Technological and Biotechnological Strategies Applied to Drought-Resilient Vegetable Production

Sandra Pérez Álvarez
Eduardo Fidel Héctor Ardisana *Editors*

DeepScience

Technological and Biotechnological Strategies Applied to Drought-Resilient Vegetable Production

Sandra Pérez Álvarez

Facultad de Ciencias Agrícolas y Forestales, Universidad Autónoma de Chihuahua, Km 2.5, carretera Delicias-Rosales, Campus Delicias, CD. Delicias, Chihuahua, México, CP: 33000.

Eduardo Fidel Héctor Ardisana

Facultad de Posgrado, Universidad Técnica de Manabí, Portoviejo, Ecuador

DeepScience

Published, marketed, and distributed by:

Deep Science Publishing, 2026
USA | UK | India | Turkey
Reg. No. MH-33-0658412
www.deepscienceresearch.com
editor@deepscienceresearch.com
WhatsApp: +91 7977171947

ISBN: 978-93-7185-042-1

E-ISBN: 978-93-7185-251-7

https://doi.org/10.70593/978-93-7185-251-7

Citation: Rodríguez-Llanes, Y., Pérez-Álvarez, S., Héctor-Ardisana, E.F., Cabezas-Pérez, D., Uranga-Valencia, L.P., Sánchez, E., Muñoz-Márquez, E., Talamantes-González, R.C., Romero-Alcantar, N.V., Magallanes-Tapia, M.A. & Villarreal-Ramírez, V.H. (2026). *Technological and Biotechnological Strategies Applied to Drought-Resilient Vegetable Production* (S. Pérez-Álvarez and E.F. Héctor-Ardisana, eds.). Deep Science Publishing. https://doi.org/10.70593/978-93-7185-251-7

Preface

Plants make life possible because they produce oxygen during photosynthesis while they absorb carbon dioxide from the atmosphere and they provide essential nutrients for human and animal consumption which serve as raw materials for various industrial products. The declining water resources that affect agricultural regions now restrict farmers from growing crops in those specific areas. The book focuses on two main topics which include drought-related vegetable production and technological and biotechnological methods developed to accomplish this critical objective. The first chapter presents the fundamentals of vegetable production. The second chapter examines the effects of drought on vegetable crop growth, yield, and product quality, as well as the procedures used to mitigate these effects, through the implementation of advanced water management techniques, biostimulant applications, and breeding methods that focus on developing more resilient plant varieties. The third chapter addresses the use of biotechnological approaches such as micropropagation and somatic embryogenesis as tools for propagation and *in vitro* studies of drought stress, transgenesis and the study of genes involved in tolerance, and research on the role of secondary metabolites in defense responses to drought stress in vegetable crops. The fourth chapter explains drought-related crop protection mechanisms which fungi and bacteria use to safeguard vegetable crops from drought damage. The research results presented here help to create better methods for using drought-affected regions to grow vegetables under challenging climatic conditions.

Dra. Sandra Pérez Álvarez

Dr. Eduardo Fidel Héctor Ardisana

Contents

About the Editors

Dra. Sandra Pérez Álvarez is Titular Professor at Faculty of Agricultural and Forestry Sciences of the Autonomous University of Chihuahua. She got her university degree in 1993 as Agronomic Engineer at the Agrarian University of Havana, Cuba, and her master degree in Plant Pathology in 2001 at Zhejiang University in China. In 2009 she graduated as Doctor in Agricultural Science at the Agrarian University of Havana, Cuba. She has 63 publications with 38 of them are in JCR journals or Scopus, 23 book chapters published, 12 of them with Springer editorial, and 4 books. She has been participated in several internationals congress. At the moment she is a member of the National System of Researchers of Mexico level 1, and also she is a member of the Mexican Society of Soil Science, AC and the Multidisciplinary Network of Desert Studies, AC.

Dr. Eduardo Fidel Héctor Ardisana (Havana, Cuba, 1962) is Agronomy Engineer (1984) and PhD in Agricultural Sciences (1996). From 1984 to 1998, he led research in Biotechnology, Genetic Breeding and Plant Physiopathology at the National Sugar Cane Research Institute (INICA) of Cuba. From 1998 to 2015, he was a principal professor at the Agrarian University of Havana (UNAH), Cuba, where he held the responsibilities of Vice Dean of Research and Postgraduate Studies and later Dean of the Faculty of Agronomy. He has served as an international advisor in Ecuador, Mexico, Venezuela, and Suriname. Based in Ecuador since 2015, he has continued to combine his research in biotechnology with teaching and attending postgraduate programs. Since 2017 he has been a Senior Professor at the Technical University of Manabí. He is the academic coordinator of the Master's program in Biotechnology, mention in Plant Biotechnology, based at the Postgraduate School and the Faculty of Agronomic Engineering of that university. He has directed more than 15 master's and doctoral theses and is the author or co-author of more than 90 scientific articles, books and book chapters, more than half of them in the area of plant biotechnology.

Authors

Dra. Yaritza Rodríguez Llanes Universidad Autónoma de Chihuahua, Chihuahua, México.

Dra. Sandra Pérez Álvarez Universidad Autónoma de Chihuahua, Chihuahua, México.

Dr. Eduardo Fidel Héctor Ardisana Facultad de Posgrado, Universidad Técnica de Manabí, Portoviejo, Ecuador.

Ing. Daniela Cabezas Pérez Universidad Autónoma de Chihuahua, Chihuahua, México.

Dra. Luisa Patricia Uranga Valencia Universidad Autónoma de Chihuahua, Chihuahua, México.

Dr. Esteban Sánchez Chávez Centro de Investigación en Alimentación y Desarrollo Unidad Delicias, Chihuahua.

Dr. Ezequiel Muñoz Centro de Investigación en Alimentación y Desarrollo Unidad Delicias, Chihuahua.

Lic. Rosa Carolina Talamantes González Universidad Autónoma de Chihuahua, Chihuahua, México.

M.A. Nancy Vyanney Romero Alcantar Centro de Investigación en Alimentación y Desarrollo Unidad Delicias, Chihuahua.

Dr. Marco Antonio Magallanes Tapia Instituto Politécnico Nacional (IPN), Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR), Unidad Sinaloa

Dr. Víctor Hugo Villarreal Ramírez Universidad Autónoma de Chihuahua, Chihuahua, México.

ABSTRACT

Vegetable production is one of the most important agricultural activities, generating numerous food, pharmaceutical, and industrial products, as well as millions of jobs worldwide. Drought stress is one of the problems that most strongly affects vegetable production, due to the alterations it causes in different physiological processes. The consequences of drought stress include reduced yields and, in many cases, plant death, which limits cultivation in affected areas. The study of the mechanisms involved in drought stress has led to the adoption of strategies aimed at mitigating its effects, including soil management, the use of biostimulants and beneficial microorganisms, and genetic improvement through different approaches. In addition to conventional breeding based on the identification of tolerant genotypes and genes involved in tolerance, the use of biotechnological tools such as plant tissue culture, transgenesis, RNA interference, and CRISPR/Cas-based genome editing has gained relevance. The development of phenotyping tools and genomics has expanded the possibilities of achieving useful results. Additional efforts have focused on the study of secondary metabolites involved in the response to drought stress, both because of their role in this process and because many of them are valuable for human nutrition, industry, agriculture, and pharmacology. From these advances, new opportunities are emerging for the management of vegetable crops aimed at their production in drought-affected areas.

CHAPTER 1

Fundamentals of Vegetable Production

Yaritza Rodríguez Llanes[1*], Marco Antonio Magallanes Tapia[2], Víctor Hugo Villarreal Ramírez[3]

[1]Postdoctoral Researcher, Universidad Autónoma de Chihuahua, Km 2.5, Carretera Delicias-Rosales, Campus Delicias, CD. Delicias, Chihuahua, México, CP: 33000, cvu945005@uach.mx (*corresponding author)

[2]Instituto Politécnico Nacional (IPN), Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR), Unidad Sinaloa, Juan de Dios Bátiz Paredes 250. Col San Joachín, Guasave, Sinaloa, México, CP: 81101

[3]Universidad Autónoma de Chihuahua, Km 2.5, Carretera Delicias-Rosales, Campus Delicias, CD. Delicias, Chihuahua, México, CP: 33000.

1. INTRODUCTION

For any human being, vegetables are an essential source of nutrition that allows the body to rebuild tissues, generate energy, maintain physiological functions, and sustain life. Because vegetables are a source of carbohydrates, minerals, fiber, and vitamins—essential elements for human nutrition, the preservation of life, and the prevention of numerous diseases—their importance is fundamental (Ocampo, 2010).

Vegetables are highly important because they represent a food source and provide employment throughout the production process (due to the number of laborers needed in both urban and rural areas), meet food demand across all social strata, and have significant economic value, both processed and fresh, in local, regional, and national markets. The wide variety of products they offer makes them a very attractive option for small and medium-sized farmers. This provides them with greater security when selling, as they can benefit from sales at markets or fairs (Guangasig-Chango, 2022).

Today, there is widespread interest in food quality issues, which has created a global trend toward increased vegetable consumption due to a growing concern for a more balanced diet. To some extent, this is based on the reduced caloric demands of modern life, characterized by greater comfort and a more sedentary lifestyle (Pérez et al., 2021).

The eight agroecological regions of the Earth are recognized as the places of origin for horticultural crops: Central China (turnip, cucumber, onion, cabbage, and broccoli); India (celery and eggplant); Central Asia (garlic, peas, broad beans, spinach, carrots, and chard); Asia Minor (radish and lettuce); the Mediterranean (parsley, cilantro, asparagus, beets, celery, and artichoke); Ethiopia (melon, watermelon, and okra); Mexico (tomato, chayote, chilacayote, serrano or jalapeño peppers, zucchini, corn, sweet potato, tomatillo, and green beans); and South America (potato). The countries that produce the most vegetables are Italy, Spain, Egypt, Brazil, Japan, Mexico, India, France, the United Kingdom, and the United States (Cárdenas-Zorro et al., 2012).

Vegetables are a key part of global agriculture and drive economic growth in any country. According to the FAO (2023), global fruit and vegetable production reached 1,966 million tons, based on the latest data from FAOSTAT for 2023. The current data shows a 1.5% increase which compares to the previous year. China, India, and the United States lead as the main producers while Spain holds the 11th position in worldwide production with 29.1 million tons. China maintained its position as the top producer in 2023 by generating 769 million tons which represents 40% of worldwide production. India occupies the second position in global production with 213 million tons which represents 11% of total output. The production volume decreased from 2022 when 245 million tons were produced. The United States holds the third position with 65 million tons which constitutes 3% of total output and matches the 2022 production level. Turkey ranks fourth among the leading countries with 53.4 million tons, down from 55.6 million tons in 2022, representing a 4% decrease. Brazil is fifth with 46.3 million tons, marking a 3.5% increase from 2022. Following them are Mexico with 37.4 million tons; Russia with 34.9 million tons; Egypt with 33.9 million tons; Indonesia with 33.8 million tons; Ukraine with 29.2 million tons; and Spain with 29.1 million tons, including fresh fruits and vegetables, wine grapes, and processing tomatoes.

With a production of nearly 70 varieties and a diverse climate that favors their cultivation, Mexico is positioned as one of the world's leading producers (Vera-Sánchez et al., 2016). National vegetable production is concentrated in several states, including Sinaloa, Sonora, Baja California, Chihuahua, Guanajuato, Jalisco, the State of Mexico, Puebla, Hidalgo, and Oaxaca (SADER, 2022).

Hoyos et al. (2012) states that, before beginning vegetable production, it is essential to keep in mind that average winter temperatures range from 2 to 19 °C, and can even drop below freezing. These temperatures make it impossible for most common crops to thrive, as they are very likely to fail to grow and may even die from sudden freezing. However, some vegetables can develop within this temperature range. In particular, it is possible to cultivate some legumes (such as broad beans and peas), flowering vegetables (such as cauliflower and broccoli), bulb vegetables (garlic and onions), and leafy vegetables (chard, lettuce, and cabbage) during the winter. These types of vegetables could die if temperatures remain below 0°C for an extended period and the ambient humidity is low; for this reason, it is essential to provide them with some type of structure to protect them from extreme temperature conditions, such as veils, PVC covers, or plastic sheeting that allows light to pass through. The harvest date for each type of vegetable will vary depending on when it was planted, its type (leaf, stem, flower, or fruit), and the care it receives throughout its development. Generally speaking, leafy vegetables grow the fastest, followed by stem vegetables, and then flower and fruit vegetables (Guangasig-Chango, 2022).

2. TYPE OF VEGETABLES

According to Mondragón-Sosa (2014) vegetables they are specified as follows (Table 1).

Table 1: Classification of vegetables

Classification of vegetables		
According to the edible part	Fleshy roots	Beet, sweet potato, jicama, radish, potato, turnip, and carrot.
	Leaves	Chard, celery, watercress, cilantro, cabbage, spinach, epazote, lettuce, parsley, turnip greens, quelite quintonil, romerito, and purslane.
	Fruits	Eggplant, zucchini, chayote, chilacayote, chili pepper, bell pepper, strawberry, tomato, melon, cucumber, watermelon, tomatillo, and xoconostle.
	Seeds	Pea, green bean, corn, okra, and fava bean. Stems: asparagus and prickly pear cactus.
	Bulb vegetables	Garlic, onion, shallot leek.
	Seed vegetables	Pea, green bean, corn (sweet corn), okra, and fava bean.
	Stem vegetables	Asparagus and cactus pad (nopalito).
According to their behavior in response to temperature	Cool-season vegetables (0°C to 18°C)	Swiss chard, garlic, broccoli, onion, cilantro, shallot, cauliflower, cabbage, epazote, asparagus, spinach, lettuce, turnip, parsley, leek, and radish.
	Temperate-season vegetables (6°C to 24°C)	Artichoke, celery, watercress, beetroot, zucchini, chayote, chilacayote, green bean, corn, huazontle, cactus pad (nopalito), potato, turnip greens (quelite nabo), quelite quintonil, romerito, tomato, xoconostle, and carrot.

	Warm-season vegetables (12°C to 30°C)	Eggplant, sweet potato, chili pepper, jicama, strawberry, tomato (jitomate), melon, okra, cucumber, and watermelon
According to their response to photoperiod	Long-day vegetables:	These require more than 14 hours of light (long-day conditions): Spinach and carrot.
	Short-day vegetables	These require 10 or fewer hours of light (short-day conditions): Potato.
	Day-neutral vegetables	Flowering is not influenced by day length: Eggplant, tomato, and chili pepper.
According to taxonomic family	Amaryllidaceae	Onion, garlic
	Asteraceae or Compositae	Lettuce
	Brassicaceae or Cruciferae	Cabbage, radish
	Cucurbitaceae	Squash, pumpkin, cucumber
	Solanaceae	chili pepper, tomato, bell pepper, and eggplant

3. CHARACTERISTICS OF VEGETABLES AND THEIR MANAGEMENT

Vegetables are defined as herbaceous plants cultivated for both personal consumption and sale in domestic and international markets, thereby generating additional household income. These biennial or annual plants are grown using intensive agricultural practices, and their products, whether consumed raw (fresh) or processed (cooked or preserved), are considered vegetables. They have a high water content, ranging between 75% and 95% of their composition, as well as fiber, vitamins, and minerals; they have a low energy content (less than 100 kcal/100 g); and a short postharvest shelf life. Additionally, they exhibit high yield per unit area and generally have a high economic value in the market (Cárdenas-Zorro et al., 2012).

Natalini et al. (2021) state that vegetables are characterized by being very delicious and flavorful. Although they do not provide significant sources of macro and micronutrients in the human diet, they offer specific benefits to different parts of the human body as well as to animals. On the other hand, Ocampo (2010) mentions that for the body to maintain high immunity, a daily intake of a variety of vegetables is necessary, containing the vitamins and minerals required to reactivate the body's immune system.

Likewise, each vegetable contains a wide variety of different nutrients, which possess specific qualities that promote better functioning of different parts of the body (Pérez et al., 2021). For example, broccoli aids in eliminating bacteria that infect the lungs because it contains a compound called sulforaphane; tomato contains fibers and nutrients that positively affect blood flow and help control healthy cholesterol levels, thus preventing heart diseases; carrot is characterized by its high content of carotene, provitamin A, and vitamins C and K; its consumption protects the visual organ by preventing macular degeneration and cataracts, also slows aging, helps prevent cancer, and contributes to skin care by maintaining a tan due to its high concentration of beta-carotene; chili peppers increase the body's immunity; lettuce helps protect bones due to its high vitamin K content, prevents anemia because it contains folic acid, stimulates good intestinal function by providing fiber that increases satiety, and helps reduce the glycemic index of meals by lowering carbohydrate absorption.

Additionally, according to Natalini et al. (2021) and studies by food scientists (bromatologists), vegetables contain macro and microelements (Table 2) that benefit the nutrition of both humans and animals.

Table 2: Macro and microelements, nutritional components, and general composition of vegetables.

Category	Component	Examples / Description
Minerals	Iron	Turnip, radish, squash, spinach, cabbage, lettuce, mushrooms, artichoke.
	Magnesium	Onion, green beans, beans.
	Phosphorus	Carrot, tomato, broccoli.
	Calcium	Lettuce, cabbage, spinach, watercress, spinach, chard, cucumbers.
	Potassium	Artichoke, beetroot, mushrooms.
	Trace elements	Zinc, manganese, chromium, iodine, cobalt, selenium, copper, sodium (present in smaller quantities).
Proteins	—	Lentils, broad beans, green beans, garlic, peas.
Nutrients	—	Onion, locoto (a type of chili), cauliflower, cabbage, beetroot, chard.
Fiber	—	Oats, grain.
Starches	—	Beetroot, onion, carrot.
Energy	—	Vegetables have a low caloric content.
Composition	—	The majority are sugars, polysaccharides, and, to a lesser extent, proteins and fats.
General properties	—	Vegetables are rich in solvent content and insoluble fiber.

Cholesterol	—	They do not contain cholesterol, being of plant origin.
Vitamins	Vitamin A (as carotene)	Carrots, tomato, spinach, red cabbage.
	L-ascorbic acid	Bell pepper, cauliflower, Brussels sprouts.
	Folic acid	Green vegetables, cabbages.
	B-complex vitamins	All vegetables.
Cooking effects	—	Water-soluble nutrients (B-complex vitamins and L-ascorbic acid) are lost due to breakdown; vitamins A and C may also be lost due to heat.

Generally speaking, for vegetable roots to grow properly, they need soft, loose, and well-draining soil. They require fertile, well-drained soil to prevent waterlogging, which can hinder root development by impeding oxygen circulation. To grow vigorously and healthily, they need adequate levels of moisture and nutrients. They prefer sandy loam soils because these offer optimal drainage and aeration; conversely, they do not like clay or heavy soils. An adequate amount of water should be maintained, but not excessively, to achieve a balance between moisture and aeration. The soil should also contain macronutrients and micronutrients (for example, phosphorus, nitrogen, and potassium). Fertilization plays an important role in routine care (Tapia-Naranjo et al., 2015; Mondragón-Sosa, 2014).

Most vegetables need direct sunlight for their growth because this provides the vital energy needed for their photosynthesis process. Also, many horticultural crops need to be grown in temperatures that range from 20 to 30°C but this standard temperature range shows significant variability. Extreme cold and extreme heat conditions will disrupt the processes of flowering, plant growth, and fruit production. The plant needs continuous water supply from the time of its initial planting until it reaches its complete growth stage. The system provides regular watering which maintains soil moisture at a level that enables plants to absorb water and nutrients without experiencing waterlogging. The two main irrigation methods used in agriculture are sprinkler and furrow irrigation which both enable farmers to manage their water resources. Excessive soil moisture creates conditions that prevent proper aeration while it stops roots from growing properly. The microorganisms present in water can transmit diseases to crops which makes water quality protection essential (Mondragón-Sosa, 2014; Sión-Macías and Carvajal-Mera, 2014).

Farmers have two methods available to plant vegetables which include transplanting and direct sowing. Direct sowing involves planting seeds directly into their permanent growing spots which is recommend for planting short-cycle species and large seeds. The method provides multiple options for seed distribution which include broadcasting, row planting, mound planting, and single seed placement. The substrate needs to maintain moisture while the seeds should be sown at a depth of 0.5 to 1 cm (Tapia-Naranjo et al., 2015). The successful establishment process requires bed or furrow preparation through proper leveling methods. The factors that determine vegetable production include three elements which are soil type, vegetable varieties, and production system. Transplanting moves germinated plants from their initial growth zones which include seedbeds and greenhouses to their final growing sites which will support their complete vegetative growth cycle. The soil fertility together with the crop genetic composition will determine the suitable plant population and density for farming (Sión-Macías and Carvajal-Mera, 2014).

Consistent with Ali et al. (2024) a nursery or seedbed is an area where plants undergo their initial growth phase until they reach the proper stage for transplanting. The trays, boxes, pots, and other small containers that have a minimum depth of 10 centimeters should receive coverage to protect their internal conditions of humidity and temperature. The containers must be designed to enable water to flow out of them. The substrate needs to have a lightweight and fertile and consistent and well-draining property. Transplanting is normally done about 30 days after sowing, when the seedling has developed true leaves and healthy roots. The seedling is carefully removed from the nursery, protecting the stem and roots (root ball), and transplanted into the garden bed or container, in which the substrate has been loosened and moistened beforehand.

Kumar-Verma et al. (2023) recommend planning the desired production throughout the year before sowing, whether directly or in seedbeds, considering both the species and the quantity, and taking into account the crop's optimal planting season. A planting calendar aims to achieve continuous production through staggered sowings. Cultural practices include irrigation, weeding, fertilization, staking, and monitoring for pests and diseases, which manifest as changes in leaf color or physical damage such as defoliation, broken plants, or damaged stems. Plants have varying nutrient requirements depending on the species, which they absorb from the land. In order to avoid nutrient loss and maintain soil productivity, applying organic matter such as compost, vermicompost, composted manure is recommended.

Ali et al. (2024) argue that the most important nutrients are the macronutrients (N, P, K, Ca, Mg, and S), and that micronutrients such as iron, copper, and zinc are also required. Nitrogen promotes growth, but in excess it delays ripening; its deficiency causes yellowing.

Phosphorus improves fruit development and quality, and it lack causes reddish spots. Potassium aids in ripening and protects against diseases, and its deficiency causes leaf burn. Organic fertilizers improve soil structure, increase moisture, reduce erosion, and promote the activity of microorganisms, contributing to sustainable agriculture.

Regarding fertilization, researchers such as Kumar-Verma et al. (2023) and Tapia-Naranjo et al. (2015) recommend that growing leafy and flowering vegetables requires higher amounts of nitrogen during their development compared to other nutrients; for fruiting vegetables, a greater amount of nitrogen is needed after transplanting until flowering, after which their demand for calcium, potassium, and phosphorus increases compared to other nutrients; with respect to the root, bulb, and rhizome vegetables, proper development require good fertilization during soil preparation and add compost or vermicompost during the development stage.

Among the main pests affecting vegetables are: *Empoasca spp*. (leafhoppers, they eat the foliage of vegetables), *Diabrotica speciosa* (diabrotica beetle, the larvae emerge from the soil and feed on the foliage; the adults feed on the stigmas of the flowers), *Phyllobrotica limbata* (sage beetle, the adults feed on the styles of the flower and therefore affect fruit set), *Phyllophaga spp.* (white grub, it feeds on the root or sucks the sap, causing galls or perforations in the root), *Conoderus spp.* (wireworms, they feed on the roots of plants; this manifests as stunted growth; root, bulb, and tuber vegetables are the most affected), *Trichoplusia ni* (cabbage looper, the larvae feed mainly on the foliage, producing irregular holes of considerable size, reducing the leaf area), *Spodoptera frugiperda* (armyworm, it feeds and causes considerable damage to the foliage and fruit), *Liriomyza spp.* (leafminer, they produce continuous mines in the leaves, which are linear and irregular, whitish or greenish in color, when the population is large; large insects that can damage the entire leaf and cause defoliation*), Bemisia tabaci* (whitefly, identified by flying in the crop when it is shaken, they measure around 2 mm; they suck sap and are a virus vector), *Pieris rapae* (cabbage caterpillar (larva and adult), this pest mainly attacks brassicas (cabbage, broccoli and cauliflower), it feeds on the foliage and if the population is allowed to grow it can cause total loss of the plant), *Plutella xylostella* (cruciferous moth (larva and adult), the adults feed on the nectar of brassica flowers and the larvae on the foliage, they defoliate the plant), *Myzus persicae* (aphid, identified as a curling on the leaves; it feeds on the sap of stems and leaves and the main problem is that it is a virus vector), *Frankliniella occidentalis* (thrips, scrapes and sucks the cellular contents of the tissues, it produces superficial whitish lesions on the epidermis of the leaves and fruits) (Mondragón-Sosa, 2014; García-Hernández et al., 2009).

Diseases are triggered by fungi, bacteria, and viral pathogens. Definitive control of these organisms is difficult because most control products are contact fungicides that attack plant tissues. Once an attack begins, the best course of action is to remove the infested plants. Therefore, all actions taken to prevent disease are preventative. The most common symptoms of disease include plant necrosis, rot, the appearance of white or black mold, and changes in the color of stems or leaves. The most common fungal diseases are powdery mildew, downy mildew, early and late blight, botrytis, rhizoctonia, and fusarium. The most common bacterial diseases are *Xanthomonas* and *Erwinia*. To prevent bacterial and fungal attacks, composting crop residues, removing diseased plants, avoiding excessive moisture, and avoiding handling plants after visiting other production areas are recommended. For virus prevention, it is recommended to have good control of aphids such as whiteflies and lice, which are the main transmitters (Kumar-Verma et al., 2023).

4. VEGETABLE PRODUCTION METHODS

The fundamental methods for growing vegetables are traditional agriculture, which uses soil and may require the application of pesticides and fertilizers; organic agriculture, which employs natural practices to achieve sustainability and avoids synthetic chemicals; hydroponics, which consists of growing vegetables in nutrient-rich water instead of soil; and aeroponics, a hydroponic technique that grows plants with aerial roots to which a nutrient solution is applied through misting (Table 3) (Albuja et al., 2021).

Table 3. Methods of vegetable production

Methods of vegetable production	
Traditional agriculture	The most widely used technique, which involves cultivating plants in soil while practicing crop rotation.
Organic agriculture	A production approach designed to achieve sustainability through the exclusion of synthetic pesticides and fertilizers.
Hydroponics	A soilless cultivation system in which plants grow in an aqueous solution enriched with all the essential nutrients for their development.
Aeroponics	A hydroponic system where plant roots are suspended in the air and periodically sprayed with a fine mist containing water and dissolved nutrients

Next, each of the aforementioned methods will be described in detail:

- Traditional agriculture

The vegetable production method is based on combining and rotating crops, using organic fertilizers (such as manure), applying organic matter to the soil, and irrigating by flooding. Its level of mechanization is quite low, as it relies on ancestral knowledge passed down from parents to children and on local resources. Crop rotation in a given area is essential to conserve soil fertility, and control pests and diseases. A combination of plants with different properties is used to attract beneficial insects and keep others away. The land is prepared to ensure good drainage, and organic matter is added to improve its fertility. For certain vegetables that require special attention during germination, seedbeds or trays with fertilized soil are used. Local seeds, that is, those adapted to local conditions, are prioritized. Ripe vegetables are harvested manually, using simple tools such as a knife or simply by pulling them up by hand. It can be described as a low-tech system, as it does not employ modern or advanced technology. Also, it is dependent on local resources and is based on the use of materials and knowledge existing in the community. Similarly, it promotes practices that benefit sustainability, such as crop diversification and avoiding burning plant waste (Ali et al., 2024; Victor et al., 2024).

- Organic farming

Organic vegetable farming is based on integrated management and the avoidance of synthetic pesticides and genetically modified organisms. It relies on sustainable practices such as crop rotation, the use of organic fertilizers and manure to improve soil fertility, biological pest control through natural enemies (such as beneficial insects), disease prevention strategies, and intercropping to protect the ecosystem and optimize resource use. Crop rotation in an area preserves soil fertility and breaks pest and disease cycles. On the other hand, utilization of well-rotted manure, compost, and other organic components augments moisture retention, provides nutrients for soil enrichment, and improves soil structure. Manually removing weeds, mechanical weed control, and mulching cover the soil, thereby preventing weeds from competing. Conversely, water cycle disposal techniques are employed for erosion prevention and conservation of soil moisture. Here, this system yields food without any genetically modified organisms or agrochemicals, minimizing soil and water pollution and rehabilitating healthy ecosystems. Organic practices contribute to the regeneration and conservation of soil fertility over an extended period. Natural resource management aims to be holistic, minimizing the use of external and non-renewable inputs (Martínez-Sánchez et al., 2019; Alcívar-Cobeña et al., 2018).

- Soilless cultivation

Hydroponics is a technique for cultivating plants without soil, but rather aqueous solutions containing essential nutrients. Plants develop when the roots are submerged in water or an inert medium, allowing them to directly absorb all the necessary nutrients. To grow, plants require water and mineral nutrients, as well as pH and salinity regulation. The most common hydroponic systems are those that use substrates and those that employ the Nutrient Film Technique (NFT). The first option is suitable for leafy greens, such as lettuce, as it nourishes the roots with a thin layer of solution; the second method, on the other hand, involves using inert materials, such as coconut fiber or perlite, to provide support for the plants and aeration for the roots.

Depending on the procedure, inert substrates like coconut fiber, perlite, vermiculite, or rockwool are used to provide structure for the plants. Nutrient Film Technique (NFT) relies on placing plants in sloped channels where a thin stream of nutrient solution continuously flows over the roots. It is an effective method for growing herbs and strawberries. The plants are grown in a substrate, such as rockwool or fiber. They are watered continuously using a drip irrigation system that keeps the substrate moist. The substrate periodically stimulates root growth. This method allows for multiple harvests and shorter growing cycles. Water is recycled and reused, which reduces overall consumption. Since no soil is used, pest problems are minimized, lowering the need for pesticides. However, handling the equipment and nutrient solution requires technical knowledge, which is a disadvantage (Panzo et al., 2025; Albuja et al., 2021).

- Aeroponic

Aeroponics is a technique for growing plants without soil, which enhances water and oxygen uptake. This allows plants to grow faster and more efficiently in controlled environments. The roots are suspended in a fine mist or spray of water and nutrients, which provides them with high levels of oxygen. The roots contain a combination of water, nutrients, and oxygen that accelerates the plant growth cycle.

There are different types of aeroponic systems: high-pressure systems, which use pumps and nebulizers to generate a very fine mist, facilitating efficient nutrient absorption; and low-pressure systems, which use lower-pressure nozzles and pumps to create larger droplets. Aeroponics consumes significantly less water than conventional growing methods.

When nutrients are applied correctly, their effectiveness increases. Faster plant growth and a greater number of plants in the same space result in higher productivity. It can be grown almost anywhere, making it perfect for urban areas and places where space or water is limited. One disadvantage is that the system requires energy for irrigation and pumps, making it vulnerable to power outages. When the substrate is inadequate, roots are prone to stress and desiccation during system failures. Therefore, continuous monitoring of both the irrigation system and the nutrient solution is crucial (Ali et al., 2024; Torres-Hernández, 2016).

5. CONCLUSIONS

Agriculture is one of the world's most important economic activities needed to feed millions of humans. Increased vegetable productivity results from new production areas plus the application of the latest technologies throughout the production cycle, from irrigation systems to mechanization.

Vegetable production within less than a span of a decade has been transformed from tradition to high-tech. This change is vital to ensure food security and global trade. Vegetables have intrinsic importance in the human diet, providing essential nutrients. They are valuable for producers and exporters worldwide, from the kitchen garden scale on up through to heavy industries employing facilities such as greenhouses.

In realizing health and well-being and supplying labor, diversifying rural economies, and feeding fresh and healthy food into cities, this sector, farmers' livelihoods, is at the same time involved in vegetable production. Vegetable production is significant in a larger global trend involving concepts like sustainability, organic farming, and technological development that are aimed at some level at mitigating the challenges of climate change, resource scarcity, and building stronger economic food systems.

REFERENCES

Albuja, V., Andrade, J., Lucano, C., Rodríguez, M. (2021). Comparativa de las ventajas de los sistemas hidropónicos como alternativas agrícolas en zonas urbanas. *Minerva Minerva: Multidisciplinaria de Investigación Científica, 2*(4). https://doi.org/10.47460/minerva.V2i4.26.

Alcívar-Cobeña, J. L., Osejos-Merino, M. A., Jaramillo-Véliz, J. J., Valverde-Lucio, Y. A., Orlando-Indacochea, N. F. (2018). Producción hortícola orgánica y su incidencia ambiental en la nutrición familiar rural. *Polo Del Conocimiento, 3*(7). https://doi.org/10.23857/pc.v3i7.573.

Ali, A., Niu, G., Masabni, J., Ferrante, A., Cocetta, G. (2024). Integrated Nutrient Management of Fruits, Vegetables, and Crops through the Use of Biostimulants, Soilless Cultivation, and Traditional and Modern Approaches—A Mini Review. *Agriculture*, *14*(8), 1330. https://doi.org/10.3390/agriculture14081330.

Cárdenas-Zorro, G.A., Pinzón-Ramírez, H., Patricia-Pulido, S., Gómez de Enciso, C., Henríquez-Henríquez, S. A., Vélez-Sánchez, J. E., Forero de La Rotta, M. C., Benavides-Rosero, M.A., Mora-Medina, H. R., Herrera-Arévalo, A., Escobar-Velásquez, H., Sánchez-León, G. D., Enrique-Flórez, L., González, G., Wyckhuys, K., Salamanca, C., Zamudio, A., Jiménez, J., Gil. R., Fuentes, L. E., Niño, N., … Ligarreto-Moreno, G.A. (2012). Manual para el cultivo de hortalizas. *Produmedios*. Colombia. 59 p.

Food and Agriculture Organization of the United Nations. (2023). The State of Food and Agriculture 2023: Revealing the true cost of food to transform agrifood systems (FAO Report). *Food and Agriculture Organization of the United Nations.* https://doi.org/10.4060/cc7724

García-Hernández, J. L., Cepeda, R. V., Servín-Villegas, R., Murillo-Amador, B., Rueda-Puente, E. O., Salazar-Sosa, E., ... Troyo-Diéguez, E. (2009). Manejo de plagas en la producción de hortalizas orgánicas. *Tropical and Subtropical Agroecosystems, 10*(1), 15-28. https://www.redalyc.org/pdf/939/93911243002.pdf.

Guangasig-Chango, A. M. (2022). Evaluación del efecto de temperatura en el cultivo de hortalizas Lechuga crespa (*Latuca sativa*), Papa nabo (*Brassica rapa*), Nabo (*Brassica napus*) bajo cubierta plástica y campo abierto en el campus CEASA, cantón Latacunga, provincia de Cotopaxi. [Proyecto de investigación. Universidad Técnica de Cotopaxi. Facultad de Ciencias Agropecuarias y Recursos Naturales]. Repositorio UTC. http://repositorio.utc.edu.ec/handle/27000/9456.

Hoyos García, D., Morales Osorio, J. G., Chavarría Ardila, H., Montoya Ríos, A. P., Correa Londoño, G., Jaramillo Villegas, S. D. C. (2012). Acumulación de grados-día en un cultivo de pepino (*Cucumis sativus* L.) en un modelo de producción aeropónico. *Revista Facultad Nacional de Agronomía Medellín, 65*(1), 6389-6398.

INEGI (Instituto Nacional de Estadística, Geografía e Informática). (2022). Guía para la interpretación cartográfica del clima. Accessed on 6 November, 2025. http://www.inegi.org.mx/geo/contenidos/recnat/edafologia/default.aspx.

Kumar-Verma, A., Gupta, A., Kumar, D., Kumar-Sharma, D. (2023). Practical manual of horticulture crops: vol.01: *Production Technologies*. Imprint: NIPA. Publisher: XYZ Publishing. 350 p. https://doi.org/10.59317/9789390083596.

Martínez-Sánchez, J., Salinas-Cruz, E., Morales-Guerra, M., Vásquez-Ortiz, R., Noriega-Cantú, D. H., Contreras-Hinojosa, J. R. (2019). Escuelas de campo y producción de hortalizas orgánicas en una comunidad Tzotzil. *Agro Productividad, 12*(4). https://doi.org/10.32854/agrop.v0i0.1354.

Mondragón-Sosa, L. (2014). Hortalizas: Manejo integral al alcance de todos. 1ra Edición Instituto de Investigación y Capacitación Agropecuaria, Acuícola y Forestal del Estado de México. ICAMEX. Secretaria de Desarrollo Agropecuario. 41 p. https://icamex.edomex.gob.mx/sites/publicaciones/2014/HORTALIZAS.pdf

Natalini, A., Acciarri, N., Cardi, T. (2021). Breeding for nutritional and organoleptic quality in vegetable crops: The case of tomato and cauliflower. *Agriculture*, *11*(7), 606. https://doi.org/10.3390/agriculture11070606.

Ocampo, I. J. C. A. (2010). Manual Básico Producción de Hortalizas. *Portal frutícola*. *Chiapas-México: sn,* 30 p.

Panzo, C. G., de la Cruz, M. C., Cruz, R. D. H., Huerta, L. H. (2025). Producción Hidropónica de Hortalizas bajo el Sistema NFT y Huerto Tradicional. *Revista Científica de Salud y Desarrollo Humano,* *6*(1), 494-511. https://doi.org/10.61368/r.s.d.h.v6i1.492.

Pérez, E. G., Meraz, M. R., Ku, J. C., López, R. F., Valdez, L. M. M. (2021). Aportaciones del Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias al mejoramiento genético de hortalizas. *Revista mexicana de ciencias agrícolas, 25*, 1-13. https://dialnet.unirioja.es/metricas/documentos/ARTREV/8164203.

SADER, (2022). Secretaría de Agricultura y Desarrollo Rural. Mayor cosecha de frutas, hortalizas y forrajes impulsan producción agrícola de México. Venustiano Carranza, México. Publicación de prensa, 1 p. https://www.gob.mx/agricultura/prensa/mayor-cosecha-de-frutas-hortalizas-y-forrajes-impulsan-produccion-agricola-de-mexico.

SIAP (Instituto Nacional de Estadística, Geografía e Informática). (2024). Producción anual agrícola. Accessed on October 28, 2025. https://www.gob.mx/agricultura/dgsiap/prensa/sistema-de-informacion-agroalimentaria-de-consulta siacon?idiom=es.

Sión-Macías, F., Carvajal-Mera, T. (2014). Manual de cultivos hortícolas. [Portoviejo, EC: INIAP, Estación Experimental Portoviejo]. 16 p. Repositorio INIAP. http://repositorio.iniap.gob.ec/handle/41000/1304.

Tapia-Naranjo, A., Romero-Brito, O., Vázquez-Romero, C., González-Hernández, E., Celaya-Mendoza, E. (2015). Manual técnico para la producción de hortalizas, huevo de gallina y carne de conejo en unidades de producción familiar. *Biblioteca Digital*, 10269. 58 p. https://vun.inifap.gob.mx/BibliotecaWeb/_Content?/=10269.

Torres-Hernández, M. (2016). Manual para la producción de cultivos aeropónicos. [Universidad Técnica Nacional. Dirección de investigación, Sede Central, Alejuela, Costa Rica] 27 p. Repositorio UTN. htpps://repositorio.utn.ac.cr/14f6b28d-fd7a-4392-9835-87bd09e0cc52.

Vera-Sánchez, K. S., Cadena-Iñiguez, J., Latournerie-Moreno, L., Santiaguillo-Hernández, J. F., Rodríguez-Contreras, A., Basurto-Pena, F. A., Ríos-Santos, E. (2016). Conservación y utilización sostenible de las hortalizas nativas de México. *Servicio Nacional de Inspección y Certificación de Semillas* (SNICS), México.73 p.

Víctor M., Guillén P., Sarmiento, A., Martínez-Herrera, O. E. (2024). Características y comparación de los sistemas de producción agrícola en campo, invernaderos y recintos de ambiente controlado con iluminación artificial (PFAL). *PRISMA Tecnológico. 15*(1). 7 p. https://doi.org/10.33412/pri.v15.1.2859.

CHAPTER 2

Drought and Global Vegetable Production

Daniela Cabezas Pérez, Sandra Pérez Álvarez*, Luisa Patricia Uranga Valencia

Universidad Autónoma de Chihuahua, Km 2.5, Carretera Delicias-Rosales, Campus Delicias, CD. Delicias, Chihuahua, México, CP: 33000, a339749@uach.mx, spalvarez@uach.mx, luranga@uach.mx

1. INTRODUCTION

The range of environmental conditions that plants encounter during their growth, such as extreme temperatures, salinity, and particularly water deficit, limits their ability to reach optimal agricultural yield (Jiang et al., 2025; Lamaoui et al., 2018). The agricultural industry faces its most severe challenges from drought because this condition directly reduces plants' ability to perform photosynthesis, absorb nutrients, and maintain their production capacity (Gupta et al., 2020; Fahad et al., 2017). Climate change will lead to more frequent and severe drought events because rising temperatures will change precipitation patterns and increase the rate of water loss through evapotranspiration (Lesk et al., 2022).

Drought occurs when a region experiences extended periods without sufficient water because of two main factors: decreased rainfall and increased demand for water evaporation which causes soil moisture to diminish and harms both plant growth and agricultural output (Mukherjee et al., 2023). The high-water requirements and shallow root systems of vegetable production systems make them extremely vulnerable to drought stress, which results in significant reductions in both yield quantity and quality. Consequently, this chapter is aimed to analyze how drought affects vegetable crop yield and quality, together with research on sustainable water management methods, which improve water usage efficiency and the development of drought-resistant vegetable crops through scientific research that combines physiological studies with genomics, CRISPR technology and advanced breeding techniques.

2. DROUGHT IMPACTS ON VEGETABLE YIELD AND QUALITY

Weather variability plays an enormous role in helping determine both crop productivity and quality in the market. Climate change has induced irregular rainfall patterns in recent decades, as a result of the increase in levels of atmospheric CO_2. These disturbances in the precipitation cycle are programmed to lead to changes in every manner possible, consequently impacting spatio-temporal distributions (Yang et al., 2019). Water deficits usually grow out of rainfall deficits. Nevertheless, severe drought occurrences can also result from intense solar radiation, persistently periodic high temperatures, and excessive dry winds that triggering soil moisture loss (Cohen et al., 2021).

Most developing countries are particularly susceptible to shifting weather patterns. Changes in low and erratic rainfall patterns are severely reducing agricultural productivity, further exacerbating food insecurity and threatening people whose livelihoods depend on crop production (Dinko and Bahati, 2023; Warner and Afifi, 2014).

Drought stress adversely affects plant growth and development at multiple levels, which include seed germination and morphological traits, as well as essential plant functions like water balance, photosynthesis, respiration, and overall metabolic processes (Zhao et al., 2020; Tiwari and Yadav, 2020; Saux et al., 2020; Seleiman et al., 2019) (Figure 1).

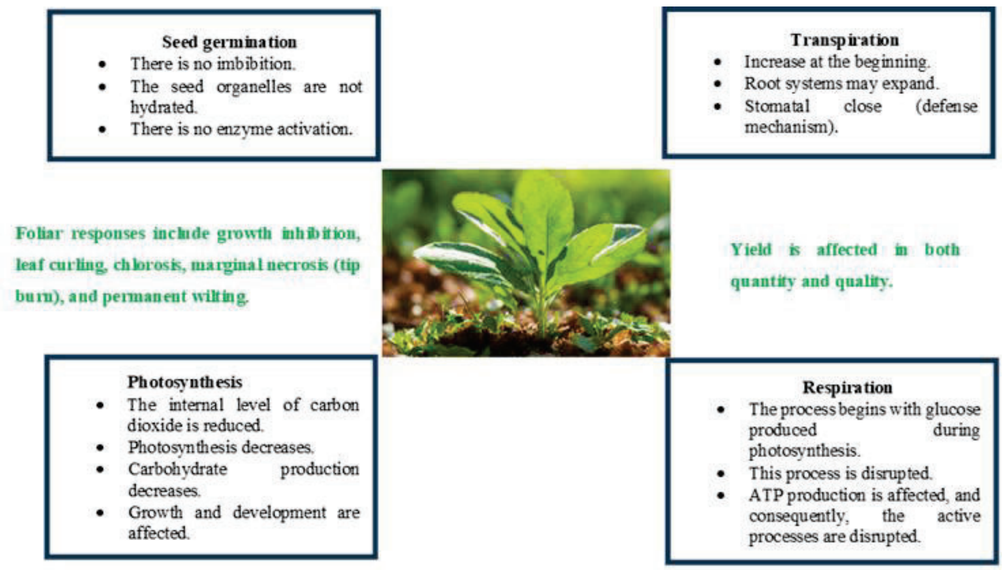

Figure 1. Influence of drought conditions on plant growth and developmental processes.

Drought acts as a vital environmental factor which restricts agricultural development because it affects crops during their initial period of seed germination and their early growth stage (Iqbal et al., 2020). The germination of seeds functions as an essential growth period for terrestrial plants, which determines whether their seedlings will exist through to adulthood (Chakma et al., 2019). Water deficit conditions prevent plants from taking up water, which results in impaired germination and reduced seedling strength during their first growth period because they experience drought stress during this time (Lu et al., 2022; Hussain et al., 2018).

During the early phase of germination, the lack of water prevents proper imbibition, which leads to failure in organelle hydration and metabolic process activation. Moreover, drought conditions restrict the mobilization and translocation of reserve nutrients from the cotyledons or endosperm to the growing embryo, resulting in a decrease in both plumule length and biomass growth (Bahar et al., 2025). Drought stress has been widely recognized to decrease percentage germination and hinder the early growth of plants in different vegetable crops. During germination, red chili (*Capsicum annuum* L.) seeds are highly vulnerable to environmental stresses like pathogen attack, salinity, and drought, which can lead to poor stand establishment, followed by greatly reduced yield. Clawing is, therefore, extremely detrimental to seedling development; some seed-trays have been reported to promote best growth performance on chili seedlings at 80% field capacity (FC) (Maphalaphathwa and Nciizah, 2025).

Kurniawan et al. (2025) also stated, that as a result of water deficit, seed germination and seedling growth in tomato (*Solanum lycopersicum* L.) were hampered. Nevertheless, these negative effects could be ameliorated through mature seed priming with salicylic acid (SA); thus, higher concentrations (100 μM) resulted in good germination rates and enhanced seedling performance under drought stress conditions.

Steiner and Zuffo (2019) studied drought effects caused by polyethylene glycol (PEG) on germination and early seedling development of four horticultural crops which included carrot (*Daucus carota* L., cv. Nantes), arugula (*Eruca sativa* Miller, cv. Cultivada), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai cv. Crimson Sweet], and eggplant (*Solanum melongena* L., cv. Embú). Their findings demonstrated that watermelon and carrot show higher drought vulnerability than eggplant and arugula, while germination rates decrease through all osmotic potential increases. The water stress tolerance of eggplant and arugula crops reaches -0.2 MPa, which allows them to maintain seed germination, yet their shoot and root development face restrictions. The germination process of watermelon and eggplant seeds reaches total inhibition at an osmotic potential of -0.8 MPa, while carrot seed germination reaches total inhibition at an osmotic potential of -0.4 MPa. Severe drought conditions restrict both seed germination and early seedling development in vegetable crops.

Beyond germination, drought also disrupts physiological processes in mature plants. A key response is stomatal closure, which is a vital plant drought avoidance mechanism for limiting transpiration. When crops experience drought conditions, this response may or may not trigger stomatal closure in these plants, resulting in the reduction of transpiration rates. Consequently, CO_2 uptake is restricted, which affects the supply of carbohydrates, and reduces the net photosynthesis rates of plants (Bhargava and Sawant, 2013). Drought stress also affects chlorophyll content through photo-oxidation and degradation processes (Yang et al., 2014). The decrease in photosynthesis with a diminution in sugar production hampers plant growth and reproductive development and eventually lowers the yield (McLaughlin and Boyer, 2004). A notable example of these effects was reported by Khamis et al. (2025) on Amaranthus (*Amaranthus caudatus* Speg) and wheat (*Triticum aestivum* L.) subjected to drought. These findings established a profound decrease in stomatal conductance by 43.9% and 55.5% in Amaranthus and wheat, respectively, and transpiration rates by 40.1% and 60.4%, respectively. The Fv/Fm ratios in the parameter determining photosynthetic efficiency declined by 26.4% and 52.4% in Amaranthus (*Amaranthus* L., 1753) and wheat (*Triticum* L., 1753), respectively. These results therefore infer some facts: that wheat, being a C3 species, tends to show stronger stomatal and photochemical constraints under drought as mitigation measures relative to those in Amaranthus, an ad hoc C4 species. Also, C4 plants are characterized by an energy-requiring carbon-concentrating feature, which limits photorespiration, thereby enhancing photosynthetic capabilities and productivity when compared with C3 plants [Karami et al., 2025; Guidi et al., 2019; Tsutsumi et al., 2017].

Drought conditions lead to reduced respiration rates across various plant parts, which include roots, leaves, shoots, flowers, and whole plants (Hussain et al., 2019). This stress also causes major changes to plant metabolic pathways, which include the processes of photosynthesis and respiration. The process of photosynthesis gets blocked when water supply decreases, but plants show more complicated patterns of breathing their needs. Respiration occurs as a constant ongoing biological function which generates both ATP and carbon skeletons needed by cells to sustain their functions and handle environmental challenges (Mazahery-Laghab et al., 2003). Drought causes plants to increase their respiration-to-assimilation ratio, which shows that plants need to spend more carbon resources to stay alive (Ayub et al., 2014). Mitochondrial electron transport shifts to the alternative oxidase (AOX) pathway because this pathway produces less ATP but prevents oxidative damage by decreasing reactive oxygen species (Singh and Agrawal, 2015). Research shows that different species display different respiration patterns because wheat and maize maintain their respiration levels or increase them during drought conditions (Fang et al., 2022; Xu et al., 2022), while other species completely stop breathing during their mild stress period. Root respiration decreases during extended drought because plant roots lose their capacity to breathe, which leads to decreased ATP production and growth restrictions (Kim et al., 2020). Drought response studies show that respiration plays an important role through its various effects, while respiration remains essential for understanding how plants deal with environmental pressures.

2.1 Drought effect on growth and yield

Drought is undoubtedly the stress that has most affected crops over time, and this has a direct impact on food production. This stress directly affects plant morphology, from reducing its size to reallocating biomass from stems and leaves to the roots (Eziz et al., 2017).

As deduced by research, the longer the drought, the more severe its impact on plants is. Especially in a non-linear manner, plant biomass and the rates of survival decline as the duration of drought increases. Garssen et al. (2014) found that substantial reductions in plant size started to occur once droughts surpassed 30 days. In a number of the reviews conducted in collaboration, drought durations of between 40 and 80 days resulted in over 50% of the loss of plant biomass. Long-term droughts significantly decrease plant survival rates, especially when they exceed one month in duration and are high in severity. A plant that had undergone a 30-day mild drought has a 75% survival probability compared to a plant that had not undergone any drought, and this probability reduces to 32% under severe famine conditions.

Drought effects on aboveground crop biomass, as a notable agent of their growth, impacts agricultural production and food security. For example, rice (*Oryza sativa* L.) and wheat (*Triticum* L.) suffered 27.5% and 25% loss of biomass, respectively, during a single severe drought event, while corresponding reductions in yield were reported to be 25.4% and 25.2% (Zhang et al., 2018).

One of the essential biological activities that get most affected by drought is cell expansion, especially with respect to reduced cell turgor pressure (Ozturk et al., 2021). This results in an impaired level of plant growth due to the affected water distribution from the xylem to adjacent elongating cells (Dietz et al., 2021). Water stress has been previously shown to affect electron transport across membranes, reduce the rate of photosynthetic assimilation, increase the level of oxidative damage due to reactive oxygen species, reduce light absorption, and reduce water-use efficiency (Kumar et al., 2022).

Several data summarized by Khan et al. (2025) clearly demonstrate that drought stress incidence causes a significant decline in crop productivity through various stages in crops like *Zea mays* L., *O. sativa*, and *Triticum aestivum* L. There is a huge difference in the percentage range of yield losses from one crop to another due to the mentioned mechanism at different growth stages. *Zea mays* L. shows yield losses reaching from 17% to 92%, especially during the vegetative growth, reproductive, and grain-filling phases; *O. sativa* exhibits a decrease of 30% and 92% in yield in the reproductive and grain-filling stages, respectively, while producing up to 63.5% losses in its reproductive stages. For *T. aestivum*, yield reductions range from 20% to almost 73% during the reproductive and grain-fill stages, indicating that drought spells during critical periods of plant growth result in reduced grain production. Neck out the fact that this type of inconformity betrays the three major cereal crops as not-so-resilient cultivars against the worst enemy of drought, which is another call for drought-tolerant lines.

Compared to wheat, rice is very sensitive to drought because it is grown under water-demanding conditions. Water deficiency in rice means less grain quality, fewer tillers, and incomplete grain filling. Drought stress results in significantly reduced total yield and elevated sterility in the spikelet (Arouna et al., 2023; Ding et al., 2020). The high sensitivity to the availability of water is a great challenge in regions susceptible to erratic rainfall and limited water resources.

Some examples of how drought affects growth in primary crops are: In rice (*O. sativa*), drought stress unfavorably disturbs vegetative growth by the reduction of parameters like plant height, biomass, and leaf area. It also induces physiological changes, like stomatal closure, leaf-tip drying, and root shortening (Ghouri et al., 2022; Ganie and Ahammed, 2021; Mishra and Panda, 2017); Maize (*Z. mays*) under drought exhibits various growth limitations, including reduced plant height, diameter, dry and fresh weight (Balbaa et al., 2022; Naghavi et al., 2013), shortened stem (Ahmad et al., 2021), and root-system modifications occurring along with stunted growth (Ranjan et al., 2022; Hussain et al., 2020). Delayed silking affects both grain yield and kernel development (Notununu et al., 2022).

Some examples, specifically in horticultural crops, highlight the harmful effects of drought on the growth development, and therefore the yield of these crops. Inadequate water supply during crucial growth stages of chili peppers (*C. annuum*) leads to plant development problems, which make the plants more susceptible to diseases and pests while producing smaller fruit, which results in reduced crop yield (Islam et al., 2023).

Red onions are plants that require sufficient water for their growth and development, making them susceptible to drought (Ginting et al., 2024). The main impact of this stress leads to reduced water potential, which prevents the growing cells from developing the essential turgor pressure required for their growth. Furthermore, drought stress causes a decrease in the growth of roots, stems, leaves, and fruits (Bekele et al., 2023). In a study by Purbajanti et al. (2025), the authors reported that drought stress affected agronomic parameters like, number of leaves, plant height, number of tillers, tuber weight, and crop yield, as well as, physiological parameters like water use efficiency (WUE), relative leaf water content (RLWC), and growth rate (GRC). Another study conducted on tomato (*Solanum lycopersicum* L.) again demonstrated the adverse influence of drought on yield, with a decrease of approximately 28%, and increased drought intensity also reduced plant height, stem diameter, and the number of fruits and leaves, likely due to impaired water and nutrient transport (Permatasari et al., 2026). Similar results demonstrate drought-induced reduction in productivity and growth of tomato (Turan et al., 2023; Kazemi et al., 2021; Petrović et al., 2019).

The studies presented demonstrate that drought stress has a severe impact on horticultural crops because it interrupts their vital physiological functions and developmental pathways. The observed reductions in plant height, fruit number, and biomass together with yield, across various species underscore the urgent need for developing drought-resilient cultivars and implementing efficient water management strategies to ensure stable crop productivity under increasingly arid conditions.

3. METHODOLOGIES TO MITIGATE DROUGHT TOLERANCE IN VEGETABLE

Drought stress represents one of the most critical environmental constraints which affects vegetable production throughout the world particularly, under the increasing variability of climate patterns. The root systems of vegetables run shallow while their water needs remain high, which creates a special risk for water shortages during their most important growth periods. The agricultural industry needs to develop effective methods which will help them reduce drought stress because this issue directly impacts their ability to produce high-quality nutritional crops. The methodologies include physiological mechanisms (changing the photosynthetic rates, increasing Water-Use Efficiency (WUE) and osmotic potential), conventional breeding and biotechnological tools, biostimulants, and plant growth regulators (Ain et al., 2025). The combination of these approaches leads to improved physiological resilience, which achieves better water utilization and creates Multiple levels of adaptive responses including changes in morphology and biochemical composition and molecular components. This section will provide information about methods to enhance drought tolerance in vegetable crops.

3.1 Water-Use Efficiency (WUE) and osmotic potential

Under water deficit conditions, water use efficiency (WUE) becomes a critical physiological parameter to consider because plant biomass production depends on water consumption. Crops that exhibit higher WUE will produce more biomass from each unit of water they consume which enables them to endure drought conditions better. The higher WUE plants show better dry condition productivity together with greater economic returns than the lower WUE plants (Stanhill, 1986).

Certain plant species have evolved C4 or CAM photosynthetic pathways instead of the C3 that predominates in most crops, resulting in greater WUE. The C4 and CAM pathways decrease water loss through transpiration while plants maintain their current level of photosynthesis or improve it, which enables plants to endure drought conditions in desert regions (Kumar et al., 2017). Plants develop these physiological characteristics because they help their WUE by enabling them to create biomass under conditions of restricted water supply.

Under drought conditions, plants will use osmotic adjustment mechanisms to survive. Osmoregulation involves the accumulation of compatible solutes, including proline and glycine betaine, which help preserve cell turgor and stabilize cellular functions during water deficit. The two methods work together to help plants withstand water scarcity while they continue to grow in challenging situations (Ain et al., 2025).

The process of soil aeration functions as a vital component which impacts WUE during periods of drought. The process of adequate soil aeration enables plants to develop root systems that reach greater depths and wider areas, which allows them to access water from deeper soil layers, thus increasing their overall WUE. The combination of better soil structure and increased oxygen levels enables roots to breathe and absorb water, which proves vital for sustaining agricultural output during times of water scarcity (Andrade et al., 2009).

Drought stress causes *Amaranthus cruentus* L. to decrease its relative water content (RWC), which leads to reduced gas exchange and lower WUE and decreased leaf nitrate levels (Cechin et al., 2022). The water-deficit conditions lead *Amaranthus caudatus* L. to develop better water use efficiency and maintain its stomatal conductance while it produces more carotenoids and continues growing. The organism displays adaptive responses which result from its C4 metabolic pathway providing it enhanced photosynthetic efficiency (Pulvento et al., 2022).

3.2 Osmotic adjustment

Osmotic adjustment has emerged as a major adaptive mechanism to resist drought stress, in which the accumulation of solutes within plant cells assists in upholding turgor pressure and hence continuing turgor-based physiological processes in low water potential situations (Kumar and Elston, 1992).

Furthermore, plants regulate intracellular ion levels and preserve osmotic equilibrium through a mechanism known as osmoregulation, which improves their physiological flexibility and enhances their ability to survive under stress conditions (Ozturk et al., 2021). The mentioned osmotic adjustment is aimed at sustaining stomatal conductance, photosynthesis, and leaf-life-span, besides saving the appearance of water-impaired shoot tip. The osmotic process will also help to decrease flower abscission, make roots stronger, and perhaps upgrade the plant's ability to withdraw water from the soil (Turner et al., 2001). This process involves the accumulation of compatible osmolytes within the cells in response to diminished external water potentials. The greater the solute concentration, the more negative becomes the cellular osmotic potential, which therefore produces a more concentrated saline system, allowing water to automatically flow into the cells, thereby preserving turgor pressure. With the basic version, osmotic adjustment in fixation is critical for crucial physiological activities, such as the opening of stomata, carbon assimilation, higher growth, and root-elongation into deeper-layer soil. The continuous growth of roots imparts soil exploration, thereby giving an opportunity to gain water at greater depths during drought. In this connection, the present observation of varied osmotic adjustment potential in vegetable crop genotypes implies an indirect tool for their future breeding program for greater drought tolerance (Chatterjee and Solankey, 2015).

The process of osmotic adjustment is accompanied by the accumulation of osmolytes, including proline, glycerol, mannitol, and glycine, betaine, among others, in plants (Jogawat, 2019; Dikilitas et al., 2020). According to Nahar and Ullah (2017) the proline concentration, and also the content of sucrose, glucose, ascorbic, fructose, citric acid, and malic acid increased significantly in tomato under water stress.

Stresses like drought, cold, heavy metals, and salinity cause an accumulation of proline. Several plant species have been described throughout the literature for having better drought tolerance on account of the accumulation of proline, such as soybean (*Glycine max* L. Merr.)

(Iqbal et al., 2019), lettuce seedlings (*Lactuca sativa* L.) (Shin et al., 2021), pepper (*Capsicum* spp.) (Mahmood et al., 2021), and eggplant (*Solanum melongena* L.) (Plazas et al., 2022).

Recent research has shown that osmolytes—glycine betaine (GB) and mannitol—are a highly effective strategy in reducing the effect of drought stress in tomato crops (*Solanum lycopersicum* L.). These also accumulate in the cytosol and help in osmotic adjustment and in maintaining cell turgor, in addition to shielding the photosynthetic apparatus (Decutt et al., 2025).

Fundamentally, osmotic adjustment is a prime physiological process that helps the plants in their fight against drought. It helps the plants by maintaining cellular turgor and keeping essential metabolic processes intact when water potential by the cells is low. Osmolyte accumulation, like glycine betaine, proline, mannitol, and soluble sugars, further increases the ability of crops to remain functional in stomatal conductance, photosynthesis, root growth, and overall productivity while facing macro-environmental water stress. The wide range of osmotic adjustment within a particular vegetable genotype suggests the usefulness of this trait as regards drought resistance and highlights the importance of plant breeders who focus on selection and development under drought stresses. Exploration of the osmoregulation system is one of the greatest promising areas for crop development under severe drought conditions.

3.3 Biostimulants and plant growth regulators

Plant-associated microorganisms play a crucial role in establishing plant tolerance to abiotic stress through close biological interactions. These beneficial microbes may inhabit internal tissues of plants as endophytes or remain in the root-surrounding soil as rhizosphere-associated organisms (Cruz et al., 2022). Endophytic microorganisms colonize various plant organs, either locally in the root system or systemically throughout the plant, including roots, stems, leaves, fruits, and underground organs. This kind of organism is one of the drivers of plant growth and hardiness against environmental stress through several mechanisms: improved nutrient and water uptake, improved water use efficiency, alteration of hormonal balance, increased plant vigor, and overall competitiveness (Kumar and Verma, 2018; Lata et al., 2018).

On the contrary, rhizosphere microorganisms are those living in the soil zone directly influenced by root activities. In other words, there is a symbiotic relationship in this region: plants release root exudates that provide carbon sources and energy to soil microbes, while, in turn, microbes contribute to various growth processes by synthesizing growth-promoting compounds, providing nutrients, or breaking down chemicals hostile to microbes living in soil. Thus, the interdependent relationship of these interactions actually helps endophytic and rhizospheric microorganisms improve plant adaptation to a more intolerable host environment (Lynch and Moffat, 2005).

A variety of strategies are used by microorganisms to alleviate or minimize the undesirable effects of drought on crops. Table 1 provides a synthesis of the role of selected microbes and their function in the mitigation of drought stress (Feng et al., 2025).

Table 1. Microbes and their function in the mitigation of drought stress (Modified from Feng et al. (2025).

Microorganism and crop	Experiment characteristics	Main results	References
Enterobacter aerogenes LMR696, *Rhizobium laguerreae* LMR575, and *Bacillus* LMR698 were applied to *P. vulgaris*, *Pisum sativum* L., and *Vicia faba* L.	Osmotic stress was induced by supplementing the medium with different concentrations of PEG 6000 (5%, 10%, 20%, 30%, and 35%).	The treatment improved proline, soluble sugars, and protein levels, helping to maintain membrane stability and water status, with *V. faba* exhibiting the strongest response. Inoculated plants exhibited higher chlorophyll (a, b and total) and carotenoid concentrations compared to non-inoculated or KNO_3-treated plants.	Hami et al. (2025)
Arbuscular mycorrhizal fungi (AMF) were applied to Maize (*Z. mays*)	The stress treatments consisted of different percentages of field water-holding capacity (35%, 55%, and 80%). The concentration of AMF applied was 10 mL of a suspension containing 1×10^8 CFU mL^{-1}.	Improves root colonization, water use, and hydraulic conductivity, enhancing nutrient uptake in both roots and shoots of corn.	(Khan et al., 2024)
Salinicola endophyticus EL13, *Bacillus methylotrophicus* SMT38, *Bacillus aryabhattai* SMT48, and	The stress treatments consisted of different percentages 35% of field water-holding capacity.	Improved the efficiency of the PS-II apparatus and reduced the ethylene stress by producing the ACC deaminase enzyme.	Lamaizi et al. (2023)

Aeromonas aquariorum SDT13 were applied to *S. lycopersicum*			
Glomous mosseae was applied to Chinese wildrye (*Leymus chinensis* (Trin.) Tzvelev)	The stress treatment consisted of 10% PEG, and 5 g of the AMF strain was applied.	Reduces Na^+ and Cl^- accumulation, enhances K^+ uptake, increases proline levels, and strengthens antioxidant enzyme activity.	Ravanbakhsh et al. (2018)
Chaetomium globosum ND35 was applied to Wheat (*T. aestivum*)	The stress level was set at 30% of the maximum water-holding capacity, and the microorganism was applied at a concentration of 1×10^6 CFU mL^{-1}.	Stimulates early root and shoot growth in winter wheat seedlings, accelerates progression to the three-leaf stage, enhances drought avoidance, and improves root activity and overall drought tolerance.	(Cong et al., 2015)

Six major mechanisms of action of microorganisms to enhance plant stress tolerance to drought stress have been identified, including:

a) Regulation of pathways for sensory perception and transmission of stress signals: Plants have created advanced systems which enable them to detect environmental changes and transmit information and generate suitable reactions to those changes. Their interaction with microorganisms relies on intricate chemical communication networks that operate through multiple paths instead of following direct routes (Conway et al., 2022). Certain microbial groups acquire new abilities to sustain their energy production while increasing their capacity to handle environmental stress during extended periods of abiotically induced stress (Meena et al., 2017)). The interaction among microbes and plants depends on root exudations which serve as energy sources and signaling substances. Plants produce various exudates which change during different growth stages, while stress conditions lead to additional changes in their composition and quantity (De Vries et al., 2020). Microorganisms can detect these changes, respond to stress-related signals, and recruit additional beneficial microbes, which strengthen their symbiotic relationships that support survival and development during adverse conditions (Williams and De Vries, 2019). A recent study demonstrated that inoculation with a consortium of five Glomus species (*G. macrocarpum, G. invarmaium, G. intraradices, G. xanthium,* and *G. mosseae*) significantly enhanced drought tolerance in tomato plants. AMF-treated plants exhibited greater root colonization, increased biomass accumulation, elevated chlorophyll and phosphorus content, higher levels of osmolytes, reduced oxidative damage, and lower canopy temperatures, collectively reflecting improved physiological performance under water-deficit conditions (Said et al., 2025).

b) Stimulation of gene expression and protein production: Scientists use gene regulatory techniques to develop new methods which create crops that can better withstand environmental stressors. The researchers implement these techniques by controlling how native genes respond to stress through their activation and termination from the active state. For example, endophytes provide plants with useful genetic material which includes genes that enable plants to use atmospheric nitrogen for growth through natural nitrogen-fixing processes (Khokhar-Voytas et al., 2023; Rosenblueth and Martínez-Romero, 2004).

c) Activation of antioxidant defense systems: Reactive oxygen species (ROS) are essential regulators of plant physiological processes including signaling, growth, and development (Castro et al., 2021; Farooq et al., 2019). Nevertheless, the unnecessary accumulation of ROS as a result of abiotic stresses such as drought initiates oxidative injury in lipids, nucleic acids, and proteins, thereby disturbing metabolism and subsequently inhibiting plant development (Castro et al., 2021; Mittler, 2002). The beneficial microorganisms attenuate oxidative stress by maintaining the antioxidant system of plants by producing extracellular antioxidant molecules, including superoxide dismutase (SOD), to neutralize the ROS within the rhizosphere or apoplast; and by the stimulation of plants antioxidant defense, activating stress-related signaling pathways (e.g., salicylic acid pathway) and upregulating antioxidant genes (Gul et al., 2023). This collaboration affects the development of both enzymatic antioxidant and non-enzymatic antioxidant systems to deliver protection to plants from ROS-induced cellular damage (Arora et al., 2020).

d) Regulation of phytohormone balance: During the interactions between plant and microorganisms, stress tolerance can be improved by hormones that work within the indole-3-acetic acid (IAA), abscisic acid (ABA), ethylene (ETH), salicylic acid (SA), and jasmonic acid (JA) pathways (Bastías et al., 2022). For example, in *Pseudomonas malodorata*, an upregulation in stress hormones in response to stress in root and shoot occurs, along with hormone level changes uncovered in the form of increased gibberellins (GA), IAA, cytokinins (CTK), and ABA to reduce the effects of stress (Ghosh et al., 2019).

e) Improvement of nutrient uptake and assimilation: AMF greatly contribute to increasing the plant's water absorption capacity under conditions of stress by enhancing the development of lateral roots and increasing the root surface area (Contreras-Cornejo et al., 2009). Another way in which AMF contributes to enhanced nutrient uptake is the spread of external mycelium, magnifying the overall surface area through which nutrients can be taken up (He et al., 2022). Likewise, many types of microorganisms such as *Rhizobium*, *Pseudomonas*, *Penicillium*, *Aspergillus,* and *Bacillus* are considered as phosphate-solubilizing bacteria (PSBs) (Sharma et al., 2016). These microbes emit organic acids, which acidify the soil around them, thus enabling the solubilization of mineral-bound phosphate to enhance its availability for uptake by plants (Rodríguez and Fraga, 1999).

f) Enhancement of photosynthetic efficiency: Exogenous microorganisms enhance photosynthetic performance by improving water uptake efficiency and reducing oxidative stress through ROS scavenging (Khan et al., 2024). Also, they help to harmonize the plant's water balance and photosynthesis by regulating stomatal conductance so that excessive transpiration can be minimized by an inoculated crop (Huot et al., 2014).

In summary, biostimulants together with plant growth regulators function as effective tools which help plants withstand drought conditions. The compounds enable plants to grow and produce more during water scarcity because they modulate physiological, biochemical, and molecular processes—including antioxidant activity, osmotic adjustment, hormone balance, and photosynthetic efficiency. Their integration into sustainable agricultural practices offers a strategic approach to mitigate the adverse effects of climate variability while reducing dependence on intensive inputs. However, further research is needed to optimize application strategies, understand genotype-specific responses, and validate their effectiveness under field conditions.

3.4 Conventional breeding

The development of a single target trait resistant variety through conventional breeding requires more than ten years to complete because the process involves multiple time-consuming steps. The process of identifying and selecting desirable phenotypic and genotypic characteristics requires extensive time and effort because multiple favorable traits must be combined into a single cultivar (Tabasum et al., 2025).

The primary goal of plant breeding programs is to improve crop performance during drought conditions. Breeders need to understand genetic mechanisms that control drought tolerance because this knowledge enables them to create better genotypes through traditional breeding methods. The traditional method for dealing with environmental stress requires scientists to choose genotypes which show consistent performance across different agricultural conditions after conducting multiple field tests and using statistical methods to assess their results. The evaluation of drought-affected environments requires the measurement of traits which decrease the difference between potential yield and actual crop output (Kumar et al., 2012).

Levitt (1972) defined drought tolerance as the ability of crops to sustain their vital functions during periods of water shortage when their plant tissues maintain low water content.

Abundant genetic variation should be present in plant germplasms targeted toward the occurrence of breeding programs and improvement in drought, given that high genetic variability serves as a tool toward the best achievable selection outcome (Rauf and Sadaqat, 2008). However, the primary goal of any breeding program is to maximize economic yield. Nevertheless, the traits that determine economic yield have different impacts on enhancing yield under irrigated conditions and drought stress. Those traits that increase productivity under adequate conditions may not necessarily confer a survival advantage in water-stressed environments. Furthermore, direct approaches to increase grain or fruit yields under drought have a low amount of heritability and restricted genetic potential. Thus, breeders are keen to select secondary traits associated with drought tolerance like root architecture, water use efficiency, osmotic adjustment, and phenological plasticity, which have an indirect contribution to increasing the stability of yield in drought-prone situations (Kumar et al., 2023). Figure 2 shows a generality of conventional breeding in vegetable crops.

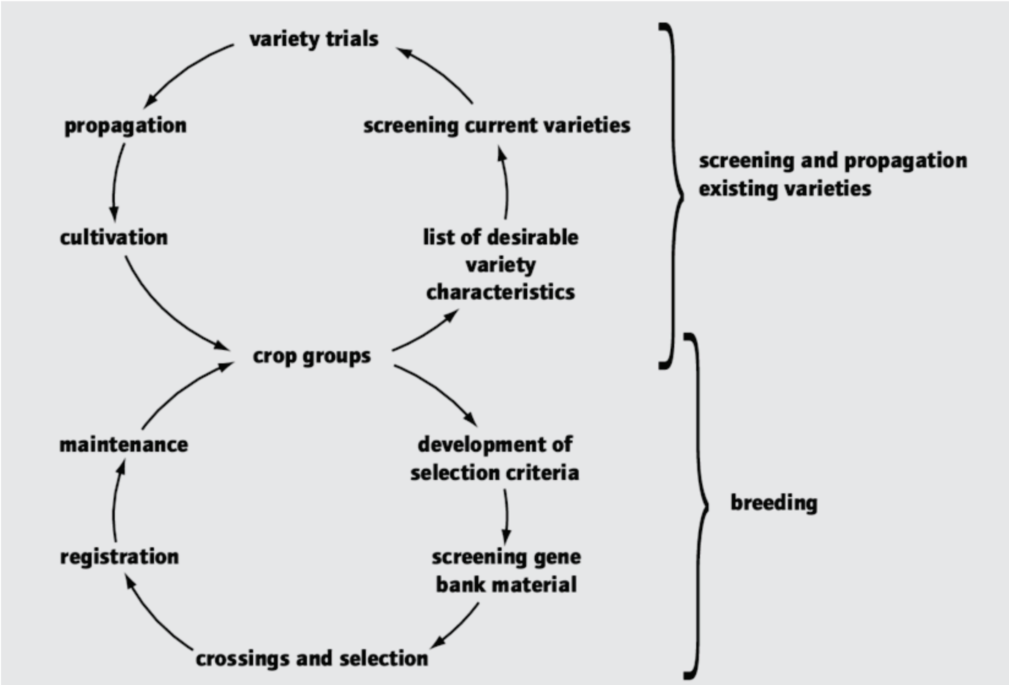

Figure 2. General framework of conventional breeding in vegetable crops.

Several cultivars of globally significant horticultural crops have been identified as drought-tolerant genotypes and species according to Kumar et al. (2023), and some examples are: in tomato, *S. habrochaites, S. esculentum* var. cerasiforme, *S. Pimpinellifoloium, S. cheesmanii, S. hirsutum, S. chilense, S. sitiens* and *S. habrochaites*; in chili, *C. baccatum* var. pendulum, *C. eximium*, and *C. chinense*; in water melon, *Citrullus colocynthis* (L.) Schrad, and in onion, *Allium fistulosum*, *A. munzii*. Other result was the identification by Lazcano-Ferrat and Louatt, (1999) of drought tolerance traits using interspecific hybridization of *Phaseolus vulgaris* L. with *Phaseolus acutifolius* A. Gray. *P. acutiflous* offers drought stress resistance traits; viz., morphology and functional adjustments allow it to finish its life cycle successfully and maintain crop yield under hot and arid environmental conditions.

Compared to other genotypes tested, the potato genotypes Alpha, Bintje, *Solanum acaule* Amargo, *Solanum demissum* Lindl. and *Solanum stenotonum* Juz. & Bukasov were significantly more drought tolerant. In particular, *S. acaule* and *S. demissum* also displayed a high level of drought resistance under both *in vitro* conditions and greenhouse pot experiments (Arvin and Donnelly, 2008).

In brief, conventional breeding is a priority for developing drought tolerance in vegetable crops. The effectiveness of conventional breeding in this regard depends on available sources of genetic variability within cultivated and wild germplasm, selection of appropriate adaptation-related traits, and identification of these traits in testing. Although selection for drought yield is usually limited by limited heritability in water-limited conditions, there have been significant achievements from selecting for the secondary traits associated with stress tolerance. However, conventional breeding requires a large amount of time and effort, and therefore in order to accelerate the breeding programs, increase selection precision and make breeding for drought-tolerant vegetable varieties faster, more efficient and able to give good results, the integration of biotechnological tools, for instance molecular markers, marker-assisted selection, and genome editing are equally essential.

4. BUILDING DROUGHT-RESILIENT VEGETABLES: FROM PHYSIOLOGY TO GENOMICS, CRISPR, AND SMART BREEDING

The development of drought-resistant vegetable crops has become essential because of climate change and rising water shortages. The solution to this problem needs a comprehensive method that starts with research on how plants react to water shortages and ends with the deployment of cutting-edge genomic techniques, CRISPR genome editing, and contemporary breeding methods. The combination of traditional agricultural practices with the latest technological advancements enables the rapid creation of vegetable crops that can withstand environmental stress, which guarantees ongoing agricultural output and food safety during times of worsening climate conditions.

Building on these advanced approaches, transgenic methods to study plant responses to environmental challenges have been widely used. Scientists have used mutant strains with enhanced and reduced gene activity to study essential genes that control drought resistance (Yang et al., 2022; He et al., 2021; Li et al., 2021; Zhao et al., 2021). Cross-species gene transfer has become a common method used to enhance crop stress tolerance through the transfer of these particular genes. Some results about transgenic methods include the study by Yang et al. (2022) in which a functional analysis of *GmNAC12* in soybean (*G. max*) was performed by overexpressing and knocking down lines, and gene overexpression resulted in a marked enhancement in drought tolerance, while knocking out *GmNAC12* practically abrogated survival, thereby confirming that *GmNAC12* acts to positively regulate drought stress factors. In another example conducted on broccoli *(Brassica oleracea* var. italica Plenck, 1794), the resulting transgenic plants overexpressed the *bolTLP1* gene, which encodes a thaumatin-like protein (mainly associated with defense responses). Consequently, the lines ultimately exhibited drought resistance, associated with alterations in stress-related pathways, including ABA-dependent signaling and antioxidant responses. These results demonstrate the potential of targeted genetic manipulation to improve tolerance to water stress and encourage the use of hybridization and genomic tools for the development of drought-tolerant plant varieties (He et al., 2021).

Based on these strategies, methods of stress tolerance-related transgenic methodologies have also been applied using genes from other species. For example, the model plant *Arabidopsis thaliana* L. was used to carry the carrot (*Daucus carota* L.) carotenoid hydroxylase gene (*DcBCH1*), and the resulting transgenic plants showed drought tolerance through influencing carotenoid biosynthesis, augmenting antioxidant capacity, and increasing abscisic acid (ABA) levels. The results suggest that *DcBCH1*-transgenic plants display increased drought survival rates, reduced malondialdehyde (MDA), elevated lutein and β-carotene levels, thus making it a good choice to confer drought tolerance to crops as a promising target (Li et al., 2019).

Moreover, similar improvements in drought tolerance have been reported in crop species such as tomato. Overexpression of the transcription factor SlGATA17 in transgenic tomato (*S. lycopersicum*) enhances drought tolerance by activating the phenylpropanoid pathway and increasing phenylalanine ammonia-lyase (PAL) activity. This modification promotes metabolite accumulation, strengthens stress resistance, and represents a promising approach for developing drought-tolerant, high-quality tomato germplasm (Zhao et al., 2021).

Complementary to gene overexpression strategies, gene silencing efforts through antisense RNA technologies, RNA interference (RNAi), or other similar technologies have frequently been used to discern between gene functions under stressful conditions following severe stressors generated by the introduction of particular environmental factors. These applications involve targeting the expression of a given gene by interfering with the delivery or production of mRNA, which requires a vital gene product for the specific structure of the cellular process (Deleavey and Damha, 2012). For instance, Chen et al. (2025) showed that silencing the *SlERF. F5* gene (an ethylene response factor) in tomatoes increases drought, salt, and cold stress tolerance, resulting in the negative regulation of the regulatory system. Thus, the knockdown plants showed higher chlorophyll content and better water retention, in addition to a lesser extent of lipid peroxidation (lower MDA content) as compared to wild plants when exposed to stress.

Similarly, another study showed that the tomato gene *SlGRAS4* was functionally characterized as a key regulator of drought tolerance. Silencing induced by RNAi increased sensitivity to drought, while over-expression lent tolerance towards such stress. As a result, transgenic plants over-expressing *SlGRAS4* (regulates drought response through the ABA signaling pathway) had less drastic ROS accumulation and up-regulation of antioxidant genes in stressful conditions. It is, hence, reasonable to infer that *SlGRAS4* enhances drought tolerance prior to its induction of an up-surged ROS removal and the *SnRK2-AREB* signaling pathway (Liu et al., 2021).

In another example, functional analysis of the tomato (*S. lycopersicum*) gene *SlNAC11* using RNAi transgenic plants revealed that the drought resistance of a gene-silenced plant was indeed diminished considerably, owing to decreased and altered concentration of chlorophyll, reduced germination, and increased oxidative damage from throttling. These results show that *SlNAC11* functions as a positive controller for drought stress resistance, thereby affirming the importance of gene-silencing techniques to bring success in enhancement efforts towards stress tolerance in crops (Wang et al., 2017).

Besides transgenic methods and RNAi approaches, the development of genome editing tools, exemplified by CRISPR/Cas, has emerged as a powerful tool for detailed gene editing of genes modulating stress responses. RNAi studies have proved that gene silencing accelerates drought sensitivity and helps differentiates between their role in regulating ROS homeostasis or ABA signaling. A much more precise and reliable gene targeting platform, CRISPR/Cas entails knockout or activation within genes in an organism. Such technologies consider the importance of targets of stress regulation in defining the range of expression work according to RNAi and overexpression, thus facilitating the building of drought-resistant crops (Tabasum et al., 2025).

Recent studies on horticultural crops have shown the successful editing of the genome by CRISPR/Cas to improve drought tolerance. The application of a reverse genetics approach for generating loss-of-function mutants by silencing *BnaA9.NF-YA7* has been evaluated by Wang et al. (2024) with the help of CRISPR/Cas9 in canola (*Brassica napus* L.). It was revealed that *NFYA7* is a negative regulator in drought resistance, as it influences ABA signaling by blocking stomatal closure and preventing water regulation. An interaction network analysis of the drought-responsive and ABA genes (*BnaABF3* and *BnaABF4*) and *BnaA9.NF-YA7* depicts that *BnaA9.NF-YA7* functions as a key player in sustaining ABA signaling during water stress. Also, Ramírez-Gonzales, et al. (2021) recently showed that overexpression of the long non-coding RNA *StFLORE* in the potato (*Solanum tuberosum*

L.) collectively enhances drought tolerance through the regulation of stomatal density and guard cell functions, while, in contrast, CRISPR/Cas9 editing of *StFLORE* results in increased drought sensitivity. Similarly, the CRISPR/Cas9-induced GID1a mutation (GIBBERELLIN-INSENSITIVE DWARF1a) functioned well as the GA receptor in tomato and further strongly affected plant growth and germination, reducing transpiration; the increase in leaf water content under water-deficit conditions enhanced drought tolerance (Illouz-Eliaz et al., 2020; Illouz-Eliaz et al., 2019).

Additional research demonstrated that *SlNPR1* functions in drought resistance by using tomato plants with CRISPR/Cas9 mutations. The expression analysis confirmed that drought conditions strongly activate *SlNPR1* expression, which indicates that this gene functions in stress response mechanisms. The functional tests demonstrated that *slnpr1* mutants showed less ability to withstand drought conditions because they maintained wider stomatal openings and suffered more electrolyte loss and total malondialdehyde and hydrogen peroxide levels while showing less antioxidant enzyme activity than wild-type plants. The mutants displayed decreased expression levels of important drought stress-related genes *SlGST SlDHN* and *SlDREB* which demonstrated that *SlNPR1* positively controls drought resistance mechanisms (Li et al., 2019).

The combination of transgenic techniques, RNA interference (RNAi) technology, and CRISPR/Cas genome editing methods has enhanced scientists' understanding of how plants respond to drought conditions. These technologies have enabled researchers to discover and control essential genes that regulate reactive oxygen species (ROS) and abscisic acid (ABA) signal transduction and plant stress response mechanisms. The transgenic and RNAi approaches have helped investigators understand plant functions, yet CRISPR/Cas provides superior accuracy and effectiveness for advancing agricultural research. The combination of these tools establishes a solid base for creating drought-resistant plant breeds varieties, which will serve as effective methods to support environmentally sustainable farming practices in response to climate change.

5. CONCLUSIONS

In conclusion, drought stress is one of the most pressing problems for vegetable yield and quality on a global scale, given its disruption of such crucial plant physiological processes as photosynthesis, water relations, and nutrient uptake. The understanding of these effects has spurred the search for mitigation strategies, including interventions in the field, by way of biostimulant products and/or beneficial microorganisms. Progress in plant physiology and molecular biology has determined a number of stress-signaling pathways up-regulated in response to abiotic stress by two stresses, namely ABA-dependent stress signal transduction cascades and ABA-independent pathways regulated by ROS.

Besides, state-of-the-art biotechnological methods such as transgenics, RNA interference, and CRISPR/Cas genome editing have greatly enhanced the discovery and manipulation of genes for drought tolerance. The possibility of engineering better-performing vegetable crops that perform well in water-limited environments has been triggered by these and previous tools, in addition to genomics, phenotyping, and smart breeding strategies. Ultimately, the integration of physiological understanding with genomics will have potential to achieve to achieve sustainable vegetable cropping systems to serve food security in the context of growing climate stresses.

REFERENCES

Ahmad, H. T., Hussain, A., Aimen, A., Jamshaid, M. U., Ditta, A., Asghar, H. N., Zahir, Z.H. (2021). Improving resilience against drought stress among crop plants through inoculation of plant growth-promoting rhizobacteria. In: Husen, A. (eds) Harsh Environment and Plant Resilience. Springer, Cham. https://doi.org/10.1007/978-3-030-65912-7_16

Ain, Q., Fatima, S.A., Amna, S., Aslam, I., Saeed, R.M.F., Javed, M.F., Bilal, M., Ahmad, M., (2025). Integrative strategies for enhancing drought tolerance in crops: advances in physiology, genetics, and agronomic practices. *Current Research in Agriculture and Farming*, **6**(2), 1-17. http://dx.doi.org/10.18782/2582-7146.254

Andrade, J. L., Cervera, J. C., Graham, E. A. (2009). Microenvironments, water relations, and productivity of CAM plants. In Perspectives in biophysical plant ecophysiology: A tribute to Park S. Nobel. Universidad Nacional Autónoma de México, México, pp. 95-120.

Arora, N.K., Fatima, T., Mishra, I., Verma, S. (2020). Microbe-based inoculants: Role in next Green Revolution. In Environmental concerns and sustainable development; Shukla, V., Kumar, N., Eds.; Springer: Singapore, pp. 191-246. https://doi.org/10.1007/978-981-13-6358-0_9

Arouna, A., Dzomeku, I. K., Shaibu, A.-G., Nurudeen, A. R. (2023). Water management for sustainable irrigation in rice (Oryza sativa L.) production: A review. *Agronomy*, *13*, 1522. https://doi.org/10.3390/agronomy13061522

Arvin, M.J., Donnelly, D.J. (2008). Screening potato cultivars and wild species to abiotic, stresses using an electrolyte leakage bioassay. *Journal of Agricultural Sciences and Technology*, **10**, 33-42.

Ayub, G., Zaragoza-Castells, J., Griffin, K.L., Atkin, O.K. (2014). Leaf respiration in darkness and in the light under pre-industrial, current and elevated atmospheric CO_2 concentrations. *Plant Science*, *226*, 120-130. https://doi.org/10.1016/j.plantsci.2014.05.001

Bahar, A. A., Faried, H. N., Ullah, S., Ali, A. (2025). Understanding drought stress, its effects, and tolerance mechanism for sustainable vegetable production. In: Sustainable and innovative vegetable production in times of climate change. Springer, Singapore. pp. 345-363. https://doi.org/10.1007/978-981-96-6283-8_18

Balbaa, M. G., Osman, H. T., Kandil, E. E., Javed, T., Lamlom, S. F., Ali, H. M., Kalaji, H.M., Wróbel, J., Telesiñski, A., Brysiewicz, A., Ghareeb, R.Y., Abdelsalam, N.R., Abdelghany AM. (2022). Determination of morpho-physiological and yield traits of maize inbred lines (*Zea mays* L.) under optimal and drought stress conditions. *Frontiers in Plant Science, 13*, 959203. https://doi.org/10.3389/fpls.2022.959203

Bastías, D.A., Balestrini, R., Pollmann, S., Gundel, P.E. (2022). Environmental interference of plant–microbe interactions. *Plant Cell Environment*, **45**, 3387-3398. https://doi.org/10.1111/pce.14455

Bekele, T., Assefa, S., Tekleab, S. (2023). Effect of deficit irrigation levels at different growth stages on yield and water productivity of furrow irrigation on onion (*Allium cepa* L.) in Silte Zone, Ethiopia. *Journal of Science Development*, *11*(1), 12-25.

Bhargava, S., Sawant, K. (2013). Drought stress adaptation: Metabolic adjustment and regulation of gene expression. *Plant Breeding, 132*, 21-32. https://doi.org/10.1111/pbr.12004

Castro, B., Citterico, M., Kimura, S., Stevens, D. M., Wrzaczek, M., Coaker, G. (2021). Stress-induced reactive oxygen species compartmentalization, perception and signalling. *Nature Plants*, **7**, 403-412. https://doi.org/10.1038/s41477-021-00887-0

Cechin, I., da Silva, L.P., Ferreira, E.T., Barrochelo, S.C., de Melo, F.P.d.S.R., Dokkedal, A.L., Saldanha, L.L. (2022). Physiological responses of *Amaranthus cruentus* L. to drought stress under sufficient-and deficient-nitrogen conditions. *PLoS ONE*, **17**, e0270849. https://doi.org/10.1371/journal.pone.0270849

Chakma, P., Hossain, M.M., Rabbani, M.G. (2019). Effects of salinity stress on seed germination and seedling growth of tomato: Salinity stress on seed germination and seedling growth. *Journal of the Bangladesh Agricultural University*, *17*(4), 490-499. https://doi.org/10.3329/jbau.v17i4.44617

Chatterjee, A., Solankey, S.S. (2015). Functional physiology in drought tolerance of vegetable crops—an approach to mitigate climate change impact. In Climate Dynamics in Horticultural Science - Volume 1, CRC Press, Boca Raton, FL, USA, pp. 149-171.

Chen, Y., Liao, X., Li, W., Cheng, X., Qi, B., Gao, J., Wan, F. (2025). Silencing of *SlERF.F5* affects tolerance to drought, salt and low-temperature stresses in tomato. *BMC Genomics*, **26**, 1117. https://doi.org/10.1186/s12864-025-12407-x

Cohen, I., Zandalinas, S. I., Huck, C., Fritschi, F. B., Mittler, R. (2021). Meta-analysis of drought and heat stress combination impact on crop yield and yield components. *Physiologia Plantarum, 171*, 66-76. https://doi.org/10.1111/ppl.13203

Cong, G., Yin, C., He, B., Li, L., Gao, K. (2015). Effect of the endophytic fungus *Chaetomium globosum* ND35 on the growth and resistance to drought of winter wheat at the seedling stage under water stress. *Acta Ecologica Sinica*, **35**(18), 6120-6128. https://doi.org/10.5846/stxb201401200153

Contreras-Cornejo, H.A., Macías-Rodríguez, L., Cortés-Penagos, C., López-Bucio, J. (2009). Trichoderma virens, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in Arabidopsis. *Plant Physiology*, **149**, 1579-1592. https://doi.org/10.1104/pp.108.130369

Conway, J., Walton, W. G., Salas-González, I., Law, T. F., Lindberg, C. A., Crook, L., Kosina, S. M., Fitzpatrick, C. R., Lietzan, A., Northen, T., et al. (2022). Diverse MarR bacterial regulators of auxin catabolism in the plant microbiome. *Nature Microbiology,* **7**, 1817-1833. https://doi.org/10.1038/s41564-022-01244-3

Cruz, C.C., Cardoso, P., Santos, J., Matos, D., Figueira, E. (2022). Bioprospecting soil bacteria from srid zones to increase plant tolerance to drought: Growth and biochemical status of maize inoculated with plant growth-promoting bacteria isolated from Sal Island, Cape Verde. *Plants*, **11**, 2912. https://doi.org/10.3390/plants11212912

De Vries, F. T., Griffiths, R. I., Knight, C., Nicolitch, O., Williams, A. H. (2020). Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science*, **368**(6488), 270-274. https://doi.org/10.1126/science.aaz5192

Decutt, N.A., Twumasi1, G., Ayarna, A.W., Ayeh, K.O., Fawibe, O.O., Keteku, A., Poku, S.A. (2025). Combined application of mannitol and melatonin improves water retention and biochemical parameters of drought-stressed tomato plants. Agricultural Science Digest, 1-7. http://dx.doi.org/10.18805/ag.DF-758

Deleavey, G. F., Damha, M. J. (2012). Designing chemically modified oligonucleotides for targeted gene silencing. *Chemical Biology*, **19**, 937-954. http://dx.doi.org/10.1016/j.chembiol.2012.07.011

Dietz, K. J., Zörb, C., Geilfus, C. M. (2021). Drought and crop yield. *Plant Biology*, *23*, 881-893. https://doi.org/10.1111/plb.13304

Dikilitas, M., Simsek, E., and Roychoudhury, A. (2020). Role of proline and glycine betaine in overcoming abiotic stresses. In Protective chemical agents in the amelioration of plant abiotic stress: Biochemical and molecular perspectives. Eds. A. Roychoudhury and D. K. Tripathi. Hoboken, NJ, USA, pp.1-23. http://dx.doi.org/10.1002/9781119551669.ch1

Ding, Y., Wang, W., Zhuang, Q., and Luo, Y. (2020). Adaptation of paddy rice in China to climate change: The effects of shifting sowing date on yield and irrigation water requirement. *Agricultural Water Management*, *228*, 105890. https://doi.org/10.1016/j.agwat.2019.105890

Dinko, D. H., Bahati, I. (2023). A review of the impact of climate change on water security and livelihoods in semiarid Africa: Cases from Kenya, Malawi, and Ghana. *Journal of Climate Resilience & Climate Justice, 1*, 107-118. https://doi.org/10.1162/crcj_a_00002

Eziz, A., Yan, Zh., Tian, D., Han, W., Tang, Zh. (2017). Drought effect on plant biomass allocation: A meta-analysis. *Ecology and Evolution, 7*(24), 11002-11010. https://doi.org/10.1002/ece3.3630

Fahad, S., Bajwa, A.A., Nazir, U., Anjum, S.A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., Ihsan, M.Z., Alharby, H., Wu, C., Wang, D., Huang, J. (2017), Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Sciences*, *8*, 1147. https://doi.org/10.3389/fpls.2017.01147

Fang, L., Yin, X., van der Putten, P. E., Martre, P., and Struik, P. C. (2022). Drought exerts a greater influence than growth temperature on the temperature response of leaf day respiration in wheat (*Triticum aestivum*). *Plant Cell & Environment*, *45*, 2062–2077. https://doi.org/10.1111/pce.14324

Farooq, M., Niazi, A., Akhtar, J., Saifullah, Farooq, M., Souri, Z., Karimi, N., Rengel, Z. (2019). Acquiring control: The evolution of ROS-induced oxidative stress and redox signaling pathways in plant stress responses. *Plant Physiology and Biochemistry,* **141**, 353-369. https://doi.org/10.1016/j.plaphy.2019.04.039

Feng, D., Li, W., Huang, P., Gu, M., Tang, G., Ding, Y., Cao, G., Xu, W. (2025). Mechanisms of microorganisms alleviating drought and salt stresses in plants. *Microorganisms*, **13**, 2565. https://doi.org/10.3390/microorganisms13112565

Ganie, S. A., Ahammed, G. J. (2021). Dynamics of cell wall structure and related genomic resources for drought tolerance in rice. *Plant Cell Reports*, *40*, 437-459. https://doi.org/10.1007/s00299-020-02649-2

Garssen, A., Verhoeven, J., Soons, M. (2014). Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis. *Freshwater Biology*, 59(5), 1052-1063. https://doi.org/10.1111/fwb.12328

Ghosh, D., Gupta, A., Mohapatra, S. (2019). Dynamics of endogenous hormone regulation in plants by phytohormone secreting rhizobacteria under water-stress. *Symbiosis*, **77**, 265-278. https://doi.org/10.1007/s13199-018-00589-w

Ghouri, F., Ali, Z., Naeem, M., Ul-Allah, S., Babar, M., Baloch, F. S., Chattah, W. Sh., Shahid, M. Q. (2022). Effects of silicon and selenium in alleviation of drought stress in rice. *Silicon*, *14*, 5453-5461. https://doi.org/10.1007/s12633-021-01277-z

Ginting, T.H.U., Ginting, J., Damanik, R.I.M. (2024). Morphology of shallots (*Allium ascalonicum* L.) under drought stress against salicylic acid application. *Journal Budidaya Pertanian*, 20(1), 90-98. https://doi.org/10.30598/jbdp/2024.20.1.90.

Guidi, L., Lo, Piccolo, E., Landi, M. (2019). Chlorophyll fluorescence, photoinhibition and abiotic stress: does it make any difference the fact to be a C3 or C4 species? *Frontiers in Plant Science*,*10*, 174. https://doi.org/10.3389/fpls.2019.00174

Gul, N., Wani, I. A., Mir, R. A., Nowshehri, J. A., Aslam, S., Gupta, R., Verma, S., & Aslam, S. (2023). Plant growth promoting microorganisms mediated abiotic stress tolerance in crop plants: A critical appraisal. *Plant Growth Regulation,* **100**, 7-24. https://doi.org/10.1007/s10725-022-00951-5

Gupta, A., Rico-Medina, A., Caño-Delgado, A. I. (2020). The physiology of plant responses to drought. *Science*, *368*, 266–269. https://doi.org/10.1126/science.aaz7614

Hami, A., El Attar, I., Mghazli, N., Ennajeh, S., Ait-Ouakrim, E.H., Bennis, M., Oulghazi, S., Badaoui, B., Aurag, J., Sbabou, L., Taha, K. (2025). Enhancing drought tolerance in *Pisum sativum* and *Vicia faba* through interspecific interactions with a mixed inoculum of *Rhizobium laguerreae* and non-host beneficial rhizobacteria. *Frontiers in Plant Science*, **16**, 1528923. https://doi.org/10.3389/fpls.2025.1528923

He, L., Li, L., Zhu, Y., Pan, Y., Zhang, X., Han, X., Li, M., Chen, Ch., Li, H., Wang, Ch. (2021). *BolTLP1*, a thaumatinlike protein gene, confers tolerance to salt and drought stresses in broccoli (*Brassica oleracea* L. var. Italica). *International Journal of Molecular Sciences*, **22**, 11132. http://dx.doi.org/10.3390/ijms222011132

He, X.; Shao, C.; Wu, A.; Xia, L.; Li, T.; Pei, J.; Zhang, N.; Wang, Y. (2022). Arbuscular mycorrhizal fungi enhance nutrient acquisition and reduce aluminum toxicity in *Lespedeza formosa* under acid rain. *Environmental Science and Pollution Research*, **29**, 29904-29916. https://doi.org/10.1007/s11356-021-18248-x

Huot, B., Yao, J., Montgomery, B. L., He, S. Y. (2014). Growth–defense tradeoffs in plants: A balancing act to optimize fitness. *Molecular Plant,* **7**(8), 1267-1287. https://doi.org/10.1093/mp/ssu049

Hussain, H. A., Men, S., Hussain, S., Zhang, Q., Ashraf, U., Anjum, S. A., Ali, I., Wang, L. (2020). Maize tolerance against drought and chilling stresses varied with root morphology and antioxidative defense system. *Plants*, *9*, 720. https://doi.org/10.3390/plants9060720

Hussain, H.A., Hussain, S., Khaliq, A., Ashraf, U., Anjum, S.A., Men, S., Wang, L. (2018). Chilling and drought stresses in crop plants: implications, cross talk and potential management opportunities. *Frontiers in Plant Science, 9*, 393. https://doi.org/10.3389/fpls.2018.00393

Hussain, S., Rao, M. J., Anjum, M. A., Ejaz, S., Zakir, I., Ali, M. A., Ahmad, N, Ahmad, Sh. (2019). Oxidative stress and antioxidant defense in plants under drought conditions. In: Hasanuzzaman, M., Hakeem, K., Nahar, K., Alharby, H. (eds) Plant Abiotic Stress Tolerance. Springer, Cham. https://doi.org/10.1007/978-3-030-06118-0_9

Illouz-Eliaz, N., Nissan, I., Nir, I., Ramon, U., Shohat, H., Weiss, D. (2020). Mutations in the tomato gibberellin receptors suppress xylem proliferation and reduce water loss under water-deficit conditions. *Journal of Experimental Botany*, **71**, 3603-3612. https://doi.org/10.1093/jxb/eraa137

Illouz-Eliaz, N., Ramon, U., Shohat, H., Blum, S., Livne, S., Mendelson, D., Weiss, D. (2019). Multiple gibberellin receptors contribute to phenotypic stability under changing environments. *Plant Cell*, **31**, 1506-1519. https://doi.org/10.1105/tpc.19.00235

Iqbal, M.S., Singh, A.K., Ansari, M.I. (2020). Effect of drought stress on crop production. In: New frontiers in stress management for durable agriculture. Springer, Singapore, pp. 35-47. https://doi.org/10.1007/978-981-15-1322-0_3

Iqbal, N., Hussain, S., Raza, M. A., Yang, C. Q., Safdar, M. E., Brestic, M., et al. (2019). Drought tolerance of soybean (*Glycine max* L. Merr.) by improved photosynthetic characteristics and an efficient antioxidant enzyme activities under a split-root system. *Frontiers in Physiology*, **10**. http://dx.doi.org/10.3389/fphys.2019.00786

Islam, K., Rawoof, A., Kumar, A., Momo, J., Ahmed, I., Dubey, M., Ramchiary, N. (2023). Genetic regulation, environmental cues, and extraction methods for higher yield of secondary metabolites in capsicum. *Journal of Agricultural and Food Chemistry*, *71*(24), 9213-9242. https://doi.org/10.1021/acs.jafc.3c01901.

Jiang, Z., van Zanten, M., Sasidharan, R. (2025). Mechanisms of plant acclimation to multiple abiotic stresses. *Communications Biology* ,*8*, 655. https://doi.org/10.1038/s42003-025-08077-w

Jogawat, A. (2019). Osmolytes and their role in abiotic stress tolerance in plants. In Molecular plant abiotic stress: Biology and biotechnology. Eds. D. K. Tripathi, V. P.

Singh and D. K. Chauhan. John Wiley & Sons, Hoboken, NJ, USA, pp. 91-104. http://dx.doi.org/10.1002/9781119463665.ch5

Karami, S., Shiran, B., Ravash, R. (2025). Molecular investigation of how drought stress affects chlorophyll metabolism and photosynthesis in leaves of C3 and C4 plant species: a transcriptome meta-analysis. *Heliyon, 11*(3), e42368. https://doi.org/10.1016/j.heliyon.2025.e42368

Kazemi, S., Zakerin, A., Abdossi, V., Moradi, P. (2021). Fruit yield and quality of the grafted tomatoes under different drought stress conditions. *Asian Journal of Agriculture and Biology, 2021*(1), 1-14. https://doi.org/10.35495/ajab.2020.03.164.

Khamis, G., Alsherif, E.A., Korany, S.M., Aldailami, D.A., Aloufi, A.S., Khalaf, M.H., Hamed, S.M., Maridueña-Zavala, M.G., Al Jaouni, S.K., Selim, S. (2025). Drought stress differentially influences growth, physiology, and metabolite *accumulation in Triticum aestivum* (C3) and *Amaranthus caudatus* (C4) plants. *BMC Plant Biology*, *25*, 1199. https://doi.org/10.1186/s12870-025-07022-7

Khan, A.A., Wang, Y-F., Akbar, R., Alhoqail, W.A. (2025). Mechanistic insights and future perspectives of drought stress management in staple crops. *Frontiers in Plant Science*, *16*, 1547452. https://doi.org/10.3389/fpls.2025.1547452

Khan, W., Zhu, Y., Khan, A., Zhao, L., Yang, Y-M., Wang, N., Hao, M., Ma, Y., Nepal, J., Ullah, F., Maqsood, M. U. R., Abrar, M., Xiong, Y-C. (2024). Above-and below-ground feedback loop of maize is jointly enhanced by plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi in drier soil. *Science of The Total Environment*, **917**, 170417. https://doi.org/10.1016/j.scitotenv.2024.170417

Khokhar-Voytas, A., Shahbaz, M., Maqsood, M.F., Zulfiqar, U., Naz, N., Iqbal, U., Sarà, M., Aqeel, M., Khalid, N., Noman, A., Zulfiqar, F., Al Syaad, K. M., AlShaqhaa, M. A. (2023). Genetic modification strategies for enhancing plant resilience to abiotic stresses in the context of climate change. *Functional & Integrative Genomics*, **23**, 283. https://doi.org/10.1007/s10142-023-01202-0

Kim, I., Chae, H. M., and Choi, B. (2020). Effects of experimental throughfall exclusion on soil respiration in a continental coniferous stand, South Korea. *Forests*, *11*, 972. https://doi.org/10.3390/f11090972

Kumar, A., Elston, J. (1992). Genotypic differences in leaf water relations between *Brassica juncea* and *B. napus*. *Annals of Botany*, **70**, 3-9. https://doi.org/10.1093/oxfordjournals.aob.a088436

Kumar, A., Verma, J.P. (2018). Does plant—Microbe interaction confer stress tolerance in plants: A review? *Microbiology Research*, **207**, 41-52. https://doi.org/10.1016/j.micres.2017.11.004

Kumar, M. R., Bahadur, V., Kumar, L. V. (2023). Breeding for drought tolerance in vegetable crops: A review. *Environment and Ecology*, **41**(2A), 996-1001.

Kumar, R., Harikrishna, Barman, D., Ghimire, O. P., Gurumurthy, S., Singh, P. K., Chinnusamy, V., Padaria, J. C., Arora, A. (2022). Stay-green trait serves as yield stability attribute under combined heat and drought stress in wheat (*Triticum aestivum* L.). *Plant Growth Regulation*, *96*, 67-78. https://doi.org/10.1007/s10725-021-00758-w

Kumar, R., Shekhar, Sh. S., Singh, M. (2012). Breeding for drought tolerance in vegetables. *Vegetable Science*, **39**(1), 1-15.

Kumar, V., Sharma, A., Soni, J. K., Pawar, N. (2017). Physiological response of C3, C4 and CAM plants in changeable climate. *The Pharma Innovation*, **6**(9, Part B), 70.

Kurniawan, A., Noviandi, W. D., Maulidah, N. I., Mullatif, I. A., Rahmandhias, D. T., Karim, M. F., Shyu, D. J. (2025). Mitigating drought stress effects in tomato through seed priming and foliar application of salicylic acid: Impacts on germination and plant growth. *Journal of Ecological Engineering, 26*(4), 369-382. https://doi.org/10.12911/22998993/200337

Lamaizi, S., Meddich, A., Boutasknit, A., Anli, M., Lahbouki, S., El Fels, L., Ouhdouch, Y., Hafidi, M. (2023). Application of olive-mill-wastewater-compost in combination with symbiotic microorganisms improves the physiological, biochemical performance and tolerance of tomato (*Solanum lycopersicum*) under drought stress. *Gesund Pflanz*, **75**, 1719–1735. https://doi.org/10.1007/s10343-022-00824-x

Lamaoui, M., Jemo, M., Datla, R., Bekkaoui, F. (2018), Heat and drought stresses in crops and approaches for their mitigation. *Frontiers in Chemistry*, *6*, 26. https://doi.org/10.3389/fchem.2018.00026

Lata, R., Chowdhury, S., Gond, S.K., White, J.F. (2018). Induction of abiotic stress tolerance in plants by endophytic microbes. *Letters in Applied Microbiology*, **66**, 268-276. https://doi.org/10.1111/lam.12855

Lazcano-Ferrat, I., Louatt, C.J. (1999). Relationship between relative water content, nitrogen pools, and growth of Phaseolus vulgaris L. and *P. acutifolius* A. Gray during water deficit. *Crop Science*, **39**, 467-475.

Lesk, C., W. Anderson, A. Rigden, O. Coast, J. Jägermeyr, S. McDermid, K.F. Davis, M. Konar. (2022). Compound heat and moisture extreme impacts on global crop yields under climate change. *Nature Reviews Earth & Environment*, *3*, 12, 872-889, https://doi.org/10.1038/s43017-022-00368-8

Levitt, J.B. (1972). Responses of plants to environmental stresses. Academic Press, New York.

Li, R., Liu, C., Zhao, R., Wang, L., Chen, L., Yu, W., Shen, L. (2019). CRISPR/Cas9-mediated slnpr1 mutagenesis reduces tomato plant drought tolerance. *BMC Plant Biology*, **19**, 38. https://doi.org/10.1186/s12870-018-1627-4

Li, T., Liu, J. X., Deng, Y. J., Xu, Z. S., Xiong, A. S. (2021). Overexpression of a carrot *BCH* gene, *DcBCH1*, improves tolerance to drought in *Arabidopsis thaliana*. *BMC Plant Biology*, **21**, 475. http://dx.doi.org/10.1186/s12870-021-03236-7

Lu, Y., Liu, H., Chen, Y., Zhang, L., Kudusi, K., Song, J. (2022). Effects of drought and salt stress on seed germination of ephemeral plants in desert of northwest China. *Frontiers in Ecology and Evolution*, *10*, 1026095. https://doi.org/10.3389/fevo.2022.1026095

Lui, Y., Wen, L., Shi, Y., Su, D., Lu, W., Cheng, Y., Li, Z. (2021). Stress-responsive tomato gene *SlGRAS4* function in drought stress and abscisic acid signaling. *Plant Science*, 304, 110804. https://doi.org/10.1016/j.plantsci.2020.110804

Lynch, J.M., Moffat, A. (2005). Bioremediation-Prospects for the future application of innovative applied biological research. *Annals of Applied Biology*, **146**, 217-221. https://doi.org/10.1111/j.1744-7348.2005.040115.x

Mahmood, T., Rana, R. M., Ahmar, S., Saeed, S., Gulzar, A., Khan, M. A., Wattoo, F. M, Wang, X., Branca, F., Mora-Poblete, F., Sousa, G.M., Du, X. (2021). Effect of drought stress on capsaicin and antioxidant contents in pepper genotypes at reproductive stage. Plants 10, 1286. http://dx.doi.org/10.3390/plants10071286

Maphalaphathwa, M., Nciizah, A.D. (2025). Nutrient seed priming effects on water stress tolerance and nutrient uptake of chilies (*Capsicum annum* L.). *Agronomy, 15*, 930. https://doi.org/10.3390/agronomy15040930

Mazahery-Laghab, H., Nouri, F., Abianeh, H. Z. (2003). Effects of the reduction of drought stress using supplementary irrigation for sunflower (*Helianthus annuus*) in dry farming conditions. Agronomy and Horticulture, 81-86. SID. https://sid.ir/paper/19479/en

McLaughlin, J.E., Boyer, J.S. (2004). Sugar-responsive gene expression, invertase activity, and senescence in aborting maize ovaries at low water potentials. *Annals of Botany*, *94*, 675-689. https://doi.org/10.1093/aob/mch193

Meena, K. K., Sorty, A. M., Bitla, U. M., Choudhary, K., Gupta, P., Pareek, A., Singh, D. P., Prabha, R., Sahu, P. K., Gupta, V. K., Singh, H. B., Krishanani, K. K., Minhas, P. S. (2017). Abiotic stress responses and microbe-mediated mitigation in plants: The omics strategies. *Frontiers in Plant Science*, **8**, 172. https://doi.org/10.3389/fpls.2017.00172

Mishra, S. S., Panda, D. (2017). Leaf traits and antioxidant defense for drought tolerance during early growth stage in some popular traditional rice landraces from Koraput, India. *Rice Science*, *24*, 207-217. https://doi.org/10.1016/j.rsci.2017.04.001

Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science,* **7**(9), 405-410. https://doi.org/10.1016/S1360-1385(02)02312-9

Mukherjee, A., Dwivedi, S., Bhagavatula, L., Datta, S. (2023). Integration of light and ABA signaling pathways to combat drought stress in plants. *Plant Cell Reports*, *42*(5), 829-841. https://doi.org/10.1007/s00299-023-02999-7

Naghavi, M. R., Aboughadareh, A. P., Khalili, M. (2013). Evaluation of drought tolerance indices for screening some of corn (*Zea mays* L.) cultivars under environmental conditions. *Notulae Scientia Biologicae*, *5*, 388-393. https://doi.org/10.15835/nsb539049

Nahar, K., Ullah, S. (2017). Fruit quality and osmotic adjustment of four tomato cultivars under drought stress. *Asian Journal of Soil Science and Plant Nutrition*, **2**(1).

Notununu, I., Moleleki, L., Roopnarain, A., Adeleke, R. (2022). Effects of plant growth-promoting rhizobacteria on the molecular responses of maize under drought and heat stresses: A review. *Pedosphere*, *32*, 90-106. https://doi.org/10.1016/S1002-0160(21)60051-6

Ozturk, M., Turkyilmaz Unal, B., García-Caparró s, P., Khursheed, A., Gul, A., Hasanuzzaman, M. (2021). Osmoregulation and its actions during the drought stress in plants. *Physiologia Plantarum, 172*, 1321-1335. https://doi.org/10.1111/ppl.v172.2

Permatasari, N. A., Pöhnl, T., Neugart, S. (2026). Impact of drought, salinity, and their combination on growth, mineral content, and plant secondary metabolites of tomatoes (*Solanum lycopersicum* L.). *Physiologia Plantarum*, *178*, e70725. https://doi.org/10.1111/ppl.70725.

Petrović, I., Savic, S., Jovanović, Z., Stikić, R., Brunel, B., Serino, S., Bertin, N. (2019). Fruit quality of cherry and large fruited tomato genotypes as influenced by water deficit. *Zemdirbyste-Agriculture, 106*(2), 123-128. https://doi.org/10.13080/z-a.2019.106.016.

Plazas, M., González-Orenga, S., Nguyen, H. T., Morar, I. M., Fita, A., Boscaiu, M., Prohens, J., Vicente, O. (2022). Growth and antioxidant responses triggered by water stress in wild relatives of eggplant. *Scientia Horticulturae*, **293**, 110685. http://dx.doi.org/10.1016/j.scienta.2021.110685

Pulvento, C., Sellami, M.H., Lavini, A. (2022). Yield and quality of *Amaranthus hypochondriacus* grain amaranth under drought and salinity at various phenological stages in southern Italy. *Journal of the Science of Food and Agriculture*, **102**, 5022-5033. https://doi.org/10.1002/jsfa.11088

Purbajanti, E.D., Safitri, D., Wedyan, M.A., Roeswitawati, D., Savitri, E.S., Yuniati, S., Yuhana, T.M. (2025). Drought stress effect on red onion: Morphological, physiological, and yield attributes. *Sarhad Journal of Agriculture*, *39*, 91-100. https://dx.doi.org/10.17582/journal.sja/2023/39/s1.91.100.

Ramírez-Gonzales, L., Shi, L., Bergonzi, S.B., Oortwijn, M., Franco-Zorrilla, J.M., Solano-Tavira, R., Visser, R.G.F., Abelenda, J.A., Bachem, C.W.B. (2021). Potato CYCLING DOF FACTOR 1 and its lncRNA counterpart *StFLORE* link tuber development and drought response. *Plant Journal*, **105**, 855-869. https://doi.org/10.1111/tpj.15093

Ranjan, A., Sinha, R., Singla-Pareek, S. L., Pareek, A., and Singh, A. K. (2022). Shaping the root system architecture in plants for adaptation to drought stress. *Physiologia Plantarum*, 174, e13651. https://doi.org/10.1111/ppl.v174.2

Rauf, S., Sadaqat, H.A. (2008). Identification of physiological traits and genotypes combined to high achene yield in sunflower (*Helianthus annuus* L.) under contrasting water regimes. *Australian Journal of Crop Science*, **1**(1), 23-30.

Ravanbakhsh, M., Sasidharan, R., Voesenek, L.A.C.J., Kowalchuk, G.A., Jousset, A. (2018). Microbial modulation of plant ethylene signaling: Ecological and evolutionary consequences. *Microbiome*, **6**(52). https://doi.org/10.1186/s40168-018-0436-1

Rodríguez, H.; Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, **17**, 319-339. https://doi.org/10.1016/S0734-9750(99)00014-2

Rosenblueth, M., Martínez-Romero, E. (2004). *Rhizobium etli* maize populations and their competitiveness for root colonization. *Archives of Microbiology*, **181**, 337-344. https://doi.org/10.1007/s00203-004-0661-9

Said, A. F., Alwutayd, K. M., Kamal, N., Ghanem, O. M. (2025). Diversity and effectiveness of arbuscular mycorrhizal fungi species in alleviating drought stress in tomato. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, **53**(2),14382. https://doi.org/10.15835/nbha53214382

Saux, M., Ponnaiah, M., Langlade, N., Zanchetta, C., Balliau, T., El-Maarouf-Bouteau, H., Bailly, Ch. (2020). A multiscale approach reveals regulatory players of water stress responses in seeds during germination. *Plant, Cell & Environment, 43*(5), 1300-1313. https://doi.org/10.1111/pce.13731

Seleiman, M.F., Refay, Y., Al-Suhaibani, N., Al-Ashkar, I., El-Hendawy, S., Hafez, E.M. (2019). Integrative effects of rice-straw biochar and silicon on oil and seed quality, yield and physiological traits of *Helianthus annuus* L. grown under water deficit stress. *Agronomy*, *9*(10), 637. https://doi.org/10.3390/agronomy9100637

Sharma, S., Kulkarni, J., Jha, B. (2016). Halotolerant rhizobacteria promote growth and enhance salinity tolerance in peanut. *Frontiers in Microbiology*, **7**, 1600. https://doi.org/10.3389/fmicb.2016.01600

Shin, Y. K., Bhandari, S. R., Jo, J. S., Song, J. W., and Lee, J. G. (2021). Effect of drought stress on chlorophyll fluorescence parameters, phytochemical contents, and antioxidant activities in lettuce seedlings. *Horticulturae* **7**, 238. http://dx.doi.org/10.3390/horticulturae7080238

Singh, A., Agrawal, M. (2015). Effects of ambient and elevated CO_2 on growth, chlorophyll fluorescence, photosynthetic pigments, antioxidants, and secondary metabolites of *Catharanthus roseus* (L.) G Don. grown under three different soil N levels. *Environmental Science and Pollution Research*, *22*, 3936-3946. https://doi.org/10.1007/s11356-014-3661-6

Stanhill, G. (1986). Water use efficiency. *Advances in agronomy*, **39**, 53-85. https://doi.org/10.1016/S0065-2113(08)60465-4

Steiner, F., Zuffo, A. A. (2019). Drought tolerance of four vegetable crops during germination and initial seedling growth. Bioscience Journal, 35(1), 177-186. http://dx.doi.org/10.14393/BJ-v35n1a2019-41724

Tabasum, S., Nazir, G., Hussain, K., Gautam, A., Mushtaq, F., Nabi, A., Ahsan, S. (2025). Climate smart breeding of vegetable crops: A review. *Plant Archives*, **25**(1), 3298-3307. https://doi.org/10.51470/PLANTARCHIVES.2025.v25.supplement-1.450

Tiwari, Y.K., Yadav, S.K. (2020). Effect of high-temperature stress on ascorbate–glutathione cycle in maize. *Agricultural Research, 9*(2), 179-187. https://doi.org/10.1007/s40003-019-00421-x

Tsutsumi, N., Tohya, M., Nakashima, T., Ueno, O. (2017). Variations in structural, biochemical, and physiological traits of photosynthesis and resource use efficiency in Amaranthus species (NAD-ME-type C4). *Plant Production Science*, *20*(3), 300-312. https://doi.org/10.1080/1343943X.2017.1320948

Turan, M., Ekinci, M., Argin, S., Brinza, M., Yildirim, E. (2023). Drought stress amelioration in tomato (*Solanum lycopersicum* L.) seedlings by biostimulant as regenerative agent. *Frontiers in Plant Science*, *14*, 1211210. https://doi.org/10.3389/fpls.2023.1211210.

Turner, N. C., Wright Graeme, C., Siddique, K. H. M. (2001). Adaptation of grain legumes (pulses) to water limited environments. *Advances in Agronomy*, **71**, 193-231. https://doi.org/10.1016/S0065-2113(01)71015-2

Wang, J., Mao, L., Li, Y., Lu, K., Qu, C., Tang, Z., Li, J., Liu, L. (2024). Natural variation in *BnaA9.NF-YA7* contributes to drought tolerance in *Brassica napus* L. *Nature Communications*, **15**, 2082. http://dx.doi.org/10.1038/s41467-024-46271-2

Wang, L., Hu, Z., Zhu, M., Zhu, Z., Hu, J., Qanmber, G., Chen, G. (2017). The abiotic stress-responsive NAC transcription factor *SlNAC11* is involved in drought and salt response in tomato (*Solanum lycopersicum* L.). *Plant Cell Tissue Organ Culture*, **129**, 161-174. http://dx.doi.org/10.1007/s11240-017-1167-x

Warner, K., Afifi, T. (2014). Where the rain falls: Evidence from 8 countries on how vulnerable households use migration to manage the risk of rainfall variability and food insecurity. *Climate and Development, 6*, 1-17. https://doi.org/10.1080/17565529.2013.835707

Williams, A., De Vries, F. T. (2019). Plant root exudation under drought: Implications for ecosystem functioning. *New Phytologist*, **225**(5), 1899-1905. https://doi.org/10.1111/nph.16223

Xu, J., Guo, L., and Liu, L. (2022). Exogenous silicon alleviates drought stress in maize by improving growth, photosynthetic and antioxidant metabolism. *Environmental and Experimental Botany*, 201, 104974. https://doi.org/10.1016/j.envexpbot.2022.104974

Yang, C., Huang, Y., Lv, P., Antwi-Boasiako, A., Begum, N., Zhao, T., Zhao, J. (2022). NAC transcription factor *GmNAC12* improved drought stress tolerance in soybean. *International Journal of Molecular Sciences*, **23**, 12029. http://dx.doi.org/10.3390/ijms231912029

Yang, H., Huntingford, C., Wiltshire, A., Sitch, S., Mercado, L. (2019). Compensatory climate effects link trends in global runoff to rising atmospheric CO_2 concentration. *Environmental Research Letters, 14*, 124075. https://doi.org/10.1088/1748-9326/ab5c6

Yang, P.M., Huang, Q.C., Qin, G.Y., Zhao, S.P., Zhou, J.G. (2014). Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. *Photosynthetica*, *52*, 193-202. https://doi.org/10.1007/s11099-014-0020-2

Zhang, J., Zhang, S., Cheng, M., Jiang, H., Zhang, X., Peng, C., Lu, X., Zhang, M., Jin, J. (2018). Effect of drought on agronomic traits of rice and wheat: A meta- analysis.

International Journal of Environmental Research and Public Health, *15*(5), 839. https://doi.org/10.3390/ijerph15050839

Zhao, T., Wu, T., Pei, T., Wang, Z., Yang, H., Jiang, J., Zhang, H., Chen, X., Li, J., Xu, X. (2021). Overexpression of *SlGATA17* promotes drought tolerance in transgenic tomato plants by enhancing activation of the phenylpropanoid biosynthetic pathway. *Frontiers in Plant Science*, **12**. http://dx.doi.org/10.3389/fpls.2021.634888

Zhao, W., Liu, L., Shen, Q., Yang, J., Han, X., Tian, F., Wu, J. (2020). Effects of water stress on photosynthesis, yield, and water use efficiency in winter wheat. *Water, 12*(8), 2127. https://doi.org/10.3390/w12082127

CHAPTER 3

Biotechnology Applied to Drought-Resilient Vegetable Production

Eduardo Fidel Héctor Ardisana

Facultad de Posgrado, Universidad Técnica de Manabí, Portoviejo, Ecuador, ehectorardisana@gmail.com

1. INTRODUCTION

Plants that are able to grow under adverse conditions, such as drought, achieve this through the synthesis of secondary metabolites that act as physiological mechanisms of stress tolerance. Among the substances involved in drought tolerance are phenolic compounds, terpenoids, flavonoids, and nitrogen-containing compounds (Zahedi et al., 2019). An important proportion of these metabolites have applications in human nutrition, pharmacology, industry, agriculture, and other areas. For this reason, the conservation, propagation, and genetic improvement of drought-tolerant plants goes beyond purely biological and environmental purposes and have attracted increasing interest over the last two decades.

The environments in which drought-tolerant plants usually grow do not provide favorable conditions for their large-scale propagation. In addition, the seeds of many species show low germination rates or are difficult to propagate vegetatively by cuttings (Custódio et al., 2022). To overcome these limitations, accelerated micropropagation through *in vitro* culture techniques has been successfully applied. Among the *in vitro* approaches that have gained relevance in recent years is somatic embryogenesis, which has been used not only as a propagation method (Spinoso-Castillo and Bello-Bello, 2022) but also as a technology for metabolite production in bioreactors (Murthy et al., 2023). At the same time, the need to increase the yield of useful products and to select plants with outstanding performance has promoted studies based on conventional breeding as well genetic engineering tools (Martignago et al., 2020).

The fact that stress conditions stimulate the synthesis of these compounds has led to the use of stress itself, or of stress-related molecules, as elicitors to enhance the production of biological compounds of interest (Thakur et al., 2019). Recent advances in these topics, together with their future prospects, are reviewed below.

2. *IN VITRO* MICROPROPAGATION

The micropropagation of drought-tolerant species has gained importance as a means of multiplying these plants, either for the restoration of eroded soils or for the establishment of plantations with commercial interest. Different explant sources and growth regulators have been used for the multiplication of these species.

Cyamopsis tetragonoloba L. (Taub) is a legume from which a gum is obtained that is useful in food production, cosmetics, pharmaceuticals, and is even employed as a gelling agent in culture media (Babbar et al., 2005). Ahmad et al. (2013) developed a complete protocol for its multiplication using axillary buds, inducing shoot formation with thidiazuron (TDZ) and rooting with indolebutyric acid (IBA), which resulted in an acclimatization success rate of 80% for the regenerated plants.

In contrast, Rashmi and Trivedi (2014) obtained callus cultures from *Nerium odorum* L., a species resistant to high temperatures, salinity, and drought, using 2,4-dichlorophenoxyacetic acid (2,4-D) alone or combined with 6-benzylaminopurine (BAP). In addition to its use in soil recovery, this species synthesizes flavonoids and terpenoids with applications in medicine. Similarly, the propagation of *Anthyllis barba-jovis* L., a Mediterranean fabaceous species useful for soil restoration, has been achieved using seedlings obtained from seeds germinated *in vitro*, with benzyladenine (BA) during the multiplication stage and IBA for rooting (Trigka and Papafotiou, 2017).

In woody species such as *Jatropha curcas* L., the use of seeds or seed-derived tissues as explant sources has been explored as an alternative to increase micropropagation efficiency. Jokotola et al. (2025) tested seeds cut in two different ways (cut with back and cut plain) as well as embryos dissected from the seeds; the latter showed the best results, with a survival rate of 4.58 explants out of 5 (91.6%).

In addition to the presence of cytokinins in the culture medium, which stimulate shoot formation, some species require a certain amount of auxin to ensure caulogenesis. Pourhassan et al. (2023) successfully multiplied *Zamioculcas zamiifolia* (Lodd.) Engl. using 0.5 mg L^{-1} naphthaleneacetic acid (NAA) combined with 2 mg L^{-1} BA. This species is valued for its ornamental use, its ability to purify indoor air, and because its tissues contain metabolites of pharmacological interest with anti-inflammatory, antioxidant, and anxiolytic properties, such as apigenin, rosmarinic acid, and caffeic acid (Le Moullec et al., 2015).

The growth regulators used to stimulate organogenesis, as well as their concentrations, may vary among species and even among genotypes of the same species. For example, five almond genotypes responded differently to combinations of BA (0–4 mg L^{-1}), TDZ (0–2 mg L^{-1}), IBA (0.05–1 mg L^{-1}), and gibberellic acid (GA_3) (0–1 mg L^{-1}) (Rezaei et al., 2023).

Naturally occurring plant growth regulators have also been tested in the micropropagation of drought-tolerant plants, with satisfactory results. Mogilevskaya et al. (2025), working with *Prunus*, found that 24-epibrassinolide performed better than BAP in terms of shoot length, number of shoots per explant, and number of nodes of *in vitro* plants. This effect may be related to the protective role of this brassinosteroid analog against drought stress (Wang et al., 2019) and to the ability of plants of this genus to synthesize brassinosteroids (Ma et al., 2024).

The acclimatization stage of micropropagated plants largely determines the final outcome and success of the protocol; therefore, efforts have been made to increase the proportion of plants adapted to *ex vitro* conditions, for example by the use of mycorrhizae to stimulate plant establishment. Gomes et al. (2021) observed that the addition of 2 µM quercetin stimulated mycorrhization with *Tuber borchii* of *in vitro* plants of *Arbutus unedo*, a Mediterranean species with edible fruits that is highly tolerant to drought. The role of quercetin as a signaling molecule that promotes the association between mycorrhizae and roots has also been recognized (Tian et al., 2021).

3. SOMATIC EMBRYOGENESIS

Somatic embryogenesis has wide applications in increasing the efficiency of *in vitro* plant propagation systems; in addition, somatic embryos represent an excellent material for the insertion of foreign genetic information (Martínez and Corredoira, 2024), for providing material for genetic improvement through different techniques (Yuan et al., 2025), and for the study of processes such as abiotic stress. Under *in vitro* culture conditions, drought is simulated by adding substances that induce osmotic stress to the culture medium, such as polyethylene glycol, mannitol, and sorbitol, and the response to this condition is mediated by abscisic acid (ABA) (Spinoso-Castillo and Bello-Bello, 2022).

This idea is supported by the results obtained from experiments in which osmotic stress was induced during somatic embryogenesis. In date palm (*Phoenix dactylifera* L.), a species tolerant to salinity, heat, and drought, the addition of osmotic stress–inducing substances, such as polyethylene glycol and sorbitol, to the culture medium increases the multiplication, germination, and rooting of somatic embryos (Hassan and Taha, 2012; Taha, 2017). Similarly, Valencia-Lozano et al. (2021) observed that the induction of osmotic stress enhanced the vigor of root and apical meristems in *Coffea arabica* L. and promoted the maturation of somatic embryos.

The role of ABA has also been described by Walther et al. (2022) during the induction of somatic embryogenesis in Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), a drought-tolerant species. In huizache (*Vachellia farnesiana* [L.] Wight & Arn.), a xerotolerant species that grows in highly arid systems, the addition of 3% polyethylene glycol increased the frequency of somatic embryos, while 1 mg L^{-1} ABA promoted their maturation (Ibarra-López et al., 2026).

Mannitol and sorbitol have also been used as *in vitro* selective agents to obtain drought-tolerant plants from somatic embryos of *Oryza sativa* L. The frequency of somatic embryogenesis was significantly reduced when high concentrations of these compounds (150 mM) were added to the culture medium (Rajalakshmi and Vikrant, 2025), causing high lethality and, as a consequence, increasing the likelihood of recovering tolerant individuals.

4. TRANSGENIC AND GENETIC STUDIES

The polygenic nature of drought tolerance complicates both its understanding and its use in crop improvement efforts (Khan et al., 2019). Nevertheless, numerous studies have been conducted to obtain tolerant genotypes, both through transgenic approaches and through conventional breeding procedures.

Recently, substantial research has been devoted to the identification of drought tolerance–related genes and to understanding how they function. The WRKY gene family comprises numerous transcription factors involved in responses to diverse biotic and abiotic stresses, including drought tolerance (Chen et al., 2019). Consequently, their expression has been examined across multiple species.

In *Arabidopsis*, the overexpression of ZmWRKY40, a transcription factor from *Zea mays* L., confers drought tolerance, manifested as increased activity of the ROS-scavenging enzymes peroxidase (POD) and catalase (CAT) (Wang et al., 2018). By contrast, overexpression of the wheat gene TaWRKY133 in *Arabidopsis* results in diminished drought tolerance, while its silencing increases tolerance (Lv et al., 2022). Similarly, in *Arabidopsis*, the genes IgWRKY50 and IgWRKY32, derived from *Iris germanica* L., increase drought tolerance (Zhang et al., 2022). In all cases, the phenotypic expression of susceptibility is observed as reduced germination and growth, together with decreased activity of ROS-detoxifying enzymes, such as superoxide dismutase (SOD), peroxide (POD), and catalase (CAT).

Genes not belonging to the WRKY family have also shown a role in drought tolerance. Cui et al. (2018) identified a peptide (OsDSSR1) associated with tolerance to abiotic stresses in rice (*Oryza sativa* L.), including drought. Transgenic plants overexpressing this peptide show increased drought tolerance and reduced sensitivity to ABA, which is consistent with the close relationship between this phytohormone and water stress responses. In transgenic wheat plants (*Triticum aestivum* L.), overexpression of GmDREB1 from soybean (*Glycine max*) is associated with higher yields, reduced membrane damage, improved osmotic adjustment, and higher photosynthetic efficiency even under conditions of water deficit (Zhou et al., 2020). In this same species, improvements in drought tolerance had previously been reported through the introduction of genetic material from other species like soybean (Gao et al., 2005) and sunflower (González et al., 2019).

In transgenic *Arabidopsis* and wheat, TaFDL2-1a from wheat improves drought tolerance through the regulation of ABA synthesis and ROS-scavenging enzyme activity (Wang et al., 2022). Overexpression of MdFRK2, also derived from wheat, produces similar effects in transgenic apple plants (Yang et al., 2023). In the drought-tolerant soybean mutant JB18, Liu et al. (2022) identified the gene GmsHSP26, cloned it, and generated transgenic plants by transforming cotyledon nodes of the susceptible cultivar JN18 with *A. tumefaciens*. Overexpression of GmsHSP26 was associated with enzymatic responses and proline accumulation related to tolerance; in contrast, in JN18 plants in which GmsHSP26 was edited using CRISPR/Cas9, these responses were not observed.

Gene regulation of drought tolerance can also be negative, meaning that it is controlled by genes that determine susceptibility. The gene TaMpc1-D4, present in wheat (and not belonging to the WRKY group), increases susceptibility when overexpressed in transgenic *Arabidopsis* plants; conversely, silencing this gene in wheat increases drought tolerance (Li et al., 2020). Similar results had been reported for GhWRKY25, a member of the WRKY group from cotton, whose overexpression in *Nicotiana benthamiana* increases susceptibility (Liu et al., 2016).

Exploration of the genomes of drought-tolerant species is therefore an essential strategy for identifying genes useful for crop improvement. In forest species, advances have been achieved in genera such as *Quercus*, *Eucalyptus*, and *Pinus*, many species of which are drought tolerant; in contrast, much less is known about other genera such as *Prosopis*, in which several species show different degrees of tolerance, including *P. glandulosa* Torr. and especially *P. cineraria* (L.) Druce (Rai et al., 2021).

More conventional approaches have also focused on the identification of tolerant individuals through evaluation under greenhouse and field conditions (Sari et al., 2020; Viljevac Vuletić et al., 2022) or under *in vitro* conditions (Hajizadeh et al., 2023; Bektaş et al., 2024).

5. OBTAINING METABOLITES AND OTHER PROCESSES

Secondary metabolites present in plants (Yeshi et al., 2022) are classified into three main groups (Table 1).

Table 1. Groups of secondary metabolites found in plants

Group	Metabolites	Examples
Terpenoids	Plant volatiles, sterols, carotenoids, saponins, glycosides	ß-carotene, licopene, lutein
Phenolic compounds	Flavonoids, phenolic acids, lignin, lignans, coumarins, stilbenes, tannins	Kaempferol, quercetin, resveratrol
Nitrogen-contaning compounds	Alkaloids, glucosinolates, cyanogenic glycosides	Morphine, sinigrin, amygdalin

Some authors also include polyamines (putrescine, spermine, and spermidine), which are ubiquitous compounds, present in all plant cells. Although they may be considered primary metabolites because of their role in the regulation of cell division, their involvement in stress defense-particularly in drought tolerance-is well established (Blázquez, 2024; Roy et al., 2024). Some examples from each group are discussed below.

5.1. <u>Terpenoids</u>

Mibei et al. (2017) analyzed pigment profiles in 19 accessions of eggplant (*Solanum aethiopicum* and *Solanum macrocarpon*) subjected to drought conditions. Although carotenoid content increased under water stress in two accessions, drought generally caused significant reductions in both carotenoid and chlorophyll contents. This result should be considered when establishing extraction protocols for these compounds.

Within this group, ursolic and oleanolic acids, which are triterpenoids involved in plant protection against drought (Gudoytite et al., 2021), have shown anti-inflammatory, antioxidant, and anticarcinogenic effects in experimental animal and human models (Günther et al., 2026).

5.2. Phenolic compounds

Rodrigues et al. (2020) detected more than 20 phenolic compounds in chaya (*Cnidoscolus aconitifolius* Mill.) leaves, with kaempferol, quercetin, and myricetin being the most abundant. Among the extraction methods tested, Subcritical Water Extraction (SWE) and Microwave-Assisted Extraction (MAE) were the most efficient. Quercetin, among other compounds present in Tartary buckwheat (*Fagopyrum tataricum* Gaertn.), contributes to intestinal health, improved digestion, and cholesterol reduction (Luthar et al., 2021).

Neoglaziovia variegata (Arruda) Mez, native to the Caatinga region in Brazil, is an excellent example of a drought-tolerant plant with multiple potential uses. Its ability to grow in very dry and arid soils makes it suitable for the restoration of eroded areas. During the rainy season it produces berries that, although not an important part of the human diet, are edible; its leaves can be used as emergency forage for animals, and its fiber is useful for the production of different industrial and artisanal products. In addition, it contains phenolic compounds with antinociceptive, antioxidant, and photoprotective properties (Ibrahim et al., 2019; Miranda et al., 2025).

5.3. Nitrogen-containing compounds

Berberine is an isoquinoline alkaloid present in several species, particularly in the genus *Berberis* spp., from which it takes its name. It has important pharmacological applications as a hypoglycemic, antimicrobial, and anticarcinogenic agent, among others, and for this reason it has received considerable attention in countries such as Ukraine (Lykholat et al., 2019) and Turkey (Bostanci and Akalin, 2023).

Sophora alopecuroides L. is a fabaceous species native to Asia that is used in traditional medicine for its anti-inflammatory and anxiolytic properties. More recently, extracts obtained from its seeds have been shown to reduce opioid withdrawal symptoms, an effect associated with their content of alkaloids such as sophocarpine, matrine, and sophoramine (Kianbakht et al., 2020). Drought conditions stimulate alkaloid synthesis in this species (Huang et al., 2024), so the induction of this stress may contribute to increasing the yields of these biologically valuable products.

5.4. Polyamines

Spermidine is involved in protecting maize plants against water stress through its effect on increasing antioxidant compounds, that reduce oxidative processes induced by drought (Li et al., 2018). Similar results for spermidine, as well as for putrescine and spermine, have been reported in wheat, supporting the idea that the effect of polyamines on stress tolerance is not direct but rather related to a signaling role that enhances defense responses (Marcińska et al., 2020).

These are only a few examples; as noted by Yeshi et al. (2023), more than 200,000 secondary metabolites have been identified in plants, and given that more than 390,000 plant species are known, it is clear that much remains to be discovered and applied. For example, plant tissue culture, through different techniques such as callus, seedling, root, and cell cultures, combined with the use of bioreactors, is beginning to be applied for the large-scale production of useful metabolites (Espinosa-Leal et al., 2018) to increase production efficiency.

6. CONCLUSIONS

Drought is one of the main limiting factors for horticultural production on a global scale, with direct effects on crop growth, yield, and quality. Plants respond to this stress through a network of physiological, biochemical, and molecular mechanisms, including the modulation of water balance, regulation of stomatal opening, activation of antioxidant systems, and the synthesis of secondary metabolites.

The need to produce crops under drought conditions, as well as to restore soils affected by this stress, has driven research aimed at improving species to increase drought tolerance. In this context, special attention has been given to the study of genes that regulate the expression of defense mechanisms and to their incorporation into genetically modified plants with this trait through transgenic approaches.

A wide range of secondary metabolites participate in the response to water stress by reducing oxidative damage, acting as signaling molecules, or influencing cellular stability. The differential accumulation of phenolic compounds, flavonoids, terpenoids, and other bioactive molecules reflects a metabolic plasticity that varies according to species, genotype, and stress intensity. Many of these metabolites also display properties that make them relevant for human nutrition, pharmacology, industry, agriculture, and other fields.

Based on current knowledge, new opportunities have emerged for the development of more sustainable agricultural production strategies under climate change scenarios. The identification of physiological and metabolic traits associated with drought tolerance, together with their incorporation into breeding programs and adaptive agronomic practices, represents a promising approach to reduce crop vulnerability. At the same time, the integration of knowledge from genetics, biochemistry, and physiology will increase the efficiency of industrial and biotechnological processes used for the production of bioactive compounds.

REFERENCES

Ahmad, N., Faisal, M., Anis, M. (2013). Role of PGR on *in vitro* shoot propagation in *Cyamopsis tetragonoloba* L. (Taub.): a drought tolerant grain legume. *Rendiconti Lincei. Scienze Fisiche e Naturali, 24,* 7-12. https://doi.org/10.1007/s12210-012-0210-4

Babbar, SB., Jain, R., Walia, N. (2005). Guar gum as a gelling agent for plant tissue culture media. *In Vitro Cellular & Developmental Biology - Plant, 41*, 258-261. https://doi.org/10.1079/IVP2005628

Bektaş, Ü., Isak, MA., Bokzurt, T., Dönmez, D., İzgü, T., Tütüncü, M., Simsek, Ö. (2024). Genotype-specific responses to *in vitro* drought stress in myrtle (*Myrtus communis* L.): integrating machine learning techniques. *PeerJ, 12*, e18081. https://doi.org/10.7717/peerj.18081

Blázquez, MA. (2024). Polyamines: Their Role in Plant Development and Stress. *Annual Review of Plant Biology, 75* (1), 95-117. https://doi.org/10.1146/annurev-arplant-070623-110056

Bostanci, B., Akalin, E. (2023). An overview of the therapeutic potentials and safety profiles of *Berberis* species in Türkiye. *Turkish Journal of Biodiversity, 6* (2), 159-166. https://doi.org/10.38059/biodiversity.1306614

Chen, X., Li, C., Wang, H., Guo, Z. (2019). WRKY transcription factors: evolution, binding, and action. *Phytopatology Research, 1*, 13. https://doi.org/10.1186/s42483-019-0022-x

Cui, Y., Li, M., Yin, X., Song, S., Xu, G., Wang, M., Li, C., Peng, C., Xia, X. (2018). OsDSSR1, a novel small peptide, enhances drought tolerance in transgenic rice. *Plant Science, 270*, 85-96. https://doi.org/10.1016/j.plantsci.2018.02.015

Custódio, L., Charles, G., Magné, C., Barba-Espín, G., Piqueras, A., Hernández, JA., Ben Hamed, K., Castañeda-Loaiza, V., Fernandes, E., Rodrigues, MJ. (2022). Application of *in vitro* plant tissue culture techniques to halophyte species: a review. *Plants, 12,* 126. https://doi.org/10.3390/plants12010126

Espinosa-Leal, CA., Puente-Garza, CA., García-Lara, S. (2018). *In vitro* plant tissue culture: means for production of biological active compounds. *Planta, 248*, 1-18. https://doi.org/10.1007/s00425-018-2910-1

Gao, S., Xu, H., Cheng, X., Chen, M., Xu, Z., Li, L., Ye, X., Du, L., Hao, X., Ma, Y. (2005). Improvement of wheat drought and salt tolerance by expression of a stress inducible transcription factor GmDREB of soybean (*Glycine max*). *Chinese Science Bulletin, 50*, 2714-2723. https://doi.org/10.1007/BF02899641

Gomes, B., Castro, F., Santos, R., Figueiredo, P., Silva, M., Vidal, M., Ferreira, I., Nunes, J., Machado, H., Gomes, F. (2021). Effect of quercetin on mycorrhizal synthesis between *Tuber borchii* and *Arbutus unedo* L. *in vitro* plants. *Microbiology Research, 12*, 69-81. https://doi.org/10.3390/microbiolres12010007

González, FF., Capella, M., Ribichich, KK., Curín, F., Giacomelli, JJ., Ayala, F., Watson, G., Otegui, ME., Chan, RL. (2019). Field-grown transgenic wheat expressing the sunflower gene HaHB4 significantly outyields the wild type. *Journal of Experimental Botany, 70* (5), 1669-1681. https://doi.org/10.1093/jxb/erz037

Gudoityte, E., Arandarcikaite, O., Mazeikiene, I., Bendokas, V., Liobikas, J. (2021). Ursolic and oleanolic acids: plant metabolites with neuroprotective potential. *International Journal of Molecular Sciences, 22*, 4599. https://doi.org/10.3390/ijms22094599

Günther, A., Kulawik, M., Sip, S., Zalewski, P., Jarmołowska-Jurczyszyn, D., Stawicki, P., Bednarczyk-Cwynar, B. (2026). Targeting oxidative stress in carcinogenesis: oleanolic acid and its molecular pathways. *Antioxidants*, *15* (1), 67. https://doi.org/10.3390/antiox15010067

Hajizadeh, HS., Rezaei, S., Yari, F., Okatan, V. (2023): In vitro simulation of drought stress in some Iranian Damask Rose landraces. *Horticultural Science (Prague), 50*, 45-60. https://doi.org/10.17221/107/2021-HORTSCI

Hassan, MM., Taha, RA. (2012). Callogenesis, somatic embryogenesis and regeneration of date palm (Phoenix dactylifera L.) cultivars affected by carbohydrate sources. *International Journal of Agricultural Research, 7* (5), 231-242. https://doi.org/10.3923/ijar.2012.231.242

Huang, X., Rong, W., Zhang, X., Gao, Y., Zhou, Y., Su, J., Luo, H., Chu, G., Wang, M. (2024). Transcriptome and metabolome analysis reveal the dynamic changes and biosynthesis pathways of alkaloids in *Sophora alopecuroides* L. under drought stress. *Industrial Crops and Products, 212*, 118365. https://doi.org/10.1016/j.indcrop.2024.118365

Ibarra-López, A., Vázquez-Alvarado, RE., Ojeda-Zacarías, MC., Lozoya-Saldaña, H., Olivares-Sáenz, E., Treviño-Ramírez, JE. (2026). Plant regeneration of sweet acacia (*Vachellia farnesiana* [L.] Wight & Arn.) via somatic embryogenesis. *Discover Forests, 2,* 6. https://doi.org/10.1007/s44415-025-00064-7

Ibrahim, AHH., Herfindal, L., Rathe, B., Andersen, HL., Almeida, JRGS., Fossen, T. (2019). A novel poly-oxygenated flavone glucoside from aerial parts of the Brazilian plant *Neoglaziovia variegata* (Bromeliaceae). *Heliyon, 5* (3), e01369. https://doi.org/10.1016/j.heliyon.2019.e01369

Jokotola, IS., Iyekolo, B., Omaka, A., Adeboye, S., Bello, A. (2025). Enhancing *Jatropha curcas* micropropagation through optimized hypochlorite concentrations: a comparative evaluation of various explant types. *Nigerian Journal of Biotechnology, 42* (2), 1-8. https://zenodo.org/uploads/17216942

Khan, S., Anwar, S., Yu, S., Sun, M., Yang, S., Gao, Z. (2019). Development of drought-tolerant transgenic wheat: achievements and limitations. *International Journal of Molecular Sciences, 20*, 3350. https://doi.org/10.3390/ijms20133350

Kianbakht, S., Hajiaghaee, R., Akhondzadeh, S. (2020). Efficacy and safety of *Sophora alopecuroides* var. *alopecuroides* seed extract for opioid detoxification: A randomized, double-blind, and placebo-controlled clinical trial. *Phytotherapy Research, 34* (5), 1108-1113. https://doi.org/10.1002/ptr.6578

Le Moullec, A., Juvik, OJ., Fossen, T. (2015). First identification of natural products from the African medicinal plant *Zamioculcas zamiifolia* - A drought resistant survivor through millions of years. *Fitoterapia, 106*, 280-285. https://doi.org/10.1016/j.fitote.2015.09.011

Li, L., Gu, W., Li, C., Li, W., Li, C., Li, J., Wei, S. (2018). Exogenous spermidine improves drought tolerance in maize by enhancing the antioxidant defence system and regulating endogenous polyamine metabolism. *Crop & Pasture Science, 69* (11), 1076-1091. https://doi.org/10.1071/CP18271

Li, X., Tang, Y., Li, H., Luo, W., Zhou, C., Zhang, L., Lv, J. (2020). A wheat R2R3 MYB gene TaMpc1-D4 negatively regulates drought tolerance in transgenic *Arabidopsis* and wheat. *Plant Science, 299*, 110613. https://doi.org/10.1016/j.plantsci.2020.110613

Liu, S., Guan, S., Liu, J., Zhang, Y., Jiang, Y., Hu, S., Shi, A., Cong, Q., Qu, J., Dan, Y. (2022). Cloning of the soybean sHSP26 gene and analysis of its drought resistance. *Phyton-International Journal of Experimental Botany*, *91* (7), 1465-1482. https://doi.org/10.32604/phyton.2022.018836

Liu, X., Song, Y., Xing, F., Wang, N., Wen, F., Zhu, C. (2016). GhWRKY25, a group I WRKY gene from cotton, confers differential tolerance to abiotic and biotic stresses in transgenic *Nicotiana benthamiana*. *Protoplasma, 253* (5), 1265-1281. https://doi.org/10.1007/s00709-015-0885-3

Luthar, Z., Golob, A., Germ, M., Vombergar, B., Kreft, I. (2021). Tartary Buckwheat in Human Nutrition. *Plants, 10*, 700. https://doi.org/10.3390/plants10040700

Lv, M., Luo, W., Ge, M., Guan, Y., Tang, Y., Chen, W., Lv, J. (2022). A Group I WRKY Gene, TaWRKY133, Negatively Regulates Drought Resistance in Transgenic Plants. *International Journal of Molecular Sciences, 23*, 12026. https://doi.org/10.3390/ijms231912026

Lykholat, YV., Khromykh, NO., Lykholat, TY., Bobrova, OM., Didur, OO., Lykholat, OA., Sudak, VM., Legostaeva, TV., Gtytzaj, ZV., Kabar, AM., Savosko, VM., Kovalenko, IM., Davydov, VR., Suvorova, KM., Dudkina, KA., Kolinko, OM., Grygoryuk, IP. (2019). Introduction success of less common species from the genus *Berberis* L. *Ukrainian Journal of Ecology, 9* (4), 634-640.

https://www.ujecology.com/articles/introduction-success-of-less-common-species-from-the-genus-berberis-l.pdf

Ma, Y., Ma, C., Zhou, P., Gao, F., Tan, W., Huang, X., Bai, Y., Li, M., Wang, Z., Hayat, F., Shi, T., Ni, Z., Gao, Z. (2024). PmLBD3 links auxin and brassinosteroid signalling pathways on dwarfism in *Prunus mume*. *BMC Biology, 22* (1), 184. https://doi.org/10.1186/s12915-024-01985-z

Marcińska, I., Dziurka, K., Waligórski, P., Janowiak, F., Skrzypek, E., Warchoł, M., Juzoń, K., Kapłoniak, K., Czyczyło-Mysza, IM. (2020). Exogenous polyamines only indirectly induce stress tolerance in wheat growing in hydroponic culture under polyethylene glycol-induced osmotic stress. *Life, 10* (8), 151. https://doi.org/10.3390/life10080151

Martignago, D., Rico-Medina, A., Blasco-Escámez, D., Fontanet-Manzaneque, JB., Caño-Delgado, AI. (2020). Drought resistance by engineering plant tissue-specific responses. *Frontiers in Plant Science, 10*, 1676. https://doi.org/10.3389/fpls.2019.01676

Martínez, M., Corredoira, E. (2024). Recent advances in plant somatic embryogenesis: Where we stand and where to go? *International Journal of Molecular Sciences, 25*, 8912. https://doi.org/10.3390/ijms25168912

Mibei, EK., Ambuko, J., Giovannoni, JJ., Onyango, AN., Owino, WO. (2017). Carotenoid profiling of the leaves of selected African eggplant accessions subjected to drought stress. *Food Science & Nutrition, 5* (1), 113-122. https://doi.org/10.1002/fsn3.370

Miranda, FAA., Oliveira, VV., Bezerra, SDS., Osajima, JA., Silva-Filho, EC. (2025). Photoprotective properties of extracts derived from Neoglaziovia variegata (Arruda) Mez incorporated into mesoporous TiO2. *ACS Omega, 10* (44), 52820-52837. https://doi.org/10.1021/acsomega.5c06956

Mogilevskaya, IV., Zholobova, OO., Tereshchenko, TV., Grichik, EL., Melnik, SV. (2025). Osmotic stress tolerant cherry rootstock: *in vitro* propagation features. *Indian Journal of Agricultural Research, 59* (3), 458-466. https://doi.org/10.18805/IJARe.AF-822

Murthy, HN., Joseph, KS., Hahn, JE., Lee, HS., Paek, KY., Park, SY. (2023). Suspension culture of somatic embryos for the production of high-value secondary metabolites.

Physiology and Molecular Biology of Plants, 29, 1153-1177. https://doi.org/10.1007/s12298-023-01365-x

Pourhassan, A., Kaviani, B., Kulus, D., Miler, N., Negahdar, NA. (2023). Complete micropropagation protocol for black-leaved *Zamioculcas zamiifolia* (Lodd.) Engl. 'Dowon'. *Horticulturae, 9*, 422. https://doi.org/10.3390/horticulturae9040422

Rai, MK., Shekhawat, JK., Kataria, V., Phulwaria, M., Shekhawat, NS. (2021). Genomic and biotechnological interventions in *Prosopis cineraria*: current status, challenges and opportunities. *Trees, 35*, 1109-1121. https://doi.org/10.1007/s00468-020-02073-9

Rajalakshmi, P., Vikrant (2025). Evaluation of drought stress factors response on somatic embryogenesis and plantlet regeneration from mature caryopsis culture in traditional Indian black rice (*Oryza sativa* L.). *Journal of Stress Physiology & Biochemistry, 21* (4), 138-152. http://www.jspb.ru/issues/2025/N4/JSPB_2025_4_138-152.pdf

Rashmi, R., Trivedi, MP. (2014). Effect of various growth hormone concentration and combination on callus induction, nature of callus and callogenic response of *Nerium odorum*. *Applied Biochemistry and Biotechnology, 172*, 2562-2570. https://doi.org/10.1007/s12010-013-0693-1

Rezaei, A., Gharaghani, A., Shekafandeh, A., Eshghi, S. (2023). Developing a promising micropropagation method for several drought tolerant and hard-to-root wild and domesticated almond genotypes by shoot tips culture. *Erwerbs-Obstbau, 65*, 1463-1477. https://doi.org/10.1007/s10341-023-00866-z

Rodrigues, LGG., Mazzutti, S., Siddique, I., da Silva, M., Vitali, L., Ferreira, SRS. (2020). Subcritical water extraction and microwave-assisted extraction applied for the recovery of bioactive components from Chaya (*Cnidoscolus aconitifolius* Mill.). *The Journal of Supercritical Fluids, 165*, 104976. https://doi.org/10.1016/j.supflu.2020.104976

Roy, T., Pal, N., Das, N. (2024). Regulation of the polyamine pool in plants: Metabolic implications and stress mitigation, with emphasis on microbial influence. *Physiological and Molecular Plant Pathology, 132*, 102317. https://doi.org/10.1016/j.pmpp.2024.102317

Sari, L., Susetio, M., Efendi, D., Wulansari, A, Ermayanti, TM. (2020). Growth evaluation of taro cv. Bentul (*Colocasia esculenta* L.) diploid and tetraploid in the greenhouse in response to different soil water content for selection of drought tolerant plants. *IOP Conference Series: Earth and Environmental Science, 439* (1), 012049. https://doi.org/10.1088/1755-1315/439/1/012049

Spinoso-Castillo, JL., Bello-Bello, JJ. (2022). *In vitro* stress-mediated somatic embryogenesis in plants. *Methods in Molecular Biology, 2527*, 223-235. https://doi.org/10.1007/978-1-0716-2485-2_16

Taha, RA. (2017). Enhanced indirect somatic embryogenesis of date palm using low levels of seawater. In: *Date Palm Biotechnology Protocols Volume 1: Tissue Culture Applications* (Jameel M. Al-Khayri et al., eds.). Springer. https://doi.org/10.1007/978-1-4939-7156-5_6

Thakur, M., Bhattacharya, S., Khosla, PK., Puri, S. (2019). Improving production of plant secondary metabolites through biotic and abiotic elicitation. *Journal of Applied Research on Medicinal and Aromatic Plants, 12,* 1-12. https://doi.org/10.1016/j.jarmap.2018.11.004

Tian, B., Pei, Y., Huang, W., Ding, J., Siemann, E. (2021). Increasing flavonoid concentrations in root exudates enhance associations between arbuscular mycorrhizal fungi and an invasive plant. *The ISME Journal*, *15* (7), 1919-1930. https://doi.org/10.1038/s41396-021-00894-1

Trgka, M., Papafotiou, M. (2017). *In vitro* propagation of *Anthyllis barba-jovis* from seedling tissues. *Acta Horticulturae, 1189.* https://doi.org/10.17660/ActaHortic.2017.1189.94

Valencia-Lozano, E., Ibarra, JE., Herrera-Ubaldo, H., De Folter, S., Cabrera-Ponce, JL. (2021). Osmotic stress-induced somatic embryo maturation of coffee *Coffea arabica* L., shoot and root apical meristems development and robustness. *Scientific Reports, 11*, 9661. https://doi.org/10.1038/s41598-021-88834-z

Viljevac Vuletić, M., Horvat, D., Mihaljević, I., Dugalić, K., Šimić, D., Čupić, T., Jurković, V., Lepeduš, H. (2022). Photosynthetic variability of Oblačinska sour cherry ccotypes under drought. *Plants, 11*, 1764. https://doi.org/10.3390/plants11131764

Walther, M., Wagner, I., Raschke, J., Zoglauer, K., Rupps, A. (2022). Abscisic acid induces somatic embryogenesis and enables the capture of high-value genotypes in Douglas fir (*Pseudotsuga menziesii* [MIRB.] Franco). *Plant Cell Tissue and Organ Culture, 148*, 45-59. https://doi.org/10.1007/s11240-021-02159-3

Wang, B., Li, L., Liu, M., Peng, D., Wei, A., Hou, B., Lei, Y., Li, X. (2022). TaFDL2-1A confers drought stress tolerance by promoting ABA biosynthesis, ABA responses, and ROS scavenging in transgenic wheat. *The Plant Journal, 112* (3), 722-737. https://doi.org/10.1111/tpj.15975

Wang, CT., Ru, JN., Liu, YW., Yang, JF., Li, M., Xu, ZS., Fu, JD. (2018). The maize WRKY transcription factor ZmWRKY40 confers drought resistance in transgenic *Arabidopsis*. *International Journal of Molecular Sciences, 19*, 2580. https://doi.org/10.3390/ijms19092580

Wang, X., Gao, Y., Wang, Q., Chen, M., Ye, X., Li, D., Chen, X., Li, L., Gao, D. (2019). 24-Epibrassinolide-alleviated drought stress damage influences antioxidant enzymes and autophagy changes in peach (*Prunus persicae* L.) leaves. *Plant Physiology and Biochemistry, 135,* 30-40. https://doi.org/10.1016/j.plaphy.2018.11.026

Yang, J., Zhan, R., Wang, L., Li, J., Ma, B., Ma, F., Li, M. (2023). Overexpression of MdFRK2 enhances apple drought resistance by promoting carbohydrate metabolism and root growth under drought stress. *Horticultural Plant Journal, 9* (5), 884-897. https://doi.org/10.1016/j.hpj.2022.10.010

Yeshi, K., Crayn, D., Ritmejerytė, E., Wangchuk, P. (2022). Plant secondary metabolites produced in response to abiotic stresses has potential application in pharmaceutical product development. *Molecules, 27*, 313. https://doi.org/10.3390/molecules27010313

Yuan, G., Wang, D., Yu, C., Hua, J., Yin, Y., Chen, T. (2025). 5-AzaCytidine promotes somatic embryogenesis of *Taxodium* Hybrid 'Zhongshanshan' by regulating redox homeostasis. *Plants, 14,* 1354. https://doi.org/10.3390/plants14091354

Zahedi, SM., Karimi, M., Venditti, A. (2019). Plants adapted to arid areas: specialized metabolites. *Natural Product Research, 35* (19), 3314-3331. https://doi.org/10.1080/14786419.2019.1689500

Zhang, J., Huang, D., Zhao, X., Zhang, M., Wang, Q., Hou, X., Di, D., Su, B., Wang, S., Sun, P. (2022). Drought-responsive WRKY transcription factor genes IgWRKY50 and IgWRKY32 from *Iris germanica* enhance drought resistance in transgenic Arabidopsis. *Frontiers in Plant Science, 13*, 983600. https://doi.org/10.3389/fpls.2022.983600

Zhou, Y., Huang, C., Chen, M., Guo, J., Wang, Y., Min, D., Jiang, Q., Ji, H., Wang, C., Wei, W., Xu, H., Chen, X., Li, L., Xu, Z., Cheng, X., Wang, C., Ma, Y. (2020). Overexpression of soybean DREB1 enhances drought stress tolerance of transgenic wheat in the field. *Journal of Experimental Botany, 71* (6), 1842-1857. https://doi.org/10.1093/jxb/erz569

CHAPTER 4

Beneficial Microorganisms as a Tool to Improve Drought Tolerance in Horticultural Production Systems

Rosa Carolina Talamantes Gonzáles[1], Ezequiel Muñoz Márquez[2*], Nancy Vyanney Romero Alcantar[2], Sandra Pérez Álvarez[1]

[1]Universidad Autónoma de Chihuahua, Km 2.5, carretera Delicias-Rosales, Campus Delicias, Cd. Delicias, Chihuahua, México, CP: 33000.

[2]Centro de Investigación en Alimentación y Desarrollo, A.C. Avenida Cuarta Sur No. 3820, Fraccionamiento Vencedores del Desierto, Delicias 33089, Chihuahua, México. emunoz@ciad.mx (*corresponding author).

1. INTRODUCTION

Climate change causes a gradual increase in global climate variability, and the intensification, frequency, and severity of hydrometeorological phenomena such as droughts and floods severely damage practices used for human development (Landa et al., 2008; Ortega et al., 2018). Drought, in particular, is a natural phenomenon that is an essential part of the climate and to which all places on the planet are exposed. It is characterized as an inevitable and unpredictable event; it has no epicenter or defined trajectory, its advance is slow and gradual, and it can cover large geographical areas. For this reason, it is difficult to define its spatiotemporal boundaries and mitigate the damage caused by this phenomenon (Ortega, 2013). In Mexico, rainfall anomalies have been projected up to 2039. Simulations indicate a decrease in rainfall of 10 to 20% in most of the northern part of the country, and 0 to 10% in the rest of Mexico (INECC, 2025). In this regard, droughts are predicted to increase and cause greater devastation across most of the country, especially in the north, where rainfall fluctuates between 300 and 500 mm/year due to low precipitation and high temperatures (Ortega et al., 2018). This raise concerns that agricultural production will be severely affected, consequently impacting the circular economy and food security (Troyo et al., 2014).

Horticultural production is valued at over $11 billion; however, most of these crops are highly sensitive to water scarcity. This vulnerability stems primarily from the plants' anatomy, as they possess large leaf areas and high transpiration rates, in addition to being subjected to intensive growing cycles. Water stress reduces CO_2 assimilation by causing stomatal closure, disrupts carbon and nutrient partitioning, and impairs growth, flowering, and fruit set. Furthermore, it significantly impacts yield and quality. In addition, drought increases reactive oxygen species (ROS) levels and lipid peroxidation (MDA), disrupts membranes, and alters ionic homeostasis (Herrera-Flores, 2014).

Therefore, traditional strategies such as precision fertigation, mulching, and genetic improvement are essential, but their implementation is slow and costly. For this reason, the use of beneficial microorganisms emerges as a viable alternative capable of buffering the effects of drought (Figure 1), and they can achieve this through direct mechanisms such as the production of phytohormones, ACC deaminase, phosphorus (P) solubilization, nitrogen (N) fixation, and indirect mechanisms such as the induction of systemic tolerance, root remodeling, and improvement of soil physical properties through exopolysaccharides (EPS) and aggregation (Ahluwalia et al., 2021; Liu et al., 2025; Parastesh et al., 2025).

2.

Figure 1. Shows the interaction of different microorganisms that benefit the plant. From left to right: beneficial bacteria, arbuscular mycorrhizal fungi, beneficial fungi, endophytic bacteria, *Trichoderma* spp., and *Rhizobium* spp.

In different investigations, the use of microorganisms to mitigate the adverse effects of drought has been reported in crops such as tomato, chili pepper, cucumber, lettuce, and aromatic plants, in which increases in biomass and yield, greater fruit set, and improvements in quality have been observed (Ganugi et al., 2021; Zhu et al., 2022).

2. GENERAL MECHANISMS USED BY PLANTS AND ASSOCIATED MICROORGANISMS TO MITIGATE DROUGHT

Several studies have reported that, regardless of the microbial group, the mechanisms of action against drought stress are grouped into five axes:

2.1. Hormonal regulation and stress signaling. In response to drought, a systemic signal is triggered that increases the production of abscisic acid (ABA), which travels from the roots to the leaves and stems, closing the stomata (stomatal adjustment). Another defined strategy is based on the enzyme ACC deaminase; when the plant is stressed, it initiates ethylene production. Bacteria associated with the plant produce this enzyme and reduce ethylene levels. It is important to note that ethylene reduction is not always entirely advantageous, as ethylene participates in the plant's adaptive responses, such as stomatal closure, allowing the stress signal to be completed and potentially inducing water conservation and tolerance (Hecht et al., 2024). The interaction between auxins and cytokinins may also be present. Auxins promote the growth and formation of adventitious roots for greater exploration of the soil and access to deeper water. Simultaneously, the concentration of cytokinins is minimized as much as possible so as not to impede root growth (Alogi et al., 2025).

2.2. Osmotic adjustment. This physiological mechanism allows the accumulation of solutes in the cytosol to reduce the osmotic potential of cells, increasing water uptake and retention; in this way, turgor pressure is maintained and essential metabolism remains active (Furtak and Gawryjotek, 2025). The plant also activates proline biosynthesis (via glutamate) (Yu, 2025). The function of this osmolyte is to stabilize membranes, maintain protein structure, and modulate redox balance (Xu et al., 2025). It is essential to mention that if proline accumulates in large quantities, it inhibits growth; therefore, it is important that this osmoprotectant remains in balance (Dabravolski and Isayenkov, 2025; Munné-Bosch, 2025). Glycine/betaine (GB) is an osmoregulator known to protect cellular enzymatic activities and membrane integrity in plants (Singh et al., 2022). While glycine/betaine accumulators are unable to synthesize this compound in wheat and maize, the combination of commercial products and genetic engineering can manipulate normal biosynthetic processes to enable the enhancement of plant responses such as for PSII protection, water-saving, productivity, among others (Kumar et al., 2018). The accumulation of sugars and polyalcohol in osmotic adjustment not only helps create a water potential gradient but also allows the construction of carbon structures and affords energy for other vital processes, supporting basic metabolism processes (Sun et al., 2015). Another notable stabilizer relates to trehalose, protecting proteins and water retention to a great extent. Trehalose-6-phosphate (T6P) is a signal for trehalose-6-phosphate synthase (TPS) genes' overexpression that in turn stabilizes enzymes and membranes in response to dehydration (Prakash et al., 2025). Osmotic adjustment aims to uphold tissue turgor by bringing water into the cell (Gutiérrez et al., 2023). All of the metabolic support are vital to prevent cell collapse and to keep the plant alive until this is further supported by other environmental adaptations (Shehab et al., 2026).

2.3. Redox protection. According to Hasanuzzaman et al. (2017) the cellular homeostasis in the plant is getting disarranged under water stress, leading to enhanced production levels of reactive oxygen species (ROS), hydroxyl radicals (OH), superoxide anion (O2-), and hydrogen peroxide (H_2O_2). All these molecules are generated in mitochondria, chloroplasts, and peroxisomes and serve a dual purpose. When present in controlled concentrations, they act as molecular signaling molecules to activate adaptation and defense pathways; however, when this balance is disrupted, they become oxidative agents and damage nucleic acids, proteins, and lipids (Cannea and Padiglia, 2025). The plant counteracts this imbalance by activating its antioxidant system, which comprises both enzymatic and non-enzymatic mechanisms, to maintain cell integrity and plant survival (Alaswad, 2025).

The first line of defense against ROS consists of specialized enzymes that detoxify cells (Rao et al., 2025). The first enzyme is superoxide dismutase (SOD), which can break down the superoxide anion into molecular oxygen and hydrogen peroxide. Its different forms are Cu/Zn-SOD, Mn-SOD, and Fe-SOD, present in mitochondria, cytosol, chloroplasts, and peroxisomes. It reduces the formation of hydroxyl groups, which are highly toxic (Renu et al., 2023). Similarly, the enzymes catalase (CAT) and ascorbate peroxidase (APX) eliminate hydrogen peroxide by transforming it into water and oxygen (Rao et al., 2025). Another key enzyme is peroxidase, it breaks down peroxide into water through its use of ascorbate from the ascorbate-glutathione cycle while producing monodehydroascorbate (MDHA). The enzyme glutathione reductase (GR) is essential because it helps restore reduced glutathione which protects against oxidative damage while maintaining redox balance (Ozyigit et al., 2016). Bioindicators of oxidative damage need to be used which include malondialdehyde (MDA) to evaluate how well the oxidative system operates. MDA is the end product of membrane lipid peroxidation caused by excess reactive oxygen species (ROS). ROS attack polyunsaturated fatty acids and destabilize membrane function and structure (Alaswad, 2025). In addition to antioxidant defense, plants also regulate water transport through aquaporins. These membrane proteins form specialized and selective channels for water and very small solutes. Plasma membrane isoforms (PIPs) and tonoplast isoforms (TIPs) are primarily responsible for the hydraulic conductivity of the cell and tissues (Byrt et al., 2023).

2.4. Hydraulic properties and root architecture. Roots are a dynamic interface between the plant and the soil; their morphological adaptations and symbiotic interactions with rhizospheric microorganisms are key to adaptation to drought (Shoaib et al., 2022). Studies by Paul et al. (2024) indicate that biofilms and exopolysaccharides (EPS) are the basis for rhizospheric resilience to drought stress. These two substances, with their own physical, chemical, and biological properties, form a hydrated matrix surrounding microbial cells, constituting the structural basis of biofilms. The EPS matrix is crucial for the survival of rhizospheric microorganisms, as it creates a microhabitat that protects them from fluctuations in humidity, temperature, and osmotic potential (Rana et al., 2020). EPS are hydrophilic and retain large amounts of water, therefore acting as reservoirs that release water as the soil dries out (Khan and Bano, 2019). Fetsiukh et al. (2021) demonstrated that there was greater water availability with the presence of EPS, and a greater osmotic pressure in the biofilm. It is important to highlight that the root response to water stress is not an isolated phenomenon, but rather is closely linked to the hydraulic properties of the soil-plant-microorganism system (Agee et al., 2021). The plasticity of the root allows the plant to modify the density, angle, distribution, and depth of roots to capture water, and this capacity is significantly enhanced by microorganisms (Shoaib et al., 2022).

2.5. Soil/rhizosphere modification. In addition to water retention, EPS plays a key role in soil particle aggregation. The polymers act as cementing agents that bind mineral particles and organic matter, forming stable micro- and macro-aggregates. This modification of the soil's physicochemical properties has direct hydraulic consequences, such as improved porosity and aeration, increased structural stability, and enhanced permeability (Bhagat et al., 2021). EPS-producing rhizobacteria, therefore, not only directly benefit the plant but also improve the substrate in which it grows, increasing its capacity to store and supply water in the long term (Shoaib et al., 2022). For this reason, the presence of biofilms and stable aggregates in the rhizosphere modifies local moisture conditions, creating microhabitats with greater water availability than the surrounding soil. This phenomenon influences root exploration patterns, favoring lateral root growth in areas with greater water resources (Fitzpatrick et al., 2019). Likewise, the EPS matrix also acts as a reservoir and trap for nutrients, capable of chelating ions and capturing particles rich in essential elements

(Timmusk and Zucca, 2019). This creates a chemically and physically differentiated microhabitat in which biological activity intensifies during periods of drought, and communication via molecular signals between microorganisms and the plant is facilitated. This environment also protects nitrogen-fixing bacteria and mycorrhizal fungi, which enhance soil exploration capacity (Shoaib et al., 2022). Alharbi et al. (2022) found that rhizobacteria control their exopolysaccharide production through their interactions with soil particles which especially include silica. The research demonstrates that bioproducts can be developed through the combination of microorganisms with essential minerals which enhance their hydroprotective properties (Xu et al., 2018).

3. PLANT GROWTH-PROMOTING BACTERIA AND BENEFICIAL RHIZOBACTERIA

Plant growth-promoting rhizobacteria (PGPR) establish their presence in the rhizosphere through their relationship with plants. Agricultural scientists study these organisms because they can multiply quickly, they kill target organisms effectively, and they can easily be used to create bioproducts. These bacteria produce or can induce mechanisms for the reduction of ethylene (ACC deaminase), EPS and biofilms formation, phytohormones (gibberellins, IAA, and cytokinins), and the activation of the antioxidant system (Ahluwalia et al., 2021; Liu et al., 2025).

3.1. *Bacillus* spp.

This genus is one of the most widely used in horticultural production. In tomato cultivation under drought stress, Gowtham et al. (2020) demonstrated that *Bacillus subtilis* Rhizo SF48 produced ACC deaminase, increased proline and soluble sugar content, and activated the antioxidant enzymes SOD, CAT, and APX, while simultaneously reducing MDA and H_2O_2.

It is important to note that *Bacillus subtilis* produces surfactin, iturin, and fengycin, which are cyclic lipopeptides that act as signaling molecules inducing systemic resistance in plants. All of these compounds promote biofilm formation, cell membrane stabilization, and activate jasmonate, abscisic acid, and ethylene-regulated signaling pathways, thus favoring drought tolerance and protection against pathogens (Ongena and Jacques, 2008; Hashem et al., 2019; Parastesh et al., 2025).

Bacillus subtilis therefore triggers an integrated response known as induced systemic tolerance (ISR). This is a metabolic reprogramming of the plant that allows it to respond quickly and effectively to adverse conditions, reducing damage and maintaining productivity (Vurukonda et al., 2016).

3.2. *Pseudomonas* spp.

Among them are *Pseudomonas fluorescentes* and *Pseudomonas putida*, and *Pseudomonas* spp. These bacteria can modulate the expression of EPS, siderophores, and can regulate the redox state (Mekureyaw et al., 2026).

Pseudomonas spp. produce EPS, which are water-retaining compounds that also signal systemic responses. A particular example is *Pseudomonas chlororaphis* O6, which produces EPS associated with drought tolerance, specifically through changes in gene expression and physiological preparation in distal tissues. These studies reinforce the idea that the protection provided by microorganism manifests in an integrated manner (Mehmood et al., 2023). Mekureyaw et al. (2026) suggest that EPS biofilms can initiate various metabolic adjustments. For example, they improved ecophysiological parameters in tomatoes grown under water stress when the plants were inoculated with *Pseudomonas putida* KT2440. Furthermore, they observed that plants without EPS biofilms lacked the protective effect and exhibited lower enzymatic and antioxidant activity, as well as reduced transcriptional programming. This clearly connects the microbial effect with the metabolic reconfiguration of the plant under water stress conditions.

Pseudomonas spp. also synthesize siderophores, which capture iron from the rhizosphere even under drought conditions, thanks to their high affinity. They capture it before competitors and pathogens, allowing the plant to use it for electron transport, photosynthesis, and antioxidant defense (Chieb et al., 2023).

3.3. *Azospirillum* spp.

These beneficial bacteria colonize roots quickly and efficiently, fix atmospheric nitrogen, and produce phytohormones and signaling molecules that contribute to drought tolerance (Sun et al., 2025). One of their major effects on plants is root modification, promoting branching and the formation of root hairs. These modifications increase soil exploration and improve water and nutrient uptake; they are mainly associated with the bacterial production of auxins such as indoleacetic acid, lipopolysaccharides, and volatile metabolites that act as regulatory signals for root development (Pelagio-Flores et al., 2025). The research experiments showed that plants which received *Azospirillum brasilense* inoculation developed longer roots and bigger root systems together with increased total biomass and plant functions that matched the performance of plants without stress. The results demonstrate that the system achieved a significant advancement in its capacity to extract and distribute water throughout its operations. The structural changes to the plant system result in better hydraulic performance because they enhance the plant's ability to move water while sustaining its flow to the plant's upper sections (Marques et al., 2023).

Furthermore, *Azospirillum* spp. bring about physiological changes which support water status; here they alter xylem-induced hormones such as abscisic acid (ABA), jasmonates, and other signals related to stomatal control and water deprivation. Such effects were found in purple basil inoculated with *A. baldaniorum* Sp245. The *Azospirillum* inducing of beneficial effects of water use efficiency, improvement in photosynthesis, and maintenance of cell turgor (Mariotti et al., 2021).

The influences of *Azospirillum* spp. are further extended to plant metabolism, and their interaction with plant aids in the activation of metabolic pathways related to nitrogen nutrition, osmoprotectant synthesis, and antioxidant defense. Additionally, these bacteria bring forth alterations in gene expression, cell division, and developmental processes related to water, and nutrient absorption, thus implying a decisive metabolic reprogramming of the host harbor (Mancilla-Álvarez et al., 2025). At the same time, the accumulation of osmolytes in plants, such as trehalose, in inoculated *Azospirillum*, leads to better desiccation tolerance in plants and bacteria themselves. In that sense, improves plant growth and establishes relationships with dry plant survival and increased total biomass by the action of the trehalose-accumulating strains under drought stress, suggesting much deeper protection conferred by microbial interaction (Rodríguez-Salazar et al., 2009).

For all the above, *Azospirillum* spp. can be applied not only as a biofertilizer but also as an integral modulator of the soil-plant system capable of optimizing, improving, and activating metabolic and systemic mechanisms of drought tolerance, making them strong candidates for the development of key bioinoculants for sustainable agriculture under climate change conditions.

4. BENEFICIAL FUNGI

Beneficial soil fungi, especially arbuscular mycorrhizal fungi (AMF), which are obligate symbiotic associations, *Trichoderma* spp., which promote plant growth and have a biostimulant and biocontrol role, and fungal endophytes, have proven to be highly effective biological tools that improve plant drought tolerance. They are capable of activating integrated physiological, metabolic, and molecular mechanisms that increase water and nutrient uptake, promote photosynthesis, maintain hormonal balance, and reduce the accumulation of reactive oxygen species, thereby reducing oxidative damage and improving yield (Begum et al., 2019; Zhu et al., 2022).

4.1. Arbuscular mycorrhizal fungi (AMF)

Arbuscular mycorrhizae form a network of extraradical hyphae that increases the effective absorption surface area and improves access to water and nutrients in soil that is inaccessible to roots. Hyphal expansion maintains leaf hydration and photosynthesis, even during prolonged periods of drought. It increases the absorption of macro- and micronutrients that sustain metabolic function (Zhu et al., 2022). In research conducted by Leventis et al. (2021) on tomato cultivation, the fungi *Funneliformis mosseae* and *Rhizophagus irregularis*, through water regulation mechanisms and enhanced transpiration control, improved growth under both normal and deficit irrigation (Leventis et al., 2021; Zhu et al., 2022).

Furthermore, arbuscular mycorrhizal fungi activate the synthesis of osmoprotectants such as proline, soluble sugars, and phenolic compounds, which maintain cell turgor and protect macromolecular structures. Simultaneously, the enzymes superoxide dismutase, catalase, and peroxidases are activated, reducing the accumulation of reactive oxygen species (ROS) and oxidative damage (Begum et al., 2019). Studies conducted by Soussani et al. (2023) on drought- stressed tomatoes showed that arbuscular mycorrhizal fungi, along with compost and organic amendments, enhanced colonization, improved soil structure, and increased water retention. These results demonstrate that resilience depends on soil biology and agronomic management.

4.2. *Trichoderma* spp.

Fungi of the genus Trichoderma have become established as a group of beneficial fungi that play an important role in mitigating the effects of water stress. They are capable of simultaneously modulating the rhizosphere, plant metabolism, and systemic signaling (Akbari et al., 2024; Contreras-Cornejo et al., 2024). These species can colonize the rhizosphere and root tissues, promoting plant growth through the production of bioactive metabolites, phytohormones, and volatile compounds. *Trichoderma* spp. have been shown to induce changes in root architecture, increase water absorption, and improve water use efficiency, in addition to activating defense responses and metabolic pathways associated with stress (Guzmán-Guzmán et al., 2019).

From a biostimulation perspective, *Trichoderma* spp. can stimulate growth and resource utilization without necessarily requiring continuous contact with the plant, because they are capable of releasing signaling metabolites that impact the plant's endogenous hormonal network. It has been documented that, during interaction with roots, *Trichoderma* produces or induces compounds with activity similar to growth regulators (IAA-related indoles) and volatile organic compounds (VOCs) such as 6-pentyl-2H-pyran-2-one (6-PP), in addition to other signals that ultimately adjust root development, nutritional status, and water use (Contreras-Cornejo et al., 2024).

A distinctive feature for which *Trichoderma* spp. is used is its ability to induce priming, a process of preconditioning. Under this process, the plant enters a "ready" state that does not imply a permanently high constitutive defense, but rather a faster and more efficient response when stress occurs. This priming can involve protein accumulation, sensitization of signaling pathways (redox/Ca^{2+}/MAPKs), and more efficient activation of antioxidants and osmoprotection during drought. Furthermore, it has been discussed that certain priming responses induced by *Trichoderma* spp. may exhibit heritable or physiological memory components, relevant for bio-priming strategies in seeds and agronomic management (Morán-Diez et al., 2021). In line with this, omics studies in a model plant *Arabidopsis thaliana* show that *Trichoderma*-based biostimulants can reorganize the metabolome under stress (including nitrogenous compounds, phenylpropanoids, terpenes, and hormones), supporting the idea of a metabolic reprogramming compatible with systemic tolerance (Senizza et al., 2023).

Similarly, recent studies emphasize that the efficacy of *Trichoderma* spp. is not universal, but rather exhibits marked genotype-by-strain plasticity. This means that a strain can be highly effective in one genotype (or environment) and moderately effective in another, and that the magnitude of the benefit depends on host traits (basal tolerance capacity, root architecture, hormonal sensitivity, etc.) and isolate traits (colonization capacity, desiccation tolerance, metabolite profile, etc.). A clear example was presented by Rawal et al. (2022), who applied different isolates, including various species and commercial strains, to tomato plants under water stress. These showed significant differences in their ability to alleviate water deficit, and the results also depended on the tomato genotype. This type of evidence justifies, from an applied perspective, the selection of strains with consistent performance and multi-genotype/multi-environment validation.

4.3. Fungal endophytes and *Serendipita indica*

Fungal endophytes are fungi that colonize plant tissues without causing disease and have emerged as key modulators of drought tolerance. Among them, the basidiomycete *Serendipita indica* (formerly *Piriformospora indica*) stands out for its ability to establish itself in a wide range of hosts, its capacity for *in vitro* cultivation, and its effectiveness in improving plant growth and resilience to multiple abiotic stresses (Gill et al., 2016; Saleem et al., 2022).

One of the most relevant mechanisms by which fungal endophytes increase tolerance to water deficit is the improvement of the plant's water status through changes in root physiology and hydraulic conductivity. Colonization by *S. indica* promotes root development, increases water and nutrient uptake, and favors the regulation of membrane proteins related to water transport, such as aquaporins. These changes maintain water content and photosynthesis (Gill et al., 2016). In contrast to the hydrological function, these organisms stimulate major modifications in primary and secondary metabolism. *S. indica*, for instance, upregulates the accumulation of osmoprotectants proline, soluble sugar, and phenolics; simultaneously contributes in activating the total antioxidant machinery to counter oxidative damage (Jogawat et al., 2016; Saleem et al., 2022). Under such an influence, substantial hormonal reprogramming occurs, *S. indica* balances aquaporin channel levels, stomatal conductance, photosynthetic efficiency, and cellular carbon and nitrogen availability. In addition, the endophyte establishes resource acquisition (Gill et al., 2016) and triggers transporters necessary for the performance of essential metabolic functions. Thus, endophytes function as an agri-biotechnological tool that can substantially enhance the resistance of agricultural systems to water scarcity govern by climate change.

5. CONCLUSION

One of the modern biotechnological strategies that can reduce vulnerability under water-limited conditions is the use of beneficial microbes. The plant-microbe interaction is significant in terms of preservation of photosynthesis, sustainable water use, the growth of the engineered plants, and yield. The use of specific microbial consortia or bioinoculants will characterize a vital tool for maintaining the sustainability of horticulture and adaptation of these types of agriculture in the face of climate change.

REFERENCES

Agee, E., He, L., Bisht, G., Couvreur, V., Shahbaz, P., Meunier, F., Gough, M. C., Matheny, A. M., Bohrer, G., Ivanov, V. (2021). Root lateral interactions drive water uptake patterns under water limitation. *Advances in Water Resources*, **151**, 103896.

Akbari, S. I., Prismantoro, D., Permadi, N., Rossiana, N., Miranti, M., Mispan, M. S., Mohamed, Z., Doni, F. (2024). Bioprospecting the roles of *Trichoderma* in alleviating plants' drought tolerance: Principles, mechanisms of action, and prospects. *Microbiological Research*, **283**, 127665. https://doi.org/10.1016/j.micres.2024.127665

Alaswad, A. A. (2025). Transcriptomic landscapes of ornamental plants under salt and drought stress: key genes and pathways for tolerance. *Frontiers in Plant Science*, **16**, 1703649. https://doi.org/10.3389/fpls.2025.1703649

Alharbi, K., Hafez, E., Omara, A. E. D., Awadalla, A., Nehela, Y. (2022). Plant growth promoting rhizobacteria and silica nanoparticles stimulate sugar beet resilience to irrigation with saline water in salt-affected soils. *Plants*, **11**(22), 3117. https://doi.org/10.3390/plants11223117

Alongi, F., Petek-Petrik, A., Mukarram, M., Torun, H., Schuldt, B., Petrík, P. (2025). Somatic drought stress memory affects leaf morpho-physiological traits of plants via epigenetic mechanisms and phytohormonal signalling. *Plant Gene*, **42**, 100509. https://doi.org/10.1016/j.plgene.2025.100509

Begum, N., Qin, C., Ahanger, M. A., Raza, S., Khan, M. I., Ashraf, M., Ahmed, N., Zhang, L. (2019). Role of arbuscular mycorrhizal fungi in plant growth regulation: Implications in abiotic stress tolerance. *Frontiers in Plant Science*,**10**, 1068. https://doi.org/10.3389/fpls.2019.01068

Bhagat, N., Raghav, M., Dubey, S., Bedi, N. (2021). Bacterial exopolysaccharides: Insight into their role in plant abiotic stress tolerance. *Journal of microbiology and biotechnology*, **31**(8), 1045. https://doi.org/10.4014/jmb.2105.05009

Byrt, C. S., Zhang, R. Y., Magrath, I., Chan, K. X., De Rosa, A., McGaughey, S. (2023). Exploring aquaporin functions during changes in leaf water potential. *Frontiers in Plant Science*, **14**, 1213454. https://doi.org/10.3389/fpls.2023.1213454

Cannea, F. B., and Padiglia, A. (2025). Antioxidant defense systems in plants: Mechanisms, regulation, and biotechnological strategies for enhanced oxidative stress tolerance. *Life*, **15**(8), 1293. https://doi.org/10.3390/life15081293

Chieb, M., Abdelmoula, S., El Khoury, R., Vallance, J., Brigitte, C. (2023). The role of plant growth promoting rhizobacteria in plant drought stress responses. *BMC Plant Biology*, **23**, 403. https://doi.org/10.1186/s12870-023-04403-8

Contreras-Cornejo, H. A., Schmoll, M., Esquivel-Ayala, B. A., González-Esquivel, C. E., Rocha-Ramírez, V., Larsen, J. (2024). Mechanisms for plant growth promotion activated by *Trichoderma* in natural and managed terrestrial ecosystems. *Microbiological Research*, **281**, 127621. https://doi.org/10.1016/j.micres.2024.127621

Dabravolski, S. A., Isayenkov, S. V. (2025). Expansins in Salt and Drought Stress Adaptation: From Genome-Wide Identification to Functional Characterisation in Crops. *Plants*, **14**(9), 1327. https://doi.org/10.3390/plants14091327

Fetsiukh, A., Conrad, J., Bergquist, J., Timmusk, S. (2021). Silica particles trigger the exopolysaccharide production of harsh environment isolates of growth-promoting rhizobacteria and increase their ability to enhance wheat biomass in drought-stressed soils. *International Journal of Molecular Sciences*, **22**(12), 6201. https://doi.org/10.3390/ijms22126201

Fitzpatrick, C.R.; Mustafa, Z.; Viliunas, J. (2019). Soil microbes alter plant fitness under competition and drought. *Journal of Evolutionary Biology*, **32**, 438–450. https://doi.org/10.1111/jeb.13426Digital Object Identifier

Furtak, K., Gawryjołek, K. (2025). Effect of selected osmoprotectants (betaine, ectoine and inositol) on germination and initial growth of *Triticum aestivum* L. under salt stress conditions–model experiment. *Current Agronomy*, **54**(2). https://doi.org/10.2478/cag-2025-0003

Gill, S. S., Gill, R., Trivedi, D. K., Anjum, N. A., Sharma, K. K., Ansari, M. W., Ansari, A. A., Johri, A. K., Tuteja, N. (2016). *Piriformospora indica*: Potential and significance in plant stress tolerance. *Frontiers in Microbiology*, 7, 332. https://doi.org/10.3389/fmicb.2016.00332

Gutiérrez N, Pégard M, Balko C, Torres AM (2023) Genome-wide association analysis for drought tolerance and associated traits in faba bean (*Vicia faba* L.). *Frontier in Plant Science* **14**:1091875. https://doi.org/10.3389/fpls.2023.1091875

Guzmán-Guzmán, P., Porras-Troncoso, M. D., Olmedo-Monfil, V., Herrera-Estrella, A. (2019). *Trichoderma* species: versatile plant symbionts. *Phytopathology*, **109**(1), 6-16. https://doi.org/10.1094/PHYTO-07-18-0218-RVW

Hasanuzzaman, M., Nahar, K., Gill, S. S., Alharby, H. F., Razafindrabe, B. H., Fujita, M. (2017). Hydrogen peroxide pretreatment mitigates cadmium-induced oxidative stress in Brassica napus L.: an intrinsic study on antioxidant defense and glyoxalase systems. *Frontiers in Plant Science*, **8**, 115. https://doi.org/10.3389/fpls.2017.00115

Hashem, A., Tabassum, B., Abd_Allah, E. F. (2019). Bacillus subtilis: A plant-growth promoting rhizobacterium that also impacts biotic stress. *Saudi Journal of Biological Sciences*, **26**(6), 1291–1297. https://doi.org/10.1016/j.sjbs.2019.05.004

Hecht, K., Kowalchuk, G. A., Ford Denison, R., Kahmen, A., Xiong, W., Jousset, A., Ravanbakhsh, M. (2025). Deletion of ACC Deaminase in Symbionts Converts the Host Plant From Water Waster to Water Saver. *Plant, Cell & Environment*, **48**(3), 1919-1931. https://doi.org/10.1111/pce.15265

Herrera Flores, T. S., Ortíz Cereceres, J., Delgado Alvarado, A., Acosta Galleros, J. A. (2014). Contenido de osmoprotectores, ácido ascórbico y ascorbato peroxidasa en hojas de frijol sometidas a estrés por sequía. *Revista mexicana de ciencias agrícolas*, **5**(5), 859-870.

INECC (Instituto Nacional de Ecología y Cambio Climático). (2025). Secretaría de Medio Ambiente y Recursos Naturales, Gobierno de México. Accessed on February 10, 2025. https://www.gob.mx/inecc

Khan N, Bano A (2019) Exopolysaccharide producing rhizobacteria and their impact on growth and drought tolerance of wheat grown under rainfed conditions. *PLoS ONE* **14**(9): e0222302. https://doi.org/10.1371/journal. pone.0222302

Kumar, V., Khare, T., Shaikh, S., Wani, S. H. (2018). Compatible solutes and abiotic stress tolerance in plants. In. Metabolic adaptations in plants during abiotic stress, Akula Ramakrishna, A., Singh, S. G. (eds), 1st Edition, CRC Press, Boca Raton, USA. pp. 213-220.https://doi.org/10.1201/b22206-18

Leventis, G., Tsiknia, M., Feka, M., Ladikou, E. V., Papadakis, I. E., Chatzipavlidis, I., Papadopoulou, K., Ehaliotis, C. (2021). Arbuscular mycorrhizal fungi enhance growth of tomato under normal and drought conditions, via different water regulation mechanisms. *Rhizosphere*, **19**, 100394. https://doi.org/10.1016/j.rhisph.2021.100394

Mancilla-Álvarez, E., López-Buenfil, J. A., Serrano-Fuentes, M. K., Reyes-Castillo, A., Sánchez-Páez, R., & Bello-Bello, J. J. (2025). *Azospirillum brasilense* affects survival, growth and nutrient status of micropropagated sugarcane (*Saccharum* spp.) plantlets during ex vitro conditions. *Discover Plants*, **2**(1), 274. https://doi.org/10.1007/s44372-025-00357-3

Mariotti, L., Scartazza, A., Curadi, M., Picciarelli, P., Toffanin, A. (2021). *Azospirillum baldaniorum* Sp245 induces physiological responses to alleviate drought stress in purple basil. *Plants*, **10**(6), 1141. https://doi.org/10.3390/plants10061141

Marques, D.M., Magalhães, P.C., Marriel, I.E., Júnior, C.C.G., da Silva, A.B., dos Reis, C.O., de Souza, K.R.D., de Souza, T.C. (2023). Does *Azospirillum brasilense* mitigate water stress and reduce the use of nitrogen fertilizers in maize?. *South African Journal of Botany*, **156**, pp.278-285. https://doi.org/10.1016/j.sajb.2023.03.041

Mehmood, N., Saeed, M., Zafarullah, S., Hyder, S., Rizvi, Z. F., Gondal, A. S. (2023). Multifaceted impacts of plant-beneficial Pseudomonas spp. in managing various plant diseases and crop yield improvement. *ACS Omega*, **8**(25), 22296–22315. https://doi.org/10.1021/acsomega.3c00870

Mekureyaw, M. F., Pandey, C., Sorty, A. M., Hennessy, R. C., Nicolaisen, M. H., Liu, F., Nybroe, O., Roitsch, T. (2026). Biofilm formation by Pseudomonas putida KT2440 contributes to improve tomato drought stress resilience and priming for enhanced gene regulation. *Journal of Plant Physiology*, **317**, 154704. https://doi.org/10.1016/j.jplph.2026.154704

Morán-Diez, M. E., Martínez de Alba, Á. E., Rubio, M. B., Hermosa, R., Monte, E. (2021). *Trichoderma* and the plant heritable priming responses. *Journal of Fungi*, **7**(4), 318. https://doi.org/10.3390/jof7040318

Munné-Bosch, S. (2025). Rethinking phytohormone signaling hierarchies in plant stress responses. *Trends in Plant Science*, **30**(2), 123-135. https://doi.org/10.1016/j.tplants.2024.11.003

Ongena, M., Jacques, P. (2008). Bacillus lipopeptides: Versatile weapons for plant disease biocontrol. *Trends in Microbiology*, **16**(3), 115-125. https://doi.org/10.1016/j.tim.2007.12.009

Ortega, G. D., Bartolón, J., Bahena, H. C. (2018). Peligro, vulnerabilidad y riesgo por sequía en el contexto del cambio climático en México. Instituto mexicano de tecnología del agua. http://hdl.handle.net/20.500.12013/2192

Ortega-Gaucin, D. (2013). Sequía: causas y efectos de un fenómeno global, Ciencia UANL, 16(61), pp. 8-15.

Ozyigit, I. I., Filiz, E., Vatansever, R., Kurtoglu, K. Y., Koc, I., Öztürk, M. X., Anjum, N. A. (2016). Identification and comparative analysis of H_2O_2-scavenging enzymes (ascorbate peroxidase and glutathione peroxidase) in selected plants employing bioinformatics approaches. *Frontiers in Plant Science*, **7**, 301. https://doi.org/10.3389/fpls.2016.00301

Paul, S., Parvez, S. S., Goswami, A., Banik, A. (2024). Exopolysaccharides from agriculturally important microorganisms: conferring soil nutrient status and plant health. *International Journal of Biological Macromolecules*, **262**, 129954. https://doi.org/10.1016/j.ijbiomac.2024.129954

Pelagio-Flores, R., Ravelo-Ortega, G., García-Pineda, E., López-Bucio, J. (2025). A century of *Azospirillum*: plant growth promotion and agricultural promise. *Plant Signaling & Behavior*, **20**(1), 2551609. https://doi.org/10.1080/15592324.2025.2551609

Prakash, P., Saini, D. R., Jangde, S., Kamlapuri, S. S., Kumar, K. (2025). Role of osmoprotectants on alleviation of elevated CO_2 and temperature stress. In. Climate change: Impact of elevated CO_2 and temperature on crops, weeds and soil microbes, 1st Edition, CRC Press, Boca Raton, USA. pp. 199-214. https://doi.org/10.1201/9781003483854-18

Rana, K. L., Kour, D., Yadav, A. N., Yadav, N., Saxena, A. K. (2020). Agriculturally important microbial biofilms: biodiversity, ecological significances, and biotechnological applications. In New and future developments in microbial biotechnology and bioengineering: Microbial biofilms Elsevier, pp. 221-265. https://doi.org/10.1016/B978-0-444-64279-0.00016-5

Rao, M.J., Duan, M., Zhou, C., Jiao, J., Cheng, P., Yang, L., Wei, W., Shen, Q., Ji, P., Yang, Y., Conteh, O., 2025. Antioxidant defense system in plants: reactive oxygen species production, signaling, and scavenging during abiotic stress-induced oxidative damage. *Horticulturae*, **11**(5), p.477. https://doi.org/10.3390/horticulturae11050477

Renu, K., Mukherjee, A. G., Gopalakrishnan, A. V., Wanjari, U. R., Kannampuzha, S., Murali, R., Veeraraghavan, P., Vinayagam, S., Paz-Montelongo, A.G., Vellingiri, B., Madhyastha, H. (2023). Protective effects of macromolecular polyphenols, metals (zinc, selenium, and copper)-Polyphenol complexes, and different organs with an emphasis on arsenic poisoning: A review. *International Journal of Biological Macromolecules*, **253**, 126715. https://doi.org/10.1016/j.ijbiomac.2023.126715

Rodríguez-Salazar, J., Suarez, R., Caballero-Mellado, J., Iturriaga, G. (2009). Trehalose accumulation in *Azospirillum brasilense* improves drought tolerance and biomass in maize plants. *FEMS Microbiology Letters*, **296**(1), 52-59. https://doi.org/10.1111/j.1574-6968.2009.01614.x

Saleem, S., Sekara, A., & Pokluda, R. (2022). *Serendipita indica*-A review from agricultural point of view. *Plants*, **11**(24), 3417. https://doi.org/10.3390/plants11243417

Senizza, B., Araniti, F., Lewin, S., Wende, S., Kolb, S., Lucini, L. (2023). *Trichoderma* spp.-mediated mitigation of heat, drought, and their combination on the *Arabidopsis thaliana* holobiont: A metabolomics and metabarcoding approach. *Frontiers in Plant Science*, **14**, 1190304. https://doi.org/10.3389/fpls.2023.1190304

Shehab, A.A., Abdelghany, A.M., Hamoda, A., Alwakel, E.S., Farouk, A.S., Ebaid, M., Lamlom, S.F., Guo, Y. (2026). Drought Tolerance Strategies of Faba Bean Cultivars: Integrated Morphological, Physiological, and Biochemical Responses. *Journal of Soil Science and Plant Nutrition*. https://doi.org/10.1007/s42729-026-03039-5

Sherwood, S., Fu, Q. (2014). A drier future? *Science*, **343**(6172), 737-739. https://doi.org/10.1126/science.1250245

Shoaib, M., Banerjee, B. P., Hayden, M., Kant, S. (2022). Roots' drought adaptive traits in crop improvement. *Plants*, **11**(17), 2256. https://doi.org/10.3390/plants11172256

Singh, P., Choudhary, K. K., Chaudhary, N., Gupta, S., Sahu, M., Tejaswini, B., Sarkar, S. (2022). Salt stress resilience in plants mediated through osmolyte accumulation and its crosstalk mechanism with phytohormones. *Frontiers in Plant Science*, **13**, 1006617. https://doi.org/10.3389/fpls.2022.1006617

Sun, C., Gao, X., Fu, J., Zhou, J., Wu, X. (2015). Metabolic response of maize (Zea mays L.) plants to combined drought and salt stress. *Plant and soil*, **388**(1), 99-117. https://doi.org/10.1007/s11104-014-2309-0

Sun, W., Shahrajabian, M. H., Wang, N. A. (2025). A study of the different strains of the genus *Azospirillum* spp. on increasing productivity and stress resilience in plants. *Plants*, **14**(2), 267. https://doi.org/10.3390/plants14020267

Timmusk, S., Zucca, C. (2019). The plant microbiome as a resource to increase crop productivity and soil resilience: A systems approach. *Journal of the Cameroon Academy of Sciences*, **14**(3), 181-187. https://dx.doi.org/10.4314/jcas.v14i3.2

Troyo-Diéguez, E., Mercado-Mancera, G., Cruz-Falcón, A., Nieto-Garibay, A., Valdez-Cepeda, R. D., García-Hernández, J. L., Murillo-Amador, B. (2014). Análisis de la sequía y desertificación mediante índices de aridez y estimación de la brecha hídrica en Baja California Sur, noroeste de México. *Investigaciones geográficas,* **85**, 66-81.

Vurukonda, S. S. K. P., Vardharajula, S., Shrivastava, M., SkZ, A. (2016). Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiological Research*, **184**, 13–24. https://doi.org/10.1016/j.micres.2015.12.003

Xu, H., Yang, X., Liu, H. (2025). Metabolomic insights into maize salt stress response and tolerant genotypes. *Maize Genomics and Genetics*, **16**(6), 284-293. https://doi.org/10.5376/mgg.2025.16.0026

Xu, L., Naylor, D., Dong, Z., Simmons, T., Pierroz, G., Hixson, K. K., Kim, Y. M., Zink, E. M., Engbrecht, K. M., Wang, Y., Gao, C., DeGraaf, S., Madera, M. A., Sievert, J. A., Hollingsworth, J., Birdseye, D., Scheller, H. V., Hutmacher, R., Dahlberg, J., Jansson, C., Taylor, J. W., Lemaux, P. G., Coleman-Derr, D. (2018). Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *Proceedings of the National Academy of Sciences*, **115**(18), E4284-E4293. https://doi.org/10.1073/pnas.1717308115

Yu, S. (2025). Drought Tolerance in Rapeseed: Genetic mechanisms and breeding strategies. *International Journal of Molecular Evolution and Biodiversity*, **15**(2), 84-98. https://doi.org/10.5376/ijmeb.2025.15.0008

Zhu, B., Gao, T., Zhang, D., Ding, K., Li, C., Ma, F. (2022). Functions of arbuscular mycorrhizal fungi in horticultural crops. *Scientia Horticulturae*, **303**, 111219. https://doi.org/10.1016/j.scienta.2022.111219