CROP SELECTION AND GENETIC ADAPTATIONS FOR ARID CONDITIONS: ENHANCING YIELD AND TOLERANCE TO WATER SCARCITY

Abstract

Global food security and sustainable economic prosperity are increasingly threatened by climate change-induced abiotic stresses, particularly in arid and semiarid regions. With food production needing to increase by 60% by 2050, improving crop resilience to drought and water scarcity is imperative. This chapter addresses the cutting-edge advancements in crop selection and genetic adaptation strategies that enhance yield stability under extreme environmental conditions. Recent studies have elucidated the molecular, biochemical and physiological mechanisms underlying plant responses to elevated CO_2, high temperatures and drought stress. Adaptive traits such as osmotic adjustment, antioxidant defense and root system plasticity play pivotal roles in stress mitigation. This chapter synthesizes recent breakthroughs in stress physiology and genetic engineering, highlighting the potential of integrating biotechnological innovations with traditional breeding to sustain agricultural productivity in drought-prone regions. These advancements are crucial for ensuring global food security and mitigating the detrimental impacts of climate change on crop yields.

Keywords: abiotic stresses, semiarid regions, osmotic adjustment. antioxidant defense and global food security

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I. INTRODUCTION

In India, agriculture remains the principal source of livelihood for approximately 65% of the population and contributes nearly 27% to the national Gross Domestic Product (GDP). Any adverse effects on this sector could have profound economic repercussions, while also jeopardizing food security and public health. By 2025, agricultural water consumption is projected to escalate by 1.3 times. Additionally, global climate models predict an increase in the Earth's mean surface temperature ranging from 1.4 to 5.8°C over the next century. Rising temperatures induced by global warming are expected to intensify evapotranspiration, leading to accelerated soil moisture depletion, reduced water availability, and the expansion of arid and saline regions. A temperature rise of merely one degree Celsius could diminish the yields of key staple crops in India by 3–7%, with *Rabi* crops facing more substantial reductions. Furthermore, the cropping period in rain-fed agricultural zones, which constitute two-thirds of India’s total cultivable land, is anticipated to decline.

Beyond direct impacts on crop production, fluctuations in temperature and relative humidity will significantly alter the geographic distribution and population dynamics of insect pests and plant pathogens. These climatic shifts could disrupt host-pathogen equilibria, influencing disease progression rates and pathogen virulence [1]. Adapting to climate change has emerged as a critical priority in global food security discussions. Agricultural livelihoods, particularly in developing countries, are highly susceptible to fluctuations in both mean climatic conditions and variability, necessitating strategic adaptation measures. Agricultural adaptation encompasses both farm-level management interventions and broader policy and institutional reforms. Among the diverse portfolio of on-farm and off-farm adaptation strategies, crop adaptation such as transitioning to climate-resilient crop species or stress-tolerant varieties remains one of the most frequently cited and effective approaches [2, 3, 4 & 5].

The necessity of adapting crops to evolving environmental conditions is not a novel concept rather, it represents the most fundamental coevolutionary dynamic between humans and cultivated plants since the inception of agriculture [6, 7]. In a Darwinian context, crop adaptation refers to the evolutionary processes through which plant species become increasingly suited to their respective agroecosystems. In traditional farming systems, this adaptation results from a synergistic interplay between natural selection and farmer-mediated selection pressures. With the advent of modernized agriculture accelerated across the developing world through the Green Revolution of the 1960s scientific plant breeding has largely supplanted the farmer's direct role in crop development [8]. Conventional plant breeding can be succinctly described as the systematic hybridization of plants exhibiting desirable traits, followed by the selection of progeny that best integrate these traits to produce improved cultivars.

Despite advancements in breeding methodologies and shifts in the political-economic landscape, genetic diversity remains the foundational resource for crop adaptation, both in traditional on-farm selection and professional breeding programs. This critical function is encapsulated in the term *genetic resources*, which encompasses seeds, plants, and plant derivatives possessing genetic attributes valuable for breeding, research, and conservation [9]. In traditional agricultural settings, farmers procure adaptive genetic resources from their own fields, informal exchanges with fellow cultivators, or through natural gene flow from landraces and wild relatives. Conversely, in modern agriculture, plant breeders serve as intermediaries, sourcing genetic material primarily from gene banks and curated genetic stock collections to develop novel, high-performing cultivars.

Classification of Arid Zone: Arid zones have been classified using various criteria. [10] categorized arid regions based on winter temperature regimes, distinguishing between hot and cold arid climates. The Food and Agriculture Organization (FAO) defines arid zones as areas with a length of growing period (LGP) ranging from 0 to 179 days [11]. Meanwhile, the United Nations Convention to Combat Desertification (UNCCD) employs the ratio of annual precipitation to potential evapotranspiration (P/PET) as a determinant for aridity classification.

According to UNCCD parameters, arid zones are characterized by a P/PET ratio between 0.05 and 0.65. For this study, we adopted the UNCCD classification system, utilizing the Aridity Index (AI) to delineate arid landscapes into hyper-arid (AI < 0.05), arid (AI = 0.05–0.20), semi-arid (AI = 0.20–0.50), and dry sub-humid regions (AI = 0.50–0.65) [12]. Globally, hyper-arid and arid zones together constitute approximately 10.6% of the Earth's terrestrial surface, whereas semi-arid regions, which extend across all seven continents, encompass a significantly larger proportion around 15.2% of the land area. Dry sub-humid zones, in contrast, account for 8.7% of the global landmass [13].

Arid Regions in India: Arid regions in India cover approximately 317,090 sq. km, with 246,790 sq. km classified as hot arid and 70,300 sq. km as cold arid [14]. The hot arid zone extends across Rajasthan, Gujarat, Punjab, Haryana, Maharashtra, Karnataka, and Andhra Pradesh, with nearly 80% of this area concentrated in eleven districts of Rajasthan. Annual rainfall in these regions exhibits significant spatial variability, ranging from 100 mm in northwestern Jaisalmer to 450 mm along the eastern boundary of Rajasthan's arid zone. In Gujarat, rainfall varies between less than 300 mm and 500 mm, while in the Haryana-Punjab arid belt, it fluctuates between 200 mm and 450 mm. Year-to-year variability is considerable, with a coefficient of variation exceeding 70% in western Jaisalmer and Barmer, whereas it remains below 40% in Sikar and Jhunjhunu districts.

Extreme temperature fluctuations characterize the arid region. Mean maximum daytime temperatures range from 36°C to 42.9°C in the eastern part and from 38.8°C to 45.5°C in the westernmost areas [15]. Surface soil temperatures can exceed 62°C in May and June, intensifying evapotranspiration. The region receives high solar radiation [450–500 cal/cm^2/day) and experiences wind speeds of 10–20 km/h, leading to a potential evapotranspiration (PET) rate of 6 mm/day and a high mean aridity index of 78%.

These harsh climatic conditions, coupled with erratic and low precipitation, frequently result in crop failures, severely impacting agricultural productivity and rural livelihoods. The soils of western Rajasthan are predominantly sandy, with low organic matter content (0.1–0.45%), poor moisture retention, and a high infiltration rate of 9 cm/hour. Additionally, salinity and alkalinity affect nearly 45% of the unirrigated land, and surface crust formation post-light rainfall during *kharif* sowing further exacerbates soil degradation [16].

Characteristics of Arid Environments: Arid environments are defined by higher evaporation rates than precipitation, leading to persistent water shortages, frequent droughts, high climate variability, and strong wind velocities. When desertification occurs, previously non-arid regions can become arid, often resulting in biodiversity loss. The concept of aridity is based on the ratio of available water to the total water used. Due to atmospheric stability, precipitation in arid regions is typically lower than evapotranspiration, and cold winters are common. Aridity is often caused by dry, stable air masses that suppress convective currents, preventing the formation of rain clouds. Additionally, the lack of storm systems, which typically generate unstable conditions and promote upward air movement necessary for precipitation, further exacerbates dryness.

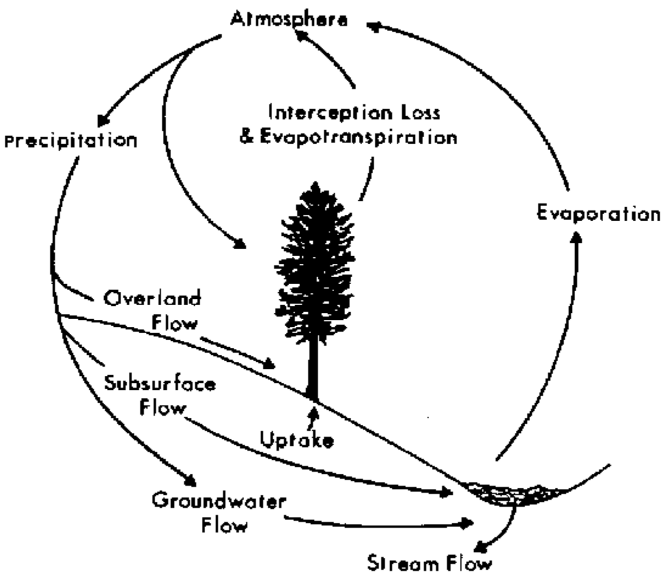


Figure 1

In hot deserts, most precipitation occurs in short, intense convectional showers, which cover small areas, making widespread rains extremely rare. In low-latitude deserts, skies are generally clear, allowing for high solar radiation. These regions also experience the greatest annual temperature variation of any tropical climate. Water loss is a significant issue in arid regions. Due to low soil infiltration capacity, heavy storms often lead to high surface runoff instead of groundwater recharge. Additionally, when rain falls on dry land, a large portion of precipitation is lost to evaporation, with up to 90% of rainfall returning to the atmosphere, leaving only 10% available for plant transpiration [17, 18]. The combination of low precipitation and high temperatures leads to high evaporation rates, resulting in aridic and xeric soil moisture regimes.

Water Scarcity and Soil Fertility in Arid Regions: Water scarcity is a critical constraint on agricultural productivity in arid regions. Due to low precipitation rates and high evapotranspiration, the availability of quality water is severely limited. This issue is further exacerbated by the ongoing global climate change, which brings about extreme weather events and extended dry periods. Optimizing agricultural practices, particularly in the realms of water management and production efficiency, is key to improving soil quality, water conservation and overall product yield [19].

In these water-scarce areas, the soils typically exhibit poor natural primary productivity and low inherent fertility. Arid soils are often alkaline and accumulate substantial concentrations of potassium (K), calcium (Ca), salt and other minerals, which can be detrimental to plant growth. In some instances, gypsic crusts form on the soil surface, supporting only specialized plant species that can tolerate these harsh conditions. The low fertility of arid soils has profound implications, notably hindering plant growth and reducing biodiversity within these environments [20].

Moreover, conventional soil fertility assessment systems, designed primarily for temperate and humid regions, fail to capture the subtle environmental nuances of arid zones [21]. Conventional systems have limited applicability and adoption potential in arid environments. As a result, there is an urgent need to develop tailored soil fertility assessment tools specific to arid regions, ensuring their practical application and fostering their adoption across arid farming communities.

Need for Crop Selection and Genetic Adaptations in Arid Conditions?

Drought is the most significant abiotic stress limiting crop yield in hot arid regions. While some plants have evolved to survive and reproduce in arid, semi-arid, and desert environments, increasing aridity reduces species diversity and potential biomass. In such regions, evaporation exceeds rainfall, severely restricting water availability for agriculture.

Plants in arid regions have developed various adaptive mechanisms to cope with water scarcity. Some species have short life cycles, enabling them to germinate, grow, and reproduce within brief periods of available moisture. Others possess deep or extensive root systems to efficiently access water over a wide area. Certain plants store water in their tissues and release it gradually, while others minimize water loss through protective wax coatings or other structural barriers. Additionally, plants with small or narrow leaves reduce transpiration, and some species have tissues capable of withstanding extreme desiccation without perishing. Crop plants in arid regions may exhibit one or a combination of these adaptations.

Another major challenge in arid regions is high temperature, primarily due to intense solar radiation. Elevated temperatures during germination can cause seedling mortality, reducing plant populations. At the flowering stage, excessive heat can lead to flower abortion, directly decreasing seed production and, consequently, crop yield.

II. CHALLENGES OF CROP PRODUCTION IN ARID REGIONS

Deficit Water Supply and Drought Tolerance Mechanisms: Adaptation of plants to water deficit is a multifaceted process that involves a range of morphological, physiological, biochemical, and molecular changes. Drought tolerance is often linked to several key traits, such as osmotic adjustment, cell membrane stability, the presence of epicuticular wax on plant surfaces, the ability to partition stem reserves to the economically important plant parts, and the regulation and stability of flowering processes. Reduced stomatal conductance and therefore lower photosynthetic rates are the main causes of the short-term yield decline caused by soil drying. However, over time, factors including changed assimilate partitioning across various plant organs and structures and lower leaf area (caused by smaller leaf size and hastened leaf senescence) become more directly accountable for significant yield loss.

Stomatal Conductance: Reductions in stomatal conductance occur as drought progresses due to internal water deficits, leading to a decline in yield. Additionally, decreased stomatal conductance reduces transpiration, causing an increase in leaf temperature. This rise in temperature can elevate maintenance respiration and photorespiration rates, further reducing crop productivity. Some genotypes exhibit variations in inherent water use efficiency, primarily due to reduced stomatal conductance (g) rather than an increase in photosynthetic capacity at a given stomatal conductance [22].

Root Development and Water Absorption: Improving the plant's ability to absorb water is another way to adapt to a water deficit. This is especially important in regions with restricted water supplies. More robust root systems that have deeper and more branched roots that can reach deeper soil water reserves can be developed to do this. In fact, the increased biomass allocation to the root system is a characteristic that distinguishes plants under water stress. By enhancing root characteristics to optimize water acquisition, water-stressed plants demonstrate avoidance mechanisms [23]. Although osmolyte accumulation (OA) is frequently thought of as a way to boost crop yields under drought, field research has not always demonstrated that OA directly increases production [24]. However, by preserving root development and enabling plants to obtain water from deeper soil levels, OA may indirectly support favorable yield responses. Harvest index (HI), water-use efficiency (WUE), and water utilization all affect crop output. Crops may have substantial residual water available to them under water stress, but they must rely on a vast root system to extract this water and increase output.

Leaf Parameters under Water Deficit: Under moderate water stress, reductions in leaf area do not always correlate with a decrease in photosynthetic rates per unit leaf area. However, as drought intensifies, there is often a significant decrease in photosynthetic efficiency per unit of leaf area. Decreased water availability is negatively correlated with a number of physiological characteristics, including leaf area index, leaf area ratio, specific leaf area, and leaf weight ratio. Furthermore, soil moisture stress has a significant impact on other important characteristics, especially during the blooming stage, such as plant height, root length, and number of pods per plant [25].

Crop Yield under Water Stress: Under water stress conditions, crop yield (**Y**) can be described by the equation:

Y=E×WUE×HIY = E \times WUE \times HIY=E×WUE×HI

Where:

- **E** = transpired water
- **WUE** = water-use efficiency
- **HI** = harvest index (the ratio of the biomass of the commercially relevant organ to the total plant biomass)

Breeding programs have successfully increased productivity primarily through harvest index (HI) improvements. However, for most annual species, HI is already close to its maximum, necessitating further increases in yield through enhanced biomass accumulation. Thus, the challenge lies in boosting the plant's capacity to produce greater amounts of dry matter per unit area, particularly under water-limited conditions.

Heat Stress and its Impact on Plants under Drought Conditions: Excessive temperature and high irradiance are common in drought conditions, making drought a multidimensional stressor that simultaneously affects multiple physiological processes in plants. One of the main consequences of heat stress is a reduction in photosynthesis, which decreases the plant’s ability to use incident solar radiation efficiently. This decline in photosynthetic activity can lead to oxidative stress, which damages plant metabolism through processes such as lipid peroxidation and the oxidation of proteins and nucleic acids. These oxidative damages manifest in leaves as chlorotic patches, which, if left unchecked, progress to necrosis, ultimately resulting in leaf abscission.

Genotypes with higher antioxidant activity, both enzymatic (e.g., increased activity of superoxide dismutase, catalase, ascorbate peroxidase, and glutathione reductase) and non-enzymatic (e.g., glutathione and ascorbate), are more drought-tolerant. These genotypes exhibit less oxidative damage compared to those with less robust antioxidant systems. The increased antioxidant capacity in such plants provides cellular protection, particularly for the photosynthetic machinery, and helps in maintaining leaf area. This maintenance of leaf area under stress is vital for the plant’s overall productivity, even in the face of severe water deficits.

Moreover, breeding programs that select for higher water-use efficiency (WUE) under water-limited conditions can significantly contribute to increased crop yields and enhanced drought resistance. WUE and transpiration efficiency are critical factors in improving plant resilience to heat stress, as they allow the plant to minimize water loss while maximizing photosynthetic efficiency. Until the biochemistry of photosynthesis is genetically improved, optimizing transpiration efficiency and WUE will remain essential strategies for reducing crop water-use and enhancing plant production under drought conditions. Thus, breeding for efficient soil moisture capture traits should be a priority in developing drought-resistant crops, as these traits directly contribute to yield improvement under heat stress and water-limited environments.

Table 1: Effects of elevated CO_2, drought, high temperature and salinity on physiological, morphological and molecular characteristics and acclimation/adaptation strategies.

Factor	**Responses to change in the growth environment**		**Acclimation/Adaptation strategies**
High CO_2	Morphological	▪ Increased plant biomass ▪ Increased LAI ▪ Increased leaf DM content	▪ Stomatal closure ▪ Resource remobilization particularly nitrogen in plant ▪ Decreased RuBisCO activity
	Physiologica	▪ Increased photosynthesis ▪ Changed respiration rates ▪ Changed photorespiration rates ▪ Reduced stomatal conductance ▪ Reduced transpiration rates ▪ Increased water use efficiency ▪ Accumulation of non-soluble carbohydrates ▪ Increased leaf nitrogen content	
	Molecular	▪ Down-regulation of key photosynthetic enzyme activities particularly RuBisCO.	
Drought	Morphological	▪ Reduced plant growth ▪ Reduced plant biomass ▪ Reduced LAI ▪ Increased leaf DM content ▪ Shorter plant height ▪ Increased root to shoot ratio	▪ Stomatal closure ▪ Increased root to shoot ratio. ▪ Increased ABA synthesis ▪ Increased osmolyte content ▪ Increased synthesis of drought-related proteins ▪ Increased anti-oxidant
	Physiologica	▪ Declined photosynthesis ▪ Changed respiration rates ▪ Reduced chlorophyll content ▪ Reduced internal CO_2 concentrations ▪ Reduced transpiration rates	
	Molecular	▪ Up-regulation of drought-responsive gene expression ▪ Down-regulation of key photosynthetic gene expression ▪ Reduced activities of key photosynthetic enzymes.	
High Temperature	Morphological	▪ Reduced plant growth ▪ Increased leaf DM content	▪ Increased synthesis of heat-shock proteins ▪ Increased
	Physiologica	▪ Declined photosynthesis ▪ Reduced photosystem II activity	

	Molecular	▪ Increased activities of starch degrading enzymes	transpiration

Crop Plants Adapted to Arid Environments: Plants that do well in arid or dry environments have developed defences against the hard climate, including the ability to grow crops. The yields that these plants can generate in arid environments and their capacity to withstand it, however, differ. Choosing the appropriate crops for arid areas usually requires a great deal of local experimentation. The creation of appropriate production systems comes next, which frequently calls for modifying indigenous systems that have amassed expertise over many years. Even while native systems might appear simple, they contain priceless knowledge, and their advancement is crucial to the survival of dry areas in the future.

The genetic improvement of crops already adapted to the stresses of aridity is key to enhancing crop productivity and stability. For instance, some drought-tolerant food crops suited to arid environments include:

- ***Zea mays*** (Corn)
- ***Sorghum bicolor*** (Sorghum)
- ***Pennisetum americanum*** (Pearl Millet)
- ***Vigna aconitifolia*** (Moth Bean)
- ***Vigna radiata*** (Mung Bean)

Although high-yielding varieties in irrigated or high rainfall areas often perform poorly in dryland conditions, these traditional crops have demonstrated a remarkable ability to adapt to water scarcity and extreme temperatures. Understanding the requirements for variety selection in dryland farming is essential, as many past attempts have failed due to the lack of proper recognition of these factors.

To survive and produce under the harsh conditions of arid regions, a variety should possess certain characteristics:

- Short life cycle to complete its growth before the onset of extreme drought
- Drought tolerance to withstand extended dry periods
- High-temperature tolerance to endure extreme heat conditions
- High water-use efficiency to maximize water utilization during scarcity
- Capacity to grow under low fertility conditions as nutrient levels in arid soils are often poor
- Salt tolerance to thrive in soils with high salinity, common in arid regions

The drought tolerance of specific food crops can vary significantly, and Table 2 provides a detailed comparison of their performance under dryland conditions.

Table 2: Drought tolerance of food crops

S. No.	Scientific Name	Common Name	Degree Of tolerance*
1	*Zea mays*	Corn	1.0
2	*Sorghum bicolor*	Sorghum	1.5
3	*Pennesitum americanum*	Pearl Millet	2.0
4	*Vigna aconitifolius*	Moth Bean	2.5
5	*Vigna radiata*	Mung Bean	2

* From 0 (no tolerance) to 3 (great tolerance), the rating ranges. Taken from Randy Creswell and Dr. Franklin W. Martin's 1993 (updated 1998) book "Dryland Farming: Crops and Techniques for Arid Regions," which was published by ECHO Staff on page 23.

Arid and Semi-Arid Climates: Sorghum and pearl millet are important crops cultivated in arid and semi-arid tropical climates where harsh environmental factors, like high soil surface temperatures, make it difficult for crops to survive and thrive. Soil temperatures in these conditions can rise above 60°C, which has a negative impact on seedling survival and germination and results in poor crop establishment.

Sorghum, despite being sensitive to high temperatures, has some genotypes capable of surviving at soil surface temperatures as high as 55°C. This characteristic makes it suitable for regions with extreme heat stress [26]. However, pearl millet has proven to be even more heat-tolerant, with some genotypes surviving in soil temperatures as high as 62°C [27]. This remarkable heat tolerance gives pearl millet a strong advantage in extreme environments.

Pearl millet has been gaining popularity as a summer crop, especially in states like Gujarat, Rajasthan, Maharashtra, Tamil Nadu, and Uttar Pradesh, where it performs well in the summer season. In Gujarat and Rajasthan, air temperatures during the summer can exceed 42°C, further exacerbating heat stress. Although pearl millet is more resilient to heat, high temperatures during flowering can still cause poor seed setting, leading to reduced grain yields. This issue has prompted the development of heat-tolerant pearl millet varieties that can endure high temperatures during the critical flowering stage, ensuring better yields.

The environment in which sorghum and pearl millet are traditionally grown, typically under rainfed conditions, is characterized by a combination of heat, water scarcity, and poor soil fertility, which makes it difficult for maize to thrive. These marginal and unproductive conditions are too harsh for maize, but sorghum and pearl millet, due to their adaptations, are able to endure and even produce under such challenging circumstances.

Table 3: Adaptive features of sorghum and pearl millet

Adaptation trait	Sorghum	Pearl millet
Drought tolerance	Superior to maize	Superior to sorghum
Water-Use-efficiency	Better than maize	Better than sorghum
Seedling heat tolerance	Superior to maize	Superior to sorghum
Reproductive heat tolerance	Superior to maize	Superior to sorghum
Crop maturity	90-130 days	62-95 days

While sorghum can withstand drought, pearl millet is considerably more drought-tolerant and uses water more efficiently than sorghum (Table 2). The water-use efficiency of pearl millet and sorghum under frequent irrigation is similar to that of maize. However, pearl millet becomes the most water-efficient crop when irrigation is reduced and drought stress increases.

Crop	**Dry matter (kg/ha/mm water)**		
	7 irrigations	**4 irrigations**	**Two irrigations**
Sorghum bicolor	15.4	16.4	14.0
Pennesitum americanum	14.6	13.8	17.9
Zea mays	15.0	12.8	11.0

Source: [28]

III. STRATEGIES FOR ENHANCING YIELD AND TOLERANCE TO WATER SCARCITY

Breeding for Water Deficit Stress: Breeding efforts need to combine increased biomass production with decreased water usage or enhanced water-use efficiency (WUE) to increase drought resistance. Reducing stomatal conductance is one such strategy that would save water but may also restrict CO_2 influx and impair photosynthetic rates, which would result in less biomass growth. Therefore, increasing photosynthetic capacity even in the presence of reduced stomatal conductance is a difficulty. Numerous tactics have been put forth to increase cultivars' photosynthetic efficiency in drought-prone environments. One tactic is to use CO_2 concentrator mechanisms, which improve CO_2 fixation and are found in organisms that use C4 metabolism. Increasing the CO_2 selectivity of the ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) enzyme is an additional strategy to reduce photorespiration losses in C3 plants. Furthermore, photosynthetic rates can be directly boosted by raising mesophyll conductivity without necessitating a rise in stomatal conductance. Lastly, increasing specific leaf mass can lead to increased productivity because it indicates a bigger quantity of photosynthetic machinery per unit leaf area. One of the main ways that plants respond to water deprivation on a cellular level is by osmotic adjustment, which is the accumulation of suitable osmolytes such proline, sorbitol, and mannitol. Plants can better withstand water stress thanks to these solutes, which support cellular processes without interfering with metabolism.

The Osmotic Adjustment has Two Main Functions

In addition to permitting a comparatively larger stomatal aperture,

i. Maintaining cell turgor in the presence of negative water potential permits the process of cell elongation; and

ii. Giving the roots a greater capacity for water uptake, which would also help maintain higher stomatal conductance.

By maximizing the photosynthetic process, osmotic adjustment results in greater biomass accumulation, making plants more productive despite limited water availability. Therefore, genotypes with a higher potential for osmotic adjustment tend to be more drought-tolerant and exhibit improved productivity under water-scarce conditions.

A situation known as drought or water deficit occurs when there is not enough moisture available to plants, which has a negative impact on vegetation. Premature senescence, floral abscission, delayed blooming and grain development, and spikelet sterility are all signs of dryness in crop plants. The ability of a genotype to produce more than other genotypes with a specific level of soil moisture is known as drought tolerance. Depending on when it happens in the plant's growth cycle, drought can be categorized as terminal, unpredictable, or a combination of both [29]. The process known as the Soil-plant-atmosphere continuum [30] replenishes the water lost through stomata, which is created by water being drawn from the soil through the root, stem, and leaf via the xylem. Climate variables that affect the quantity of available water and how it is used determine how plants behave when there is a water deficit. Depending on the species and the extent and length of the water deficit, plants might react very differently to water scarcity.

Three Main Strategies by Which Plants Can Adapt and Grow Properly under Water Deficit Conditions

1. **Drought Escape [**31**]**: This strategy involves the plant's ability to complete its life cycle before soil water is depleted. The phenology of the crop matches with the availability of soil moisture, ensuring that critical stages of growth occur when water is abundant. Examples of drought escape mechanisms include short duration, early maturity, and dormant seeds. This strategy is typically observed under terminal drought conditions, where water availability decreases towards the end of the growing season.

2. **Drought Avoidance [**32**]**: Drought avoidance refers to the plant’s ability to maintain high tissue water potential despite a shortage of soil moisture. This strategy optimizes the use of available water for dry matter production. Drought avoidance can be achieved in two ways: reducing transpiration or increasing water absorption.

   - **Water Savers:** These plants reduce transpiration by mechanisms such as stomatal closure [33], leaf drop [31], or by having smaller, thicker leaves to reduce water loss.

   - **Water Spenders:** These plants increase water absorption by improving the root system’s capacity to absorb water [31, 34]. Stress is mitigated through morphological, physiological, and biochemical barriers, including:

   - **Morphological** characteristics include awns, deep roots systems, cuticular wax, reduced leaf area, leaf rolling, and yield stability.

   - **Physiological:** Osmotic adjustment, stomatal closure, high water usage efficiency, and decreased transpiration.

- **Biochemical:** Proline, polyamines, trehalose, elevated nitrate reductase activity, and enhanced storage of carbohydrates.

3. **Drought Tolerance:** Drought tolerance is the ability to withstand water deficit with low tissue water potential. This is achieved through the maintenance of turgor via osmotic adjustment, which induces solute accumulation. This process increases cell elasticity and decreases cell size. Drought tolerance also includes mechanisms such as drought recovery, where plants regain vegetative growth vigor after water stress. Each of these strategies comes with associated costs and benefits, which can vary depending on the species, environmental conditions, available technological and the specific breeding goals.

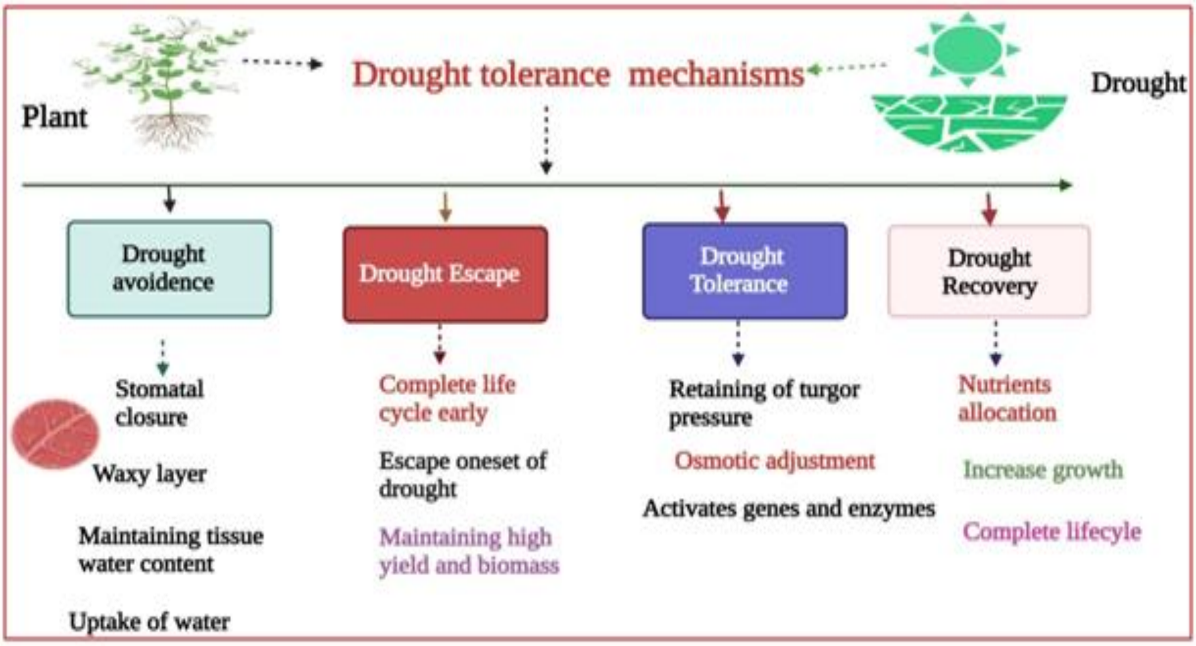


Figure 2: Drought tolerance

Breeding for Heat Stress

The threshold temperature (upper and/or lower), which varies both inter and intraspecifically, refers to the daily average temperature that causes a reduction in growth. The temperature increase above the upper limit for a period of time is sufficient to cause irreversible damage to plant growth and development is defined as heat stress, which is a complex function of the intensity, duration, and rate of temperature increase. It leads to death of cells, tissues, organs and whole plants.

The Following Circumstances Can Cause Heat Stress in Plants

- **Heat Transfer from Air**: When air temperature is high, plants absorb energy through sensible heat transfer, increasing their internal temperature.

- **Soil-Driven Heating**: Solar radiation heats the ground, raising its temperature above the air temperature, indirectly affecting plant heat stress.

- **Leaf Overheating:** Solar radiation can cause leaf temperatures to rise significantly (up to 15°C above air temperature), especially in plants with low transpiration rates, leading to heat stress.

Wilting, leaf burn, folding, or abscission are signs of heat-induced plant damage. Crops use strategies like enhanced transpiration, increased leaf reflectance, and modified leaf orientation to decrease heat absorption in order to prevent heat stress. Heat tolerance is influenced at the cellular level by factors such as increased chlorophyll content, larger leaves, stronger electrical conductivity of leaf sap, decreased stomatal density, and improved water uptake. From seeding to grain maturity, heat stress can affect crop output at any point. However, it has the greatest effect during flowering, when grain number is set, and grain filling, when final grain weight is established, especially in cereals.

Physiological Adaptations to Drought: During drought conditions, crops exhibit intricate physiological mechanisms to optimize water homeostasis, including:

(a) minimizing transpirational water loss through strategic reductions in leaf surface area and modulation of stomatal conductance [35 & 36], (b) augmenting soil water acquisition by reconfiguring root system architecture to enhance hydrotropism and rhizosphere exploration [37 & 38] and (c) executing osmotic adjustment (OA) via the intracellular accumulation of compatible solutes, thereby maintaining cellular turgor and metabolic stability under water-deficit stress [39].

Limiting Water Loss

Crops subjected to soil moisture deficits must strategically regulate transpiration to conserve available water while simultaneously sustaining adequate carbon fixation to meet energetic demands. A rapid adaptive response to dehydration involves the modulation of leaf area and stomatal conductance, effectively curtailing transpiration rates to optimize soil moisture utilization and preserve elevated leaf water potential. For instance, the drought-adaptive trait of stay-green (*Stg*) sorghum is associated with a controlled reduction in green leaf area at anthesis, suppressed tillering, and a diminutive upper leaf morphology [35]. These adaptations impart significant plasticity to canopy development, allowing dynamic modulation in response to drought severity.

Additionally, reduced stomatal conductance and transpiration rates enhance water-use efficiency, contributing to superior drought resilience in wheat [40]. In rice 36] and barley [41], a lower stomatal density further strengthens drought tolerance by optimizing water conservation. Leaf expansion is predominantly regulated by vapor pressure deficit and soil moisture availability, both of which exhibit substantial genetic variability in crop sensitivity. Consequently, leaf area measurements at any given time are an integrative outcome of prevailing environmental conditions and genotype-specific responsiveness to water-deficit stress.

Enhancing Water Uptake

The root system serves as the primary interface for soil water and nutrient acquisition while simultaneously providing structural anchorage to the plant. Within this system, coarse (or tap) roots play a crucial role in stabilizing root system architecture, regulating rooting depth, and enabling plant penetration into compacted soil layers. Conversely, fine (or lateral) roots predominantly contribute to water uptake, constituting the majority of the root system's surface area and length [42]. The structural plasticity of root architecture, along with its ability to acclimate under fluctuating environmental conditions, is a pivotal determinant of overall plant resilience [38, 43 & 44]. Under soil moisture deficit, root systems undergo strategic morphological modifications to optimize water and nutrient extraction from deeper soil strata.

Additionally, root respiration serves as a fundamental metabolic process, supplying the energy necessary for root elongation, maintenance, and the active absorption and translocation of water and solutes via the xylem. Interestingly, a reduction in root respiration and biomass under severe drought stress has been correlated with enhanced grain yield and superior drought tolerance in wheat cultivars [45]. Root system architecture is emerging as a critical focal point for crop improvement efforts; however, advancements in this domain remain limited, primarily due to the complexities associated with high-throughput root phenotyping [46, 47]. From a breeding perspective, the integration of efficient phenotyping methodologies capable of evaluating extensive mapping populations and germplasm lines is imperative for incorporating root traits into modern crop improvement programs.

Osmotic Adjustment

Osmotic adjustment (OA) is a pivotal metabolic mechanism facilitating drought adaptation by preserving cellular turgor and safeguarding essential physiological functions through the accumulation of compatible solutes [39]. This process has been extensively linked to sustained crop productivity under water-deficit conditions. For instance, wheat cultivars exhibiting high OA capacity demonstrated superior growth and yield, primarily attributed to their ability to maintain elevated leaf water potential compared to low OA counterparts.

[48) investigated eight chickpea genotypes for OA and the accumulation of key osmolytes, including sugars, proline, nitrogen, and potassium. The contribution of these osmolytes became increasingly critical as water stress intensified, particularly during the reproductive phase, where grain yield displayed a direct, positive correlation with OA and relative water content. Despite its physiological significance, OA as a selection criterion in breeding programs has been met with skepticism. This hesitation largely stems from the notion that drought-adaptive genotypes with enhanced osmotic regulation often exhibit reduced growth rates and limited biomass accumulation due to the energetic costs associated with osmolyte biosynthesis. However, under severe drought conditions, heightened osmolyte accumulation may significantly enhance crop resilience, facilitating prolonged drought endurance and enabling a more rapid and comprehensive recovery upon rehydration.

Trait-Based Breeding for Drought Adaptation

Seed yield traditionally serves as the primary selection criterion in breeding programs targeting drought adaptation. However, yield is an intricate, cumulative trait influenced by environmental interactions across various growth and developmental stages throughout the crop cycle. A conventional breeding approach that relies solely on selecting genotypes with superior absolute yields under drought is unlikely to suffice in meeting future agricultural demands [49]. The constrained genetic variability in yield among improved cultivars, substantial genotype × environment × management ($G \times E \times M$) interactions, and low heritability present formidable challenges that limit the effectiveness of direct selection for yield [50].

In contrast, genetic enhancement of adaptive traits such as biomass accumulation, harvest index, and canopy temperature through targeted modifications in leaf and root ideotypes holds immense potential to augment productivity and genetic gain under water-deficit conditions, as demonstrated in wheat [51]. Developing drought-resilient crops necessitates a concerted effort to refine these adaptive traits. A trait-based breeding approach, which prioritizes genotype evaluation based on physiological responses to water deficit during the early growth stages, offers a more precise and time-efficient strategy for enhancing drought adaptation in crops.

Context-Dependent Optimization of Leaf Area in Drought-Prone Environments

In ecosystems subjected to prolonged and intense drought episodes, genotypes exhibiting a reduced leaf area or diminished transpiration confer a strategic advantage by conserving soil moisture for critical reproductive phases, such as grain filling [52 & 53]. Studies have demonstrated that sorghum *Stay-Green* (Stg) near-isogenic lines, characterized by a constrained transpirational leaf area compared to their recurrent parent, exhibited enhanced water extraction during the grain-filling stage under extreme water scarcity. This adaptive trait translated into superior biomass accumulation, increased grain number, and elevated yield [54].

Computational simulations across diverse climatic scenarios and agronomic practices indicate that a restricted leaf area provides a substantial yield advantage under severe drought stress. However, this trait concurrently imposes a detrimental effect on biomass accumulation and overall crop productivity under more favorable hydric conditions, as observed in maize [55] and sorghum [56]. Conversely, in rainfed agricultural systems characterized by intermittent drought stress, the ability to sustain leaf area during transient soil moisture deficits emerges as a pivotal determinant of yield potential [57].

Preservation of Leaf Expansion Dynamics under Water-Deficit Conditions Bestows Four Principal Agronomic Benefits: Enhanced canopy-scale photosynthetic assimilation, particularly during the pre-anthesis phase, which directly influences grain set and yield potential [58]. Reduced soil water evaporation, optimizing water-use efficiency through preferential partitioning into transpiration [457]. Lower leaf temperature due to augmented transpiration rates, thereby mitigating heat stress and improving enzymatic activity [59]. A decline in seed abortion rates, attributable to optimized source-sink relationships that sustain reproductive success [60].

This intricate balance between leaf area modulation and drought adaptation underscores the necessity for genotype-specific optimization strategies tailored to environmental constraints.

Root Architecture and Crop Cycle Duration in Drought Adaptation

Crops grown in deep soils with low moisture content benefit from a deep, widely dispersing, and highly branching root system [50]. However, crop types with lower root biomass have often been developed as a result of breeding operations designed to increase grain yield under drought stress [61, 62]. This paradox arises because the spatial configuration of roots in deeper soil strata, rather than total root biomass or length, dictates a plant's ability to efficiently extract soil moisture. For example, chickpea genotypes exhibiting enhanced root proliferation beyond 30 cm soil depth demonstrated superior water uptake and drought resilience [63]. Consequently, deeper root systems with compact branching angles and elevated root length density in subsurface layers are pivotal for accessing water retained in deeper soil horizons, which remain hydrated while surface layers desiccate.

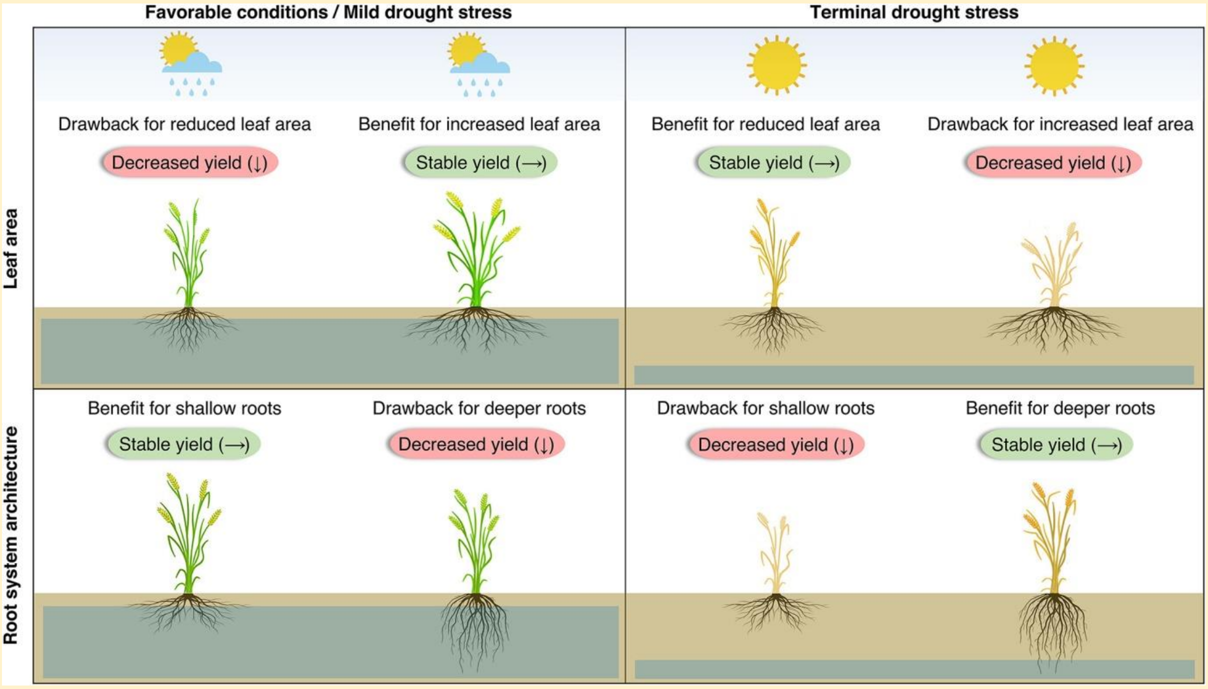


Figure 3

The impact of leaf area and root system architecture on yield varies depending on drought severity and environmental conditions. The most beneficial phenotype is highly context-dependent, influenced by factors such as climate, soil properties, and management practices. Reduced leaf area helps conserve soil moisture and lowers hydraulic gradients, providing a yield advantage under severe terminal drought. However, this trait also limits

cumulative photosynthesis throughout the crop cycle, resulting in a yield penalty under favorable conditions or mild drought stress. Similarly, deeper roots enhance water extraction from lower soil layers, offering a yield benefit in terminal drought scenarios where deep water reserves are available. Conversely, they may reduce nutrient uptake efficiency, making them less effective in conditions where nutrient foraging in upper soil layers is crucial.

However, a trade-off exists regarding nutrient acquisition. Essential yet relatively immobile soil nutrients, such as phosphorus, potassium, iron, and manganese, predominantly reside in the upper soil layers. Thus, excessive allocation of root biomass to deeper soil strata at the expense of surface-root proliferation may hinder nutrient uptake, potentially compromising crop yield [64]. Conversely, in shallow soils with sporadic rainfall or under optimal moisture regimes, a broad, horizontally expansive, and shallow root system is more conducive to maximizing crop productivity by efficiently intercepting transient moisture inputs.

A probabilistic approach to drought adaptation requires a thorough understanding of how drought-adaptive traits function in different climatic conditions. Ideally, crop varieties should be designed to integrate genetic traits that optimize leaf and root architecture while also enabling growth plasticity under water-limited conditions, similar to adaptations observed in wheat. This strategy enhances resource capture and minimizes the negative effects of environmental variability.

Due to the context-dependent nature of traits influencing yield, a two-step framework is necessary:

Identifying beneficial allelic combinations that regulate key trait responses to environmental factors.

Evaluating yield performance based on trait variations and their genetic determinants under existing climatic conditions.

A simplified genome-to-yield prediction model, previously proposed for maize, incorporates genotype-dependent sensitivities with environmental response curves. This probabilistic framework follows three major phases:

Phase 1: Establish yield response curves for soil water deficit, evaporative demand, and light availability through multi-site field trials.

Phase 2 involves utilizing genomic prediction models to assess genotype-specific sensitivity to environmental stressors.

Phase 3 extends this by predicting the yield performance of numerous genotypes under diverse field conditions, where drought severity fluctuates annually. Since farmers cannot anticipate precise environmental conditions at the time of sowing, genotype selection must be probability-driven, optimizing yield potential while mitigating risks in unpredictable climates. A probabilistic breeding approach, which accounts for the genetic variability of drought-adaptive traits and their context-dependent interactions, can enhance drought resilience in major field crops.

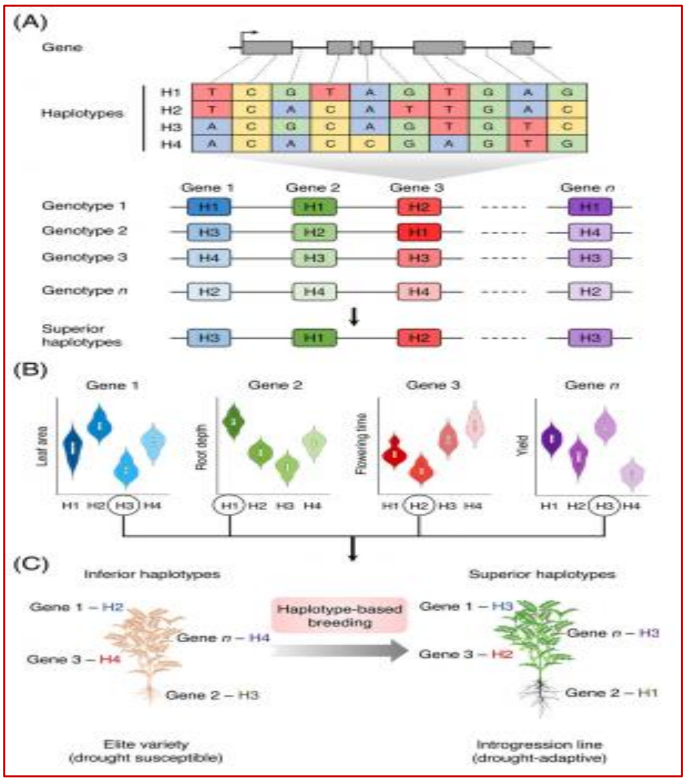
Genomic breeding offers a transformative approach to improving drought adaptation by leveraging the extensive genetic diversity stored in germplasm repositories. Advanced breeding strategies are essential to extract meaningful insights from these resources. Genomic tools have already contributed significantly to the development of stress-tolerant, high-yielding varieties in staple crops such as rice, wheat, and maize. However, many dryland crops—including pearl millet, sorghum, chickpea, pigeon pea, and cassava—have not yet fully benefited from genomic breeding. Given that these crops serve as staple foods for millions in water-scarce regions, enhancing their drought resilience through genomic approaches is critical for global food security.

IV. INTEGRATING PHENOLOGY, ROOT, AND LEAF TRAITS FOR OPTIMIZED WATER UPTAKE

The intricate interplay of phenology-related components such as the duration of the vegetative phase, flowering time, and overall crop cycle emerges as a primary determinant of water uptake efficiency. These factors exhibit complex interactions with distinct leaf and root ideotypes, suggesting that their optimization can be systematically explored through an integrative approach combining empirical experimentation and predictive modelling. Collectively, the pronounced context-dependency of both above- and below-ground plant traits underscores the necessity for targeted research that accounts for genotype × environment × management (G × E × M) interactions. This systems-based perspective is crucial for developing resilient cropping strategies that enhance yield stability under variable and unpredictable environmental conditions [66].

Harnessing Germplasm Diversity for Drought Adaptation

A fundamental limitation in the development of drought-resilient crop varieties is the restricted genetic diversity available in modern gene pools, a consequence of domestication and breeding bottlenecks [67]. As repositories of genetic variation, national and international gene banks provide a sizable collection of alleles that may be able to get beyond these restrictions. Three main categories of genetic resources can be used to study germplasm diversity: (i) crop wild relatives; (ii) isolated gene pools (such as landraces); and (iii) contemporary breeding lines.



H1	T	C	G	T	A	G	T	G	A	G
H2	T	C	A	C	A	T	T	G	A	C
H3	A	C	G	C	A	G	T	G	T	C
H4	A	C	A	C	C	G	A	G	T	G

	Gene 1	Gene 2	Gene 3		Gene n
Genotype 1	H1	H1	H2	-----	H1
Genotype 2	H3	H2	H1	-----	H4
Genotype 3	H4	H3	H3	-----	H3
Genotype n	H2	H4	H4	-----	H2
Superior haplotypes	H3	H1	H2	-----	H3

Figure 4

However, logistical and financial limitations frequently make it impracticable to phenotype huge collections of germplasm to find drought-adaptive characteristics. Choosing a strategic group of accessions that are more likely to have advantageous allelic variations is a more effective option [68]. One such approach is the Focused Identification of Germplasm Strategy (FIGS), which enhances the efficiency of detecting specific drought-adaptive traits. FIGS employs agro-ecological data to generate a priori information, enabling the targeted selection of accessions with the desired adaptive characteristics. This method has been successfully implemented in faba bean germplasm collections to identify drought-resilient genetic variations [69].

The Urgency of Genomic Innovations for Dryland Crops

Drought and desertification lead to an annual loss of 12 million hectares of cultivable land, further reducing global food grain production by 20 million tons [70]. These alarming figures underscore the need for urgent investment in modern genomic technologies to enhance drought adaptation in dryland crops. South Asia and Sub-Saharan Africa, regions disproportionately affected by drought, stand to benefit immensely from genomic innovations. Integrating genomic selection, marker-assisted breeding, and gene editing into breeding programs can help develop climate-resilient crop varieties that ensure stable yields despite fluctuating water availability. By leveraging genomic advancements and modern breeding efforts, it is possible to unlock the genetic potential of underutilized crops, fostering sustainable agriculture and ensuring global food security in the face of climate change.

Haplotype-Based Breeding: A Precision Approach for Crop Improvement

Haplotype-based breeding is an advanced genomic strategy that leverages genetic recombination to develop superior crop varieties with preferred trait combinations. Traditional breeding relies on phenotypic heritability, while QTL-based selection often includes multiple genetic variations some of which may not confer the desired traits or might even have negative effects. By focusing on haplotypes specific combinations of genomic loci associated with beneficial traits breeders can make informed selections of superior genetic variations. This precision breeding approach, also referred to as an evolution of "breeding by design," allows for the in silico development of ideal crop varieties before implementation in breeding programs [71].

Haplotype-based breeding enables the development of drought-adaptive crops by selecting superior haplotypes associated with key adaptive traits.

(A) Haplotypic variation (H1–H4) in a specific gene (gene 3) on a chromosome is illustrated, with multiple genotypes (genotype 1, genotype 2, genotype 3, and genotype n) displaying different haplotype combinations across genes (gene 1, gene 2, gene 3, gene n). Selection of superior haplotypes is based on their associated phenotypic advantages.

(B) Violin plots depict the performance of four drought-related traits—leaf area (gene 1), root depth (gene 2), time to flower (gene 3), and yield (gene n)—showing that H3 is optimal for gene 1, H1 for gene 2, H2 for gene 3, and H3 for gene n, as indicated by analysis of variance.

(C) The introgression of these superior haplotypes into an elite variety through haplotype-based breeding facilitates the development of an improved introgression line with enhanced drought adaptation.

Advantages of Haplotype-Based Breeding

Haplotype-based breeding offers several advantages, making it a powerful tool for crop improvement. One key benefit is its higher accuracy and efficiency, as it enables the assembly of favorable trait combinations at the genomic level while minimizing the risk of introducing undesirable genetic variations into breeding lines. Additionally, this approach leads to optimized crop performance, particularly for crops with extensive germplasm collections that have been thoroughly sequenced and phenotyped. It facilitates the development of drought-adaptive crop ideotypes by incorporating traits such as a small leaf area to reduce transpiration, deeper root systems for enhanced moisture access, early flowering to escape terminal drought, and higher grain yield to maintain productivity under stress. Furthermore, haplotype-based breeding is cost-effective and publicly acceptable, requiring less financial investment compared to traditional breeding methods while avoiding the public resistance often associated with transgenic modifications.

Future Potential: By assembling superior haplotype combinations in elite varieties, haplotype-based breeding presents a promising tool for developing resilient, high-yielding crops tailored to climate variability. This approach is expected to enhance food security by improving drought adaptation while maintaining economic feasibility for farmers and breeding programs.

Genome Editing

Conventional breeding is a time-consuming and difficult method because linkage drag and the random nature of recombination frequently hinder the introgression of desired features into an elite variety. A significant barrier that slows down breeding and produces unpredictable results is a heavy reliance on random or natural genetic diversity [72]. Genome editing, on the other hand, has the ability to produce precise, effective, and targeted changes in crop plants. Any crop can be used, including ones with complicated genome architecture that are difficult to breed using traditional methods [73]. Genome editing has gained attention due to the recent discovery of CRISPR-associated nuclease protein (Cas)-CRISPR-associated short palindromic repeats (CRISPR) systems [74, 75]. Through CRISPR-Cas9-mediated editing, a number of gene knockout, insertion, or replacement mutants are created in field-grown crops to enhance their drought adaption traits. Advances in genome editing technology offer the chance to take use of mutations that result in the best possible shoot and/or root architecture for future crop design. One such example is CRISPRCas9-mediated base editing, which, in the absence of a DNA repair template, may accurately alter one DNA base into another [76, 77].

Genome Editing: A Precision Tool for Crop Improvement

Genome editing offers a revolutionary approach to crop breeding by enabling precise, efficient, and targeted modifications in plant genomes. Unlike conventional breeding, which relies on random recombination and is often hindered by linkage drag, genome editing accelerates the improvement of elite crop varieties by directly modifying specific genes responsible for desirable traits [72].

Advantages of Genome Editing Over Traditional Breeding: Genome editing offers significant advantages over traditional breeding methods, primarily in terms of precision, efficiency, and speed. It allows for the targeted modification of genes controlling key agronomic traits, ensuring that only beneficial characteristics are retained while eliminating undesired genetic linkages. Unlike conventional breeding, which relies on natural genetic variation, genome editing is universally applicable to all crop species, including those with complex genomes that are difficult to improve through traditional methods. Additionally, it accelerates the breeding process by reducing dependency on natural genetic diversity, leading to shorter breeding cycles and more predictable outcomes compared to selection-based approaches.

CRISPR-Cas: A Game Changer in Genome Editing

The CRISPR-Cas9 system has emerged as the most powerful genome editing tool, enabling precise genetic modifications with various applications. It allows for gene knockouts, which disable genes that negatively impact stress tolerance. Additionally, it facilitates gene insertions and replacements, introducing beneficial traits with minimal unintended mutations [75]. Another key advantage is base editing, which enables the precise alteration of a single DNA base without requiring a repair template, providing a highly controlled approach to genetic modifications [76, 77].

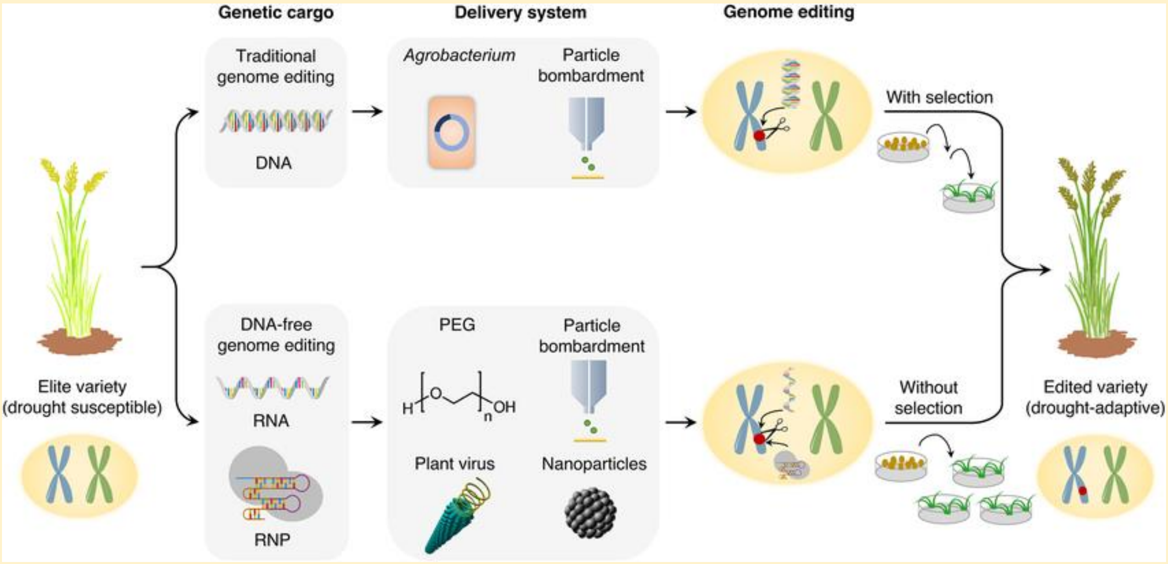


Figure 5

In order to create transgene-free plants, conventional genome editing techniques use CRISPR-Cas DNA in conjunction with selection pressure, followed by genetic segregation by selfing and crossing. On the other hand, CRISPR-Cas reagents like RNA

and ribonucleoproteins (RNPs) are used in transient delivery techniques for DNA-free genome editing. After transient expression, these chemicals break down, enabling the regeneration of modified plants free from selection pressure. DNA (deoxyribonucleic acid), mRNA (messenger RNA), RNP (ribonucleoprotein), and PEG (polyethylene glycol) are examples of common acronyms.

Applications in Drought Adaptation: Several CRISPR-edited field crops have been developed with improved drought tolerance. Technical breakthroughs in genome editing provide an opportunity to modify shoot and root architecture, enhancing water uptake efficiency and stress resilience.

Future Implications: Genome editing represents a paradigm shift in modern agriculture, enabling the development of climate-resilient crops with higher yields and improved stress tolerance. With continuous advancements in CRISPR technologies, the potential to engineer crops for food security in drought-prone regions is greater than ever.

Systems Biology-Based Breeding

Systems biology-based breeding offers an advanced approach to improving drought adaptation in crops, which is a highly complex trait influenced by a network of phytohormones, transcription factors and kinases. Understanding the interactions between these key components and their downstream targets is crucial for identifying the most suitable candidates for breeding programs. To achieve this, a systems biology approach is needed to dissect the temporal dynamics (how processes evolve over time) and spatial configurations (how processes are arranged within different parts of the plant) of these biological phenomena.

In plants, gene regulatory networks (GRNs) play a pivotal role in governing cellular processes that affect various traits, including those of agronomic importance such as drought tolerance. By studying GRNs, researchers can identify genes that are influential in drought adaptation and predict how altering these genes will affect the overall plant behavior and traits. This can enable the design of ideal crop ideotypes specific plant types optimized for particular environmental stresses. For example, only a limited number of Quantitative Trait Loci (QTLs) and candidate genes have been identified for leaf senescence, a trait that is crucial for drought tolerance, particularly in crops like wheat [78, 79 & 80]. Through systems biology, we can refine our understanding of these genes and their interactions, enhancing breeding strategies aimed at improving drought resilience in crops.

A systems biology approach is valuable for identifying genetic regulators that have the most significant impact on gene regulatory networks (GRNs), especially when traditional methods face challenges due to gene redundancies, mild-effect genes, or complex feedback loops. These obstacles can make it difficult to pinpoint the exact genes responsible for a trait's expression. By applying systems biology, we can overcome these limitations and gain insights into the intricate genetic mechanisms driving the traits of interest [81].

This approach is especially important when working with crops that have complex genomes and multigenic traits, where multiple genes interact to influence a single trait. Traditional breeding methods often struggle with these types of traits due to their complexity. However, systems-scale strategies are expected to provide a more efficient and faster route to designing ideal crop ideotypes crops optimized for specific environmental challenges, like drought. By leveraging systems biology, breeding programs can target key regulatory networks, speeding up the process of identifying and incorporating the right genetic combinations, thus improving the overall efficacy and speed of crop development.

Genomic Selection and Speed Breeding

The two ground-breaking innovations in genomic technologies that address the challenges of long breeding cycles and accelerate the development of improved crop varieties.

Genomic selection is particularly beneficial for crops with complex traits, such as drought adaptation. By estimating the genetic merit of breeding lines, genomic selection enhances the efficiency of the selection process. This approach is already being used successfully in crop breeding programs worldwide. For example, drought-tolerant maize hybrids, known as AQUAmax hybrids, have demonstrated significantly higher yields under both optimal and drought conditions. By identifying the genetic potential of breeding lines early in the process, breeders can focus on lines with the best chance of success, thereby speeding up crop improvement.

Speed breeding, on the other hand, addresses the issue of long breeding cycles by accelerating generation times. Using controlled environmental conditions, such as 22-hour-long photoperiods, speed breeding has enabled crops like wheat, barley, chickpea, and pea to achieve up to six generations per year.

This rapid cycling drastically reduces the time required to develop new varieties. When combined, **speed breeding** and **genomic selection** (referred to as "speed GS") create a powerful synergy. Genomic selection can guide breeders in selecting the best parents at each generation, ensuring that genetic gains are maximized in a shorter amount of time. This integration of **speed GS** has the potential to significantly accelerate the rate of genetic gain in crop improvement, providing faster solutions to pressing challenges such as drought and climate change.

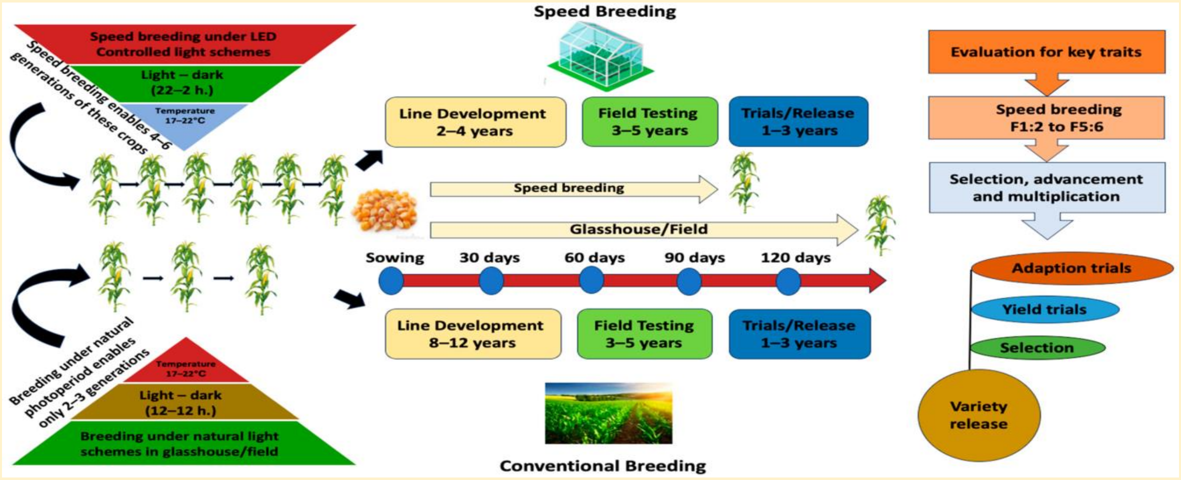


Figure 6

The efficiency of crop breeding can be significantly enhanced by combining genomic selection with speed breeding techniques. While genomic selection shortens the breeding cycle, incorporating speed breeding can further accelerate population development. In this approach, selection candidates can be evaluated for secondary traits, such as root architecture, within controlled glasshouse conditions. Plants exhibiting desirable traits can then be identified and advanced for further evaluation. By prioritizing environment-specific trait selection, plants can be better adapted to their target conditions before focusing on complex traits like yield. Additionally, phenotyping and selecting plants under speed breeding conditions within a glasshouse setting can enhance selection intensity, ultimately leading to a faster rate of genetic improvement.

V. CONCLUSIONS AND PERSPECTIVES

The continuous development of enhanced crop varieties that can sustain higher yields with minimum agronomic inputs and are better adaptable to the challenges of climate change is crucial to future food security. Drought conditions for crops can vary from mild to severe and can happen at any stage of the crop cycle. Crop responses to water deficits can also be influenced by variables such as climate, management techniques, soil depth, and water availability. This complexity makes it challenging to conceptualize a one-size-fits-all drought-adaptive crop ideotype. However, by identifying distinct traits that confer drought adaptation traits that are common across various species and environments breeders can custom-design crops suited to specific conditions.

Ultimately, custom-designed crops tailored to specific environmental and agronomic challenges will be vital in addressing the growing water demands of agriculture. They will also help maximize yield stability despite increasing environmental fluctuations. Achieving this ambitious goal will require the collective effort and collaboration of breeders, geneticists, physiologists, systems modelers and bioinformaticians.

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