

Prospects Of Developing Drought Resilience In Crop Plants Through Strategic Modifications In Root System Architecture

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Abstract

Drought alone and with associated abiotic stress such as heat and nutrient deficiency leads to significant agricultural crop loss. Thus, with changing climatic conditions, it is important to develop resilience measures in agricultural systems against drought stress. In this review, we discuss the modifications in plants while responding to drought giving special focus on roots as they are the primary sense organs in this context. Prospects of genomic crop improvement by pointing out the focus areas to engineer root system architecture and genomic regions involved in the related traits are also discussed. We have also listed instruments and software facilitating high throughput phenotyping of root system in field conditions as the phenotyping of root system architecture in the field is a challenge.

January 9, 2023

To

The Editor

Special section: Genomics of abiotic stress tolerance and crop resilience to climate change,

The Plant Genome.

Dear Prof. Varshney,

We would like to submit a **review** manuscript entitled **Prospects of developing drought resilience in crop plants through strategic modifications in root system architecture**. This review discusses the modifications in plants while responding to drought giving special focus on roots as they are the primary sense organs in this context. This review throw light on focus areas to engineer root system architecture (RSA) using genomic data and high throughput phenotypic information for drought resilience. Therefore, we find this special call an appropriate place to submit this review. We hope you will find this manuscript as a welcome addition to this special call. We will be looking forward to your views in this regard.

Regards

Shailendra Goel, Ph.D. Professor University of Delhi Delhi, India Ani A. Elias, Ph.D. Ramalingaswami fellow Institute of

Running title : Drought resilience and root system architecture

Core ideas : Drought leads to significant crop yield loss demanding engineering for resilience. Root system architecture (RSA) is the primary structure responding to drought. RSA can be engineered genetically

to modify anatomy, physiology, and morphology. Along with high-throughput phenotyping, RSA can be studied comprehensively.

Prospects Of Developing Drought Resilience In Crop Plants Through Strategic Modifications In Root System Architecture

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Abbreviations : ABA, abscisic acid; ARF7, auxin response factor 7; AQPs, aquaporins; BADH, betaine aldehyde dehydrogenase; CDPK, Ca-dependent kinases; CT, X-ray computed tomography; DEGs, differentially expressed genes; *dro1*, deeper rooting 1; EC, electrical capacitance; ERT, electrical resistance tomography; GPR, ground-penetrating radar; GSA, Gravitropic set-point angle; IAA3, indole-3 acetic acid; LEA, Late Embryogenesis Abundant; LR, lateral roots; MIP, Major Intrinsic Proteins; MRI, magnetic resonance imaging; PEG, polyethylene glycol; PIP, Plasma Membrane Intrinsic Proteins; POD, peroxide dismutase; RAM, root apical meristem; ROS, reactive oxygen species; RSA, root system architecture; RWC, relative water content; SnRK2, Snf1-related kinase; SOD, superoxide dismutase; SRL, specific root length; SUT, sucrose transporters; TIP, Tonoplast Intrinsic Proteins; QTLs, quantitative trait locus

Abstract

Drought alone and with associated abiotic stress such as heat and nutrient deficiency leads to significant agricultural crop loss. Thus, with changing climatic conditions, it is important to develop resilience measures in agricultural systems against drought stress. In this review, we discuss the modifications in plants while responding to drought giving special focus on roots as they are the primary sense organs in this context. Prospects of genomic crop improvement by pointing out the focus areas to engineer root system architecture and genomic regions involved in the related traits are also discussed. We have also listed instruments and software facilitating high throughput phenotyping of root system in field conditions as the phenotyping of root system architecture in the field is a challenge.

Keywords: drought resilience, root system, genomic crop improvement, root phenotyping

INTRODUCTION

Environmental stresses affect plant growth in multiple ways. Plants recognize and respond to these stress conditions including drought with a variety of biological signals at various stages of its growth (Takahashi and Shinozaki 2019; Takahashi et al. 2020). From 2005 to 2015 drought in developing countries caused agricultural losses of more than USD 29 billion (FAO, 2021). Drought also occurs with other stresses such as heat, nutrient deficiency, and salinity in the environment (Sehgal et al., 2018). Drought stress is often accompanied by heat stress in the field (Sehgal et al., 2018). Drought impairs transport, partitioning and uptake of nutrients, hence suppressing plant reproduction and growth (Hu and Schmidhalter 2005; Gessler et al. 2017). Due to low moisture content in soil, rate of mineralization and diffusion of nutrients towards surface of root is reduced thereby affecting plant nutrient uptake (Alam 1999; Luo et al. 2018). For example, drought stress reduced concentration of phosphorous (P) and nitrogen (N) in plant tissue as mass flow of nutrients from roots to above ground tissue has been impaired (He and Dijkstra 2014; Bista et al. 2018). During concurrent salinity stress, roots accumulate more ions such as Na⁺ and Cl⁻, reducing the hydraulic conductance in roots, thereby triggering drought conditions (Raja et al., 2020). Factors such as moisture storing capacity of soil, distribution of rainfall, and rate of evaporation are mainly responsible for determining

the extent of drought (Wery et al. 1993; Hussain et al. 2016). With changing climatic conditions, plants with higher drought resilience are preferred in agricultural systems.

The drought stress induces various kinds of responses in plants including morphological, physiological, and biochemical changes which helps them to thrive under drought stress. The first thing that plant senses during drought stress is the decreasing water potential (Christmann, Grill, and Huang 2013) because of which the roots are no longer able to absorb water from soil. This restriction of water flow through xylem and other parts of plants inhibits elongation of cell (Nonami 1998; Hussain et al. 2016). Availability of water impacts metabolic activity and, reactive oxygen species (ROS) production is increased which can alter DNA, RNA, and protein,. This also affect ATP production and disturb balance of osmotic pressure (Priestley 1986; Hussain et al 2018). Another primary response of plants during drought stress is stomata closure to prevent loss of water. Due to closure of stomata, diffusion of CO₂ does not occur in leaves thus reducing the rate of photosynthesis (Raja et al. 2020).

Generally, three types of responses are observed: drought avoidance, drought escape and drought tolerance (**Figure 1**) (Kooyers, 2015; Fang et al., 2017). Drought avoidance refers to morphological and physiological adaptations including reduced number of stomata, minimized leaf area, increased root growth, thick old leaves, cuticle wax synthesis, rolling of leaves and protection from osmotic shock under stress conditions (Lee & Suh, 2013; Y. Liu et al., 2017). Drought escapers are the ones that employ strategies such as precocious flowering, increased photosynthetic ability, increased level of nitrogen, and fast growth in order to complete its life cycle before beginning of drought stress conditions (Kooyers, 2015; Marthandan et al., 2020). In normal conditions crop cycle of longer duration is generally preferred as it enhances the absorption of sunlight but under drought conditions longer crop cycle decreases plant fitness as soil water is depleted before cycle is completed (Tardieu et al., 2018; Varshney et al., 2021). Drought tolerant ones accumulate various osmolytes such as proline and glycine and triggering phenylpropanoid pathway increasing lignin biosynthesis which helps to maintain structure of membranes and production of antimicrobial compounds such as phytoalexin (Nadeem et al., 2019; Sharma et al., 2019; Marthanandan et al., 2020; Sheoran et al., 2022).

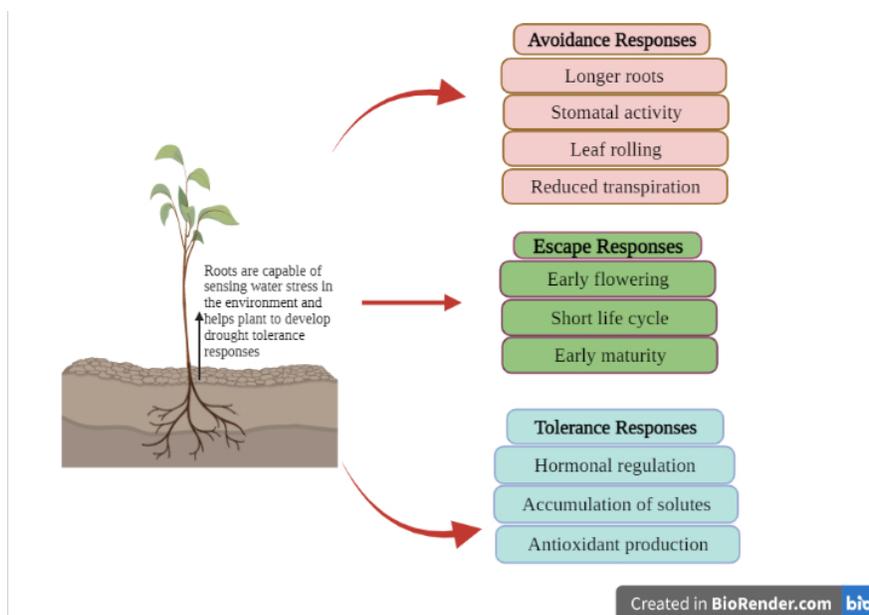


Figure 1: The plant responses to drought stress can be categorized under Escape, Avoidance and Tolerance. (Created with Biorender.com)

We initiated this review by discussing the impact of drought on plants during vegetative and reproductive

phases. Then, we elaborate on the structural adaptations of plants under drought with more focus on the root architecture as roots are the primary sense organs of drought. Genomic information which helps in crop improvement programs are also discussed. Finally, we talk about various root phenotyping methods that are useful in understanding the modifications in root architecture in field conditions.

MORPHOLOGICAL MANIFESTATIONS

Vegetative phase

Plants are severely affected by changes in environmental conditions. Plants require optimum level of water in the soil beyond which uptake of nutrients is inhibited, cell enlargement is affected, cell wall extensibility is reduced leading to loss of turgor and ultimately end of plant growth and development (Seleiman et al., 2021). On perception of any abiotic stress, a signal cascade is activated that triggers cell cycle checkpoints, which slows down the process of DNA replication, impairment of G1 to S transition and delay mitosis (Qi & Zhang, 2020). Drought stress also limits water imbibition and decreases seed vigor by disturbing osmotic balance, increasing ROS production, reducing respiration rate thus affecting seed germination (Farooq et al., 2009; Hussain et al., 2018).

Plants show immediate response to drought by decreasing rate of transpiration by reducing leaf area and stomatal activity. For instance, in stay-green (Stg) sorghum, size of upper leaves is reduced, leaf area is decreased at anthesis and lower tillering occurs in response to drought (Borrell, Mullet, et al., 2014; Varshney et al., 2021). In *Atriplex hortensis* water scarcity causes reduced fresh and dry weight of root and shoot, decreased germination and reduced length of hypocotyl (Franco et al., 2011; Kachout et al., 2021). In the following subsections we discuss the impact of drought with respect to different vegetative stages in plants.

Seedling stage

Drought can affect plants at different stages and of those germination of seeds and seedling emergence are the most critical vegetative stages (Kızılgöçü et al., 2017). Plant survival and growth are highly influenced by processes of germination and growth of seedlings (Kachout et al., 2021). Water scarcity decreases hydraulic conductivity leading to impairment of various metabolic and physiological processes impacting germination (Bareke, 2018; Marthandan et al., 2020b). Studies on various field crops such as *Pisum sativum* (pea), *Oryza sativa* (rice), *Medicago sativa* (alfalfa) has reported decreased potential of germination and reduced hypocotyl length in water stress conditions (Okcu et al., 2005; Manickavelu et al., 2006; Zeid and Shedeed, 2006). Kızılgöçü et al. (2017) reported drastic decrease in rate of germination in wheat seeds when treated with PEG 6000 solution, Islam et al (2018) also conducted similar kind of experiment and reported that rice seedlings also showed reduced germination on increasing water stress. Due to dehydration, osmotic imbalance occurs in plants leading to decreased meristematic activity impairing cell elongation and thereby impairing length of root and shoot. Less water supply towards seed also slows down the process of hydrolyzation of stored carbohydrate reserves, which ultimately affects the transport of food to developing embryo, restricting radicle emergence from seed coat, hence reducing germination (Channaoui et al., 2019). In cotton, root morphology has been shown to play significant role in conferring tolerance to drought especially at seedling stage (Singh et al., 2018; Mahmood et al., 2022). Pace et al. (1999) observed that cotton seedlings showed increased thickness and length of roots when subjected to drought stress as compared to the control seedlings.

Leaf

The leaf also undergoes drastic changes when plants counter water scarcity. The plants which are adapted to avoid drought achieve it through a string of measures such as reduction in number of metaxylem vessels, reduction in stomatal area and density, and increase in thickness of leaf (Mansoor et al., 2019). These plants also have specialized tissue to help such as thick epidermis (Mansoor et al. 2019) and well-developed bulliform cells (Balsamo et al., 2006; Hameed et al., 2009). The bulliform cells help the leaf to roll when needed thus reducing transpiration (Alvarez et al., 2008; Mansoor et al., 2019). The tissues like cortical and mesophyll parenchymatous cells help leaf attaining succulence, a well-known adaptation under water scarcity (Abdel

and Al-Rawi, 2011). Another such adaptation is sclerification (Mansoor et al., 2019; Vendramini et al., 2002) which not only provides mechanical support (Mouliya et al., 2006) but also prevent collapse of cells (Mansoor et al., 2019; Turner, 1994). Granier et al., (2000) has reported that in maize and wheat duration of cell cycle is increased under water stress condition and length of meristem is decreased in leaves. Crop yield is also reduced during drought stress due to reduction in plant height and leaf growth which ultimately reduce photosynthesis rate (Aslam et al., 2015). Delayed spikelet development and pollen abortion, has also been reported in maize plants during water stress (Lu et al., 2011; Edmeades, 2013).

A combination of drought and heat stress have drastic impact on leaves causing wilting, severe chlorosis, damage of membrane (Awasthi et al., 2014), impairment of assimilate production and photosynthesis (Roohi et al., 2013; Sehgal et al., 2017; Sita et al., 2017). Hairy leaves (Boulard et al., 2017) and trichomes on either side allow plants to tolerate water scarce conditions as they help in reducing temperature of leaf by increasing the rate by which light reflection occurs and thereby decreasing transpiration and water loss (Seleiman et al., 2021; Tiwari et al., 2021). In sorghum staygreen (Stg) near-isogenic lines, reduced leaf area allowed the plant to retain more water for later stages of grain filling and thereby resulting in increased yield (Borrell, van Oosterom, et al., 2014; Varshney et al., 2021).

Root

Water stress is primarily sensed by roots, which then transfers this signal to other organs in a plant. The response of rooting system to drought influences the impact of the stress on plants (Anderegg, 2012; Zhou et al., 2018). In response to drought, plants produce a greater number of deeper and thinner roots increasing the total absorption surface area favoring increased nutrient and water uptake (Chapman et al., 2012; Fuentealba et al., 2015; Ma et al., 2018; Zhou et al., 2018). Physiology (e.g., how root respire), architecture (e.g., depth of roots), and morphology (e.g., root diameter) (Zhou et al. 2018) of roots are modified in response to drought.

Water uptake by roots depends on two types of resistance: i) radial, the resistance experienced by water while travelling from soil to root and then to the vascular system, and ii) axial, the resistance on water travelling from root to shoot using vascular root. Rowse & Goodman (1981) studied the role of axial and radial resistance in absorption of water from soil and reported that water uptake is mainly dependent on radial resistance rather than axial resistance. Richards & Passioura (1989) conducted an experiment to modify plants for drought escape where they reduced the uptake of water in earlier water-abundant season by increasing the axial resistance with reduced diameter of xylem. This xylem modification helped in retaining soil water for later stages of grain filling leading to increased productivity. The nodal roots played an important role in this process by extracting maximum soil water from rainfall.

Reproductive phase

Reproductive stages show continuous adjustments from vegetative stages with changing environmental conditions (Onyemaobi et al., 2021). Reproductive phase is more vulnerable and results in fewer flowers with poor quality fruit and fewer seeds (Seghatoleslami et al., 2008; Pushpavalli et al., 2014). Processes such as gametogenesis, embryogenesis, and fertilization are severely affected limiting development of seeds and impairing yield (Farooq et al., 2009, 2014). Pollen fertility is seriously affected (Al-Ghzawi et al., 2009) during stress conditions, disturbing growth of pollen tube and germination (Q. Fang et al., 2010; Gusmao et al., 2012). It is also observed that under water stress, amount of non-reducing sugars is increased, and accumulation of starch is reduced leading to abortion of ovary, (Andersen et al., 2002). For example, in legumes drought decreased the seed size, and suppressed production of pods and flowers (Fang et al., 2010). In *Hordeum vulgare*, exposure of reproductive stage of growth to water stress resulted in increased root:shoot ratio and reduced root thickness (Nosalewicz et al. 2016). Similarly, *Astragalus nitidiflorus* exhibited increased seed dormancy during drought conditions (Segura et al., 2015). Drought along with heat stress has more drastic effect during early phases of reproductive development as various important biological function are affected such as anthesis, micro and megasporogenesis, growth of pollen tube, stigmatic function, fertilization and early embryo development (Prasad et al., 2008). In the following subsections, we discuss the impact of

drought on different reproductive stages in plants.

Flowering

Water plays crucial role in maintaining physiological responses in plants, thus decreasing water potential affects floral morphology and also impairs interaction with pollinators (Ullah et al., 2022). Intensity of the impact of stress varies at various stages of flower setting. For example, exposure of wheat plants to drought during post-anthesis stage, it either repressed grain maturation or left the grain completely unfilled (Dhanda & Sethi, 2002; Thakur et al., 2010) while when exposed during pre-anthesis stage cultivars showed increased drought tolerance at seed filling stage (Wang et al., 2014, 2015). The drought stress during panicle initiation and flowering stages in rice leads to drastic reduction in spikelet and grain number per panicle (Ghoneim 2018, 2020; Gaballah et al., 2022; Ishimaru et al., 2022). Some plants employ drought escape strategies by favoring early flowering, increased growth rate, higher photosynthesis capacity and preservation of reserves for seed development (Gaballah et al., 2022). Flowering, vegetative and seed maturation stages of maize are most vulnerable to water scarcity, causing yield loss up to 50, 25 and 21% respectively (Sah et al., 2020). Under drought stress, abscisic acid (ABA) accumulation occurs and suppress the source-sink relationship and hence disturbing the supply of sugars towards anthers, disrupting pollen development and inducing sterility (Ji et al., 2011). For example, previous studies have shown that accumulation of ABA at young microspore stage of pollen development inhibits expression of cell wall invertase enzyme in tapetal layers of anthers in drought stressed wheat plants (Onyemaobi et al., 2021).

Seed maturation

Seed filling is an essential stage of growth for all plants which involves assimilation of nutrients and transport of various constituents for synthesis of lipids, proteins, and carbohydrates for seed development (Barnabás et al., 2008; Awasthi et al., 2014). Grain maturation process is extremely susceptible to changes in environment affecting quantitative and qualitative traits of yield (J. Yang & Zhang, 2006). Synthesis and storage of reserves for development of seeds is highly dependent on the moisture content of storage cell and decrease in water potential during drought interferes with seed filling (Ochatt, 2015).

Source-sink relationship plays a crucial role in transfer of various constituents for development of seed and it is highly affected by drought as the stress declines the rate of photosynthesis thereby reducing source strength. Water scarcity also leads to loss of turgor pressure in phloem cell, making sucrose more viscous and resisting its flow from conducting cells to the sink (seeds) (Sevanto, 2014). Grain filling depends on transport of assimilates from vegetative sources to seeds directly either at pre- or post-anthesis stage (J. Yang and Zhang, 2006). For example, in rice and wheat assimilates from stems and sheaths provide about 10-40% of total seed weight during pre-anthesis stage (Gebbing & Schnyder, 1999). During drought and heat stress, supply of assimilates from stem increases up to 40% in seeds (Bidinger et al., 1977; Gebbing & Schnyder, 1999). Sucrose transporters (SUTs) genes play an important role in the transport of sucrose from leaves to sink. It has been reported in wheat, barley, maize, and soybean that drought alters the expression of SUT genes (Xu et al., 2018). Expression of SUT varies in different stress conditions, for example, in *Arabidopsis*, expression of AtSUT2 is upregulated under drought stress while it is downregulated under heat stress conditions (increase of about 15°C) (Xu et al., 2018). In contrast, in poplar plants, expression of PtaSUT4, a symplastic loader shows upregulation under heat stress while it is downregulated under water stress resulting in decreased transport of sucrose from source to sink (Xue et al., 2016). In lupin seeds, drought reduced the activity of cytosolic acid invertase to about five-folds thereby decreasing availability of sucrose in seeds (J.-Y. Kim et al., 2000).

Drought stress at grain maturation stage exhibited increased leaf senescence and reduced grain filling phase owing to increased ABA levels in rice and wheat (J. C. Yang et al., 2003; J. Yang & Zhang, 2006). Drought-resistant plants with stay-green trait display delayed leaf senescence (Jordan et al., 2012). At the initial stage of grain filling, drought stress reduced the germination percentage (approximately 9%) of the successive generations in soybean (Smiciklas et al., 1992). Similarly, in *Arachis hypogaea*, drought reduced germination without affecting seedling vigor (Ketrung, 1991). Drought disturbs gamete development and activates ABA

signaling which interferes with carbohydrates assimilation thereby affecting seed size and seed maturation (Sehgal et al., 2018).

ROOT SYSTEM ARCHITECTURE (RSA)

Similar to shoot traits, root traits are also important for maintaining crop yield (Ogura et al., 2019; Uga et al., 2013) and its stability (Sandhu et al., 2016) under moisture stress conditions. Drought stress leads to changes in root structure to improve uptake of water and nutrients from soil. For example, when there is heterogenous distribution of moisture in soil profile, roots are known to exhibit hydro-patterning, where auxin signaling facilitates distribution of lateral roots towards zone of higher water content (Orosa-Puente et al., 2018). In maize, root growth have been shown to play a significant role in partitioning of lateral roots in order to extract more water from depth (Robbins & Dinney, 2018). Modification of root system has been shown to increase drought tolerance in plants (Vivek et al., 2017). Deep root systems confers high drought tolerance to plants by increasing mineral and water uptake (Mahmood et al., 2022).

Plant root systems have their own complexity which is crucial to their function. Plant root systems can be categorized into four different types: (1) tap roots (coarse roots), first roots to emerge from seeds providing anchorage, deciding root depth and overall root system architecture (RSA), controlling overall penetration into soil layers (Henry et al., 2011; Wasaya et al., 2018), (2) lateral roots (fine roots), comprising majority of the total root system playing most active role in water uptake (Comas et al., 2013; Rewald et al., 2011) (3) basal roots, which originate from hypocotyl (Weinhold 1967), and (4) shoot-borne roots, are the ones that originate from shoot tissues (Esau 1965).

Studies on RSA are usually done at macro and microscale; at macroscale studies include occurrence of primary and lateral roots, their organization, and role in uptake of water and nutrient while at microscale studies include role of root hairs in increasing surface area and their assistance in uptake of water and nutrients (Bates & Lynch, 2000; Smith & De Smet, 2012). Generally, roots show plasticity in their architecture as a response to environmental factors such as availability of water and nutrient, soil salinity soil temperature, soil density and microorganism interactions (Smith and Smet 2012).

In both dicots and monocots primary roots are the first to arise from the embryonically formed meristematic tissues. At the tip of both mature and primary roots, a zone of meristematic cells (a.k.a root apical meristem) is present which keeps on dividing; giving rise to other cell types in root. Root consists of three zones in both monocot and dicot: distal root apex zone, consisting of root apical meristem (RAM); elongation zone; and differentiation zone (Jovanovic et al., 2007). A protective layer of tissues is also present at the tip of roots in both monocots and dicots known as root cap which plays a crucial role in root gravitropic responses. In the center of root cap, columella cells are present and some columella cells (statocytes), are occupied by specialized starch containing amyloplasts. Amyloplasts on perceiving the gravity stimulus, sediments on cell boundary. This abundance of amyloplasts triggers changes in auxin transport which ultimately leads to various growth responses including bending of roots towards stimulus of gravity (Smith & De Smet, 2012; Swarup et al., 2005) (**Figure 2**).

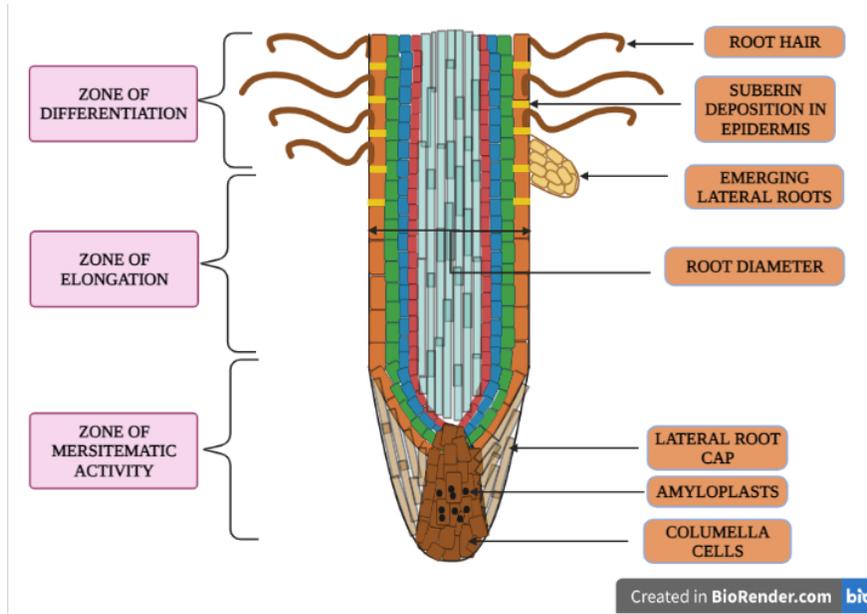


Figure 2: RSA (root system architecture) traits responsible for drought tolerance in plants. (Created with Biorender.com)

RSA in dicots

Dicots, such as *A. thaliana*, has allorhizic root system, i.e., primary roots are the first roots derived from embryo and lateral roots (LR) are formed from cells present in pericycle of primary roots. Pericycle is a layer of tissue present between endodermis and central vascular cylinder (Smith and Smet 2012). Formation of LR varies in various plant species, for instance, in *Arabidopsis*, LRs arise specifically from protoxylem patch in pericycle cells (Malamy et al., 1997; De smet et al., 2008) whereas in *Medicago* and tomato, endodermis is also involved in LR formation (Herrbach et al., 2014). Also, root vasculature in *Arabidopsis* and tomato exhibits diarch symmetry, containing only two xylem poles, whereas in *Medicago* vascular system is triarch, containing three xylem poles (Chen et al., 2018).

RSA in monocots

Monocots comprises of fibrous roots and have more complex root structure than dicots. Fibrous roots in monocots generally refers to the nodal roots along with many finer roots (Maqbool et al., 2022). Generally, in monocots the formation of shoot-borne roots a.k.a nodal roots is necessary to increase the vasculature system as monocots lack secondary thickening in roots and thereby lead to increased uptake of nutrients and water. In wheat, two types of roots are present; nodal roots which originates from basal portion of tillers and seminal roots which originates from embryonic seed part (Manske et al 2002; Wasaya et al., 2018) while only embryonic primary roots are present in rice. LR are developed from cells of pericycle, however it has been reported that in monocots such as rice and maize, pericycle cells of xylem poles are not competent to produce LR and thereby initiation of those occurs in endodermal and pericycle cells opposite phloem poles (Yu et al., 2016).

Relation of RSA with drought

Fine and coarse roots have certain morphological traits which are responsible for having significant impact on surface area and length of roots and control productivity under drought stress. Root diameter, specific root length (SRL), root surface area per dry mass and root tissue density are some of the important morphological traits that control productivity in water scarcity (Fitter 2002). Roots with small diameter and increased SRL absorbs water more efficiently by minimizing the apoplastic barrier for water entry into the xylem, thereby

increasing root hydraulic conductivity (Comas et al., 2013). The cortex formation aerenchyma is generally responsible for increasing SRL (Zhu et al., 2010). However, it has been observed in rice that aerenchyma restricts flow of water through root cortex reducing water uptake in drought stress conditions (X. Yang et al., 2012). Root hairs are more effective for uptake of nutrients and water (Suzuki et al., 2003). Root hairs maintain the hydraulic conductivity between soil and root, maximize the contact of roots with soil by minimizing surface resistance and leading to increased absorption by roots (Wasson et al. 2012). Segal et al. (2008) reported that barley mutants which lacked root hairs showed less water uptake despite having lots of branched roots.

In response to drought, plants encourage elongation of primary roots by inhibiting branching of lateral roots. More vertically structured roots are present naturally in plants that are well adapted to drought, for example in sorghum (V. Singh et al., 2010). Direction of root growth is also critical for determining effectiveness of root system. Under normal conditions, primary roots grow in response to gravity axis whereas lateral roots prefer horizontal growth while lateral roots have particular angle of emergence which is known as gravitropic set-point angle (GSA) that directs growth of lateral roots away from primary roots. Under water stress GSA undergoes changes in a way that allows enhanced uptake of nutrient and water conditions by producing longer and deeper roots (Lynch, 2013). Similarly primary roots also modulate its growth to extract maximum water from surroundings (Takahashi et al., 2009; Iwata et al., 2013).

It has been reported that response of RSA to drought varies considerably at intra- and interspecies level (Kou et al., 2022). Ability of plant to survive and maintain its yield under water scarce conditions is regarded as the plant plasticity response which confers drought tolerance to it (Gao et al., 2015; Suseela et al., 2020). Zhou et al (2018) conducted a meta-analysis based on root traits and concluded that drought drastically affect root length and its density. It enhanced diameter of roots and decreased shoot-to-root biomass ratio under drought stress.

Root architecture is dependent on plant response to the soil water and its distribution, in response to which plants make growth adjustments. Plants generally show plasticity in the distribution pattern of root, especially in deep-rooted species for example *Zea mays* and *Helianthus annuus*. Plants with low root length density (per unit volume of soil) are mainly preferred in areas where water is available in shallow layers of soil whereas for deep layers plants with high root length density are considered more efficient in breeding programs (J. Lynch, 2013; Wasson et al., 2012). Breeding for larger xylem vessels is another good strategy for increasing axial hydraulic conductivity allowing roots to grow at greater depths of soil (Wasson et al., 2012). Hydraulic conductivity is somewhat poor in many woody plants as root-xylem has higher susceptibility to cavitation (Pockman & Sperry, 2000; Comas et al., 2013). During drought conditions root pressure play significant role in repairing embolized xylem by removing water vapor and air from xylem conduits and provides important area of concern for breeders to increase drought tolerance (J. Sperry et al., 2003; J. Sperry, 2011).

It has been proposed that root traits helps in reducing the root system cost (including greater formation of aerenchyma, smaller root diameter, reduced area of living tissue, increased size of cortical cell, fewer nodal roots, root cortical senescence) and aid in promoting elongation of roots, hence increased capture of resources and deeper exploration of soil (Lynch 2013; Fonta et al., 2022). Steeper angle of root growth is known to improve drought tolerance, for example, in rice, deeper rooting 1 (*dro1*) gene which is responsible for influencing angle of root growth has been used in breeding programs and cloning experiments extensively (Uga et al. 2013; Kitomi et al. 2015; Kou et al., 2022). The number and size of metaxylem also affects drought tolerance and water use efficiency in plants. Smaller metaxylem vessels maintains less axial hydraulic conductance in roots conserving soil water while also keeping root tips hydrated (J. P. Lynch et al., 2014). Smaller metaxylem vessels increase resistance to cavitation also (Guet et al., 2015; J. S. Sperry & Saliendra, 1994). Various studies have proven the role of smaller metaxylem vessels in roots, for instance, in wheat, under drought conditions presence of smaller metaxylem vessels in seminal roots of seedlings resulted in improved yield (Richards and Passioura 1989). In maize, genotypes that had decreased metaxylem area in nodal roots and reduced axial hydraulic conductance performed better under water stress than the ones which

did not display this plasticity (Klein et al., 2020). Also in rice, it has been reported that drought-tolerant cultivars had increased number of xylem vessels under water scarcity than drought susceptible cultivars (Abd Allah et al., 2010). De Bauw et al., (2019) conducted an experiment and reported that in the *Indica* rice variety “Mudgo”, xylem vessel number and diameter increased in response to drought while in variety NERICA4, xylem vessel diameter increased but vessel number decreased with respect to water stress. Even along the root axis phenotyping variations exist in drought tolerant varieties of wheat, for instance, near the root tip fewer, larger metaxylem vessels are usually found whereas near the root base smaller metaxylem vessels are present (Kadam et al., 2015; Wasson et al., 2012). It has also been observed that at the base of lateral and nodal roots metaxylem constriction is present in rice (Hazman & Brown, 2018; Vejchasarn et al., 2016) which leads to reduced axial hydraulic conductivity which benefits rice to control the movement of water to shoot and ensuring enough water availability in root tissues, especially growing tips.

Fonta et al., (2022) studied the response of RSA and anatomy with respect to drought, where they used two rice cultivars IR64 which is high yielding, drought susceptible, *Indica* cultivar, and Azucena, low yielding, moderately drought tolerant, *Japonica* cultivar with deep rooting system. They observed that number of nodal roots decreased significantly in both the cultivars under water stress which led to increased conservation of resources for promoting root elongation and hence resulting in deeper root systems. L- type lateral roots (long, thick lateral roots) showed prominent growth at depth under drought conditions and contributed towards deeper soil exploration. Root’s ability to exploit water from the soil also depends on maintaining its fitness by reducing the cost of exploring soil by decreasing area of living tissue as fewer living cells requires less respiration per unit length (J. P. Lynch, 2011,2013). It is also reported that in maize, formation of root cortical aerenchyma or decreased living tissue area (Chimungu et al., 2014; Galindo-Castañeda et al., 2018) and senescence of root cortical cells in barley (Schneider et al., 2017) led to better adaptability under water and nutrient stress.

Production of suberin is also increased in primary roots under both water and salt stress, especially in exo- and endodermis layers where it controls loss of water (Karlova 2021). Role of suberin is generally known to be root-type specific, for example, it has been reported in grape that suberin deposition in roots provided increased tolerance to drought whereas presence of suberin in fine roots (approx. 2mm) led to increased drought susceptibility (Cuneo et al., 2020). As compared to domesticated cultivar, wild barley had increased suberin deposition in exodermis when exposed to drought, something which has also been observed in other species adapted to drought (Kreszies et al., 2020; Yang et al., 2020). Lignin deposition is also observed around mature xylem tissue which acts as a water-resistant barrier and promote drought tolerance (Xu et al., 2017; Liu et al., 2018; Sharma et al., 2020). Overexpression of lignin biosynthesis genes often produced elongated primary roots in mutants (Xu et al., 2020).

PHYSIOLOGICAL/BIOCHEMICAL RESPONSES

Plants adapt themselves to dry environments by undergoing different biochemical and physiological changes in order to maintain cell turgor. Synthesis of ABA, accumulation of various osmolytes like proline and activation of ROS scavengers including peroxidase and superoxide dismutase (SOD) are some of the common physiological response of plants to tolerate drought stress (Bari and Jones 2009; Krasensky and Jonak 2012; Y. H Yang et al. 2020; J.-K. Zhu 2002). Enzymes like protein kinases, phosphatases, ubiquitin ligases, and those involved in metabolism of phospholipids are also reported to actively participate in signaling pathways that are triggered during drought stress (J.-H. Lee and Kim 2011; Vierstra 2009; J.-K. Zhu 2002). Root’s ability to retain water is a pre-requisite for tolerating prolonged water stress, various studies have suggested that water retaining ability of roots can be preserved through waterproof barriers in roots and adjustment of osmolytes. (L. Hu et al. 2018; Kosma et al. 2014; Krasensky and Jonak 2012).

Increasing evidence suggests that plant hormone ABA play important role in regulating gene expression and various physiological responses during drought conditions (Shinozaki and Yamaguchi-Shinozaki 2007; Y. Yang et al. 2020; J.-K. Zhu 2002). Dehydration of leaf is also responsible for activating ABA responses and its biosynthesis in roots (Manzi et al. 2017), for instance, Yang et al. (2020) reported that when compared to roots, relative water content (RWC) in leaf reduced significantly, meanwhile increasing the ABA concentration

in roots, thereby it has been suggested that loss of turgor in leaves might act as important signal for accumulation of ABA in roots. In maize, ABA is known to suppress ethylene production and increases growth of shoot and root in well-watered condition whereas during dry environment, ABA has drastic effect on root-shoot ratio by promoting root growth while suppressing shoot growth (Pierik & Testerink, 2014). Root cortex in the elongation zone is known to specifically express ABA signaling intermediates namely, MIZU KUSSEI1 (MIZ1) and Snf1-related kinases (SnRK2s) which are responsible for hydrotropism (Dietrich et al., 2017; Karlova et al., 2021). When root tip senses heterogenous presence of water, it triggers MIZ1 to generate Ca^{2+} signal which is then transported to elongation zone through phloem and leads to asymmetrical distribution of Ca^{2+} according to gradient of water (Tanaka-Takada et al., 2019). Ethylene production and K^+ transport maintains the balance between Na^+/K^+ ions and thus regulates expansion of cells, turgor and development of lateral roots under osmotic and water stress (Jiang et al., 2013; Osakabe et al., 2013). Accumulation of ABA under water stress is also known to activate miRNA 165 (miR165) and miR166 to suppress transcription factors belonging to class III HD-ZIP, which are responsible for inhibiting xylem formation, thus, their inhibition results in formation of additional protoxylem under water stress conditions (Ramachandran et al., 2018). Zhang et al (2022) reported that during mild drought stress in tomato plants, length of primary roots enhanced in wild plants but failed to increase in the mutant plants lacking genes involved in biosynthetic pathway of ABA, hence concluded that ABA acts as a positive regulator of primary root growth in drought conditions.

Plant hormone auxin also promotes growth of primary roots, lateral roots, and adventitious roots (Pierik & Testerink, 2014). Columella cells are mainly responsible for controlling root angle as amyloplasts began to sediment with respect to gravity in root tips. Due to this asymmetric distribution of amyloplasts, flow of auxin is directed towards lower side of root (Karlova et al., 2021). Low amount of auxin towards upper side of roots leads to enhanced elongation and bending of root in downward direction (Ge and Chen, 2019). Hydro patterning is also dependent on Auxin Response Factor 7 (ARF7), which gets SUMOylated on perceiving the dry environment and increases its interaction with repressor indole-3-acetic acid (IAA3) thereby causing its inhibition and ultimately preventing lateral root formation (Karlova et al., 2021).

Aquaporins (AQPs) which belongs to family of major intrinsic proteins (MIP), plays important role in maintaining RSA by regulating hydraulic conductivity thereby facilitating easy passage of water across membranes (Li et al., 2014). AQPs provide enough water supply to developing primary root primordia helping them to break through endodermis and grow. Transport of water through AQPs for the emergence of lateral roots requires auxin (Péret et al., 2012a). During drought stress, reduced water potential primarily regulates expression of different AQPs; tonoplast intrinsic proteins (TIPs) and plasma membrane intrinsic proteins (PIPs) at various levels (Hachez et al. 2006; Peng et al., 2007).

Secondary metabolites such as phenolics also play significant role under drought conditions (Hessini et al., 2022). When the sugar transport to other plant parts is reduced, it results in accumulation of excess carbohydrates which is then converted to phenolics to maintain source and sink balance. With increasing concentration of phenolics, antioxidant activity also increases significantly (Rehman et al., 2022). Phenols also prevent loss of water from the cell by forming covalent bond with carbohydrates of cell wall (Hura et al., 2012). Osmolytes like proline helps to maintain water potential and turgor pressure in cells, thus preventing loss of water from cells during stress conditions (Krasensky and Jonak 2012; Y. Yang et al. 2020). It rapidly accumulates in various plants, such as wheat and watermelon in order to survive drought stress (L. Hu et al. 2018; Li et al. 2019).

Drought also has drastic effect on mineral uptake (Gunes et al., 2011; Samarah et al., 2004) and significantly decrease fixation of nitrogen in legumes such as pea (Gonzalez et al., 2001), and soybean (Serraj, 2003). These effects collectively reduce production of assimilates and their transport to maturing seeds in crops (Zare et al., 2012). Some micronutrients such as zinc plays important role in resistance to water deficit conditions (Khan et al., 2003; Yavas & Unay, 2016). Nitrogen is known to increase water absorption ability of roots and helps to maintain optimum level of leaf water content in water scarce environments (Tran et al., 2014; Kumari et al., 2022). In the presence of low moisture conditions, phosphorous (P) maintains RSA

and increases proliferation of roots in soil which enhances hydraulic conductivity in roots thereby increased uptake of minerals and nutrients (Sun et al., 2016; Tariq et al., 2017). It was reported that when phosphorous (P) was applied to wheat during the initial stages it resulted in increased production of fertile tillers, grains per spike and spikelet because of enhanced photosynthetic rate, cell elongation and division and hence also showed 28% increase in yield (Ahmed et al., 2018; Kumari et al., 2022). Potassium is also known to increase the accumulation of proline during drought stress and helps plants to cope with the situation (Yadav et al., 2019). Under abiotic stresses cytosolic Ca²⁺ level increases, activating calcium binding proteins such as Ca-dependent protein kinases (CDPK) and triggers various stress-responsive genes regulating different responses such as stomatal movement and increased potassium uptake (Choi et al., 2005; Yu et al., 2007). Increased concentration of magnesium (Mg) in leaves maintains water balance in leaves under drought stress, for instance, in *Musa acuminata*, plants affected with drought showed increased accumulation of Mg (about 28%) than control plants (Kumari et al., 2022; Mahouachi, 2009). Boron is highly beneficial for plants during drought stress as it is involved in ROS detoxification process and therefore protects plants against oxidative damage to membranes and thus plants with increased amount of boron show more resistance to drought stress and enhanced nutrient uptake (Venugopalan et al., 2021). As drought stress is known to decrease the plumule length and ultimately leading to restricted transport of nutrients to embryo, it has been reported that, application of Zinc enhanced the synthesis of hormones such as gibberellic acid and auxin under stress conditions and hence elevate plumule characteristics under water stress, for instance, Harris et al (2005) reported that seed priming with Zinc resulted in improved yield and germination in chickpea, maize and wheat. Zinc also leads to accumulation of various osmolytes, expands leaf area, improves production of photosynthetic pigments and increases leaf water content, resulting in better yield and growth (Kumari et al., 2022).

MOLECULAR RESPONSES AND GENOMIC CROP IMPROVEMENT POTENTIAL

After sensing decreasing water potential in surroundings, roots triggers various signaling pathways of transcription and transportation in aboveground and underground parts for activating defense responses (Opitz et al., 2016; Sengupta et al., 2011; Y. Yang et al., 2020). Modification in RSA to drought is dependent on intense signaling pathways and gene expressions (Janiak et al., 2016). In the following subsections we have discussed genes involved in controlling physiological responses in plants and various QTLs involved in drought responses.

Genes controlling physiological responses

Genes involved in ABA signaling pathways are most crucial for conferring tolerance against drought, which is then also followed by various other phytohormones such as salicylic acid, gibberellin, auxin, cytokinin, brassinosteroid and jasmonic acid. A root-derived peptide called “CLE25” passes, from roots to leaves and acts as signal for closing of stomata by regulating accumulation of ABA, and thereby increasing drought tolerance (Takahashi et al., 2018). In *A. thaliana* expression of CmMYB2 gene triggered ABA pathways, reducing stomatal aperture and thereby leading to enhanced drought tolerance (Shan et al. 2012). In rice, biosynthesis of ABA requires a gene *OsNCED3*, whose expression level is known to be enhanced significantly in seedlings on perception of drought stress (Liu et al 2019).

In *Chrysanthemum*, various transcription factors, such as CgDREBa, are known to activate superoxide dismutase (SOD), peroxide dismutase (POD) and proline accumulation in response to drought (Chen et al., 2011). A transcription factor, MYB, responsible for governing gibberellic acid responses, is shown to increase concentration of osmolytes in seeds under stress conditions by enhancing the accumulation of proline, sugars and production of late embryogenesis abundant (LEA) proteins, establishing water-potential gradient as a result of which water enters into seeds from the soil (Zhao et al., 2019).

Different experiments have been conducted to study molecular responses in plants with respect to drought stress. PtabZIP1-like gene increased formation of lateral roots and growth of biomass under moisture stress conditions (Dash et al., 2017). In poplar, *PagWOX11/12a*, a WUSCHEL related homeobox gene, enhanced root elongation in response to water stress (Wang et al., 2020). Orthologs of *dro1* (gene in rice controlling

angle of root growth) are found in both monocot and dicot species (Kulkarni et al., 2017), for instance, Guesman et al., (2017) reported that orthologs of *dro1* are present in *Arabidopsis* and *Prunus* and the lines overexpressing *dro1* had much deeper roots in stress conditions. Drought tolerant crops have been produced by engineering of genes encoding two enzymes, namely, beta aldehyde dehydrogenase and choline mono oxygenase which are responsible for expression of glycine betaine, which plays crucial role in configuring drought tolerance to higher plants (Zhang et al., 2008), for example, drought tolerant maize variety DH4866, has been formed by transferring beta gene from *E. coli* which led to improved production of betaine and hence tolerance to drought (Quan et al., 2004). Crops such as tobacco and soybean has also been engineered using the genes involved in biosynthesis of proline, an important osmolyte (Ronde et al., 2004; Gubis et al., 2007).

Roche et al. (2007) tried to study the expression of various genes that were responsible for signal transduction and metabolism in immature embryos and leaves of *Helianthus annuus* with the help of cDNA array and he identified around 409 DEGs out of which 82 were induced in response to drought and were organ specific. Betaine aldehyde dehydrogenase (BADH) gene is also known to be produced in sunflower with respect to salt and drought stress (Liang et al. 2017).

Leaf transcriptome profiles of *O.taihangensis* have been studied after treating with 5% and 25% PEG6000. The study revealed that differentially expressed genes (DEGs) responsible for coping with stress were being produced (Gu, H.H et al. 2019). Moreover, genes involved in trehalose biosynthesis such as *tps6*, *tps1*, *tps10* (belonging to trehalose-6-phosphate synthase family) and in sucrose metabolism such *assus3* and *sus1* also showed increased expression during drought conditions (Y. Yang et al., 2020). Various genes that are involved in biosynthesis of different amino acids such as phenylalanine, alanine, tryptophan, aspartate, glutamate, proline and arginine were also found to be upregulated under water deficient conditions (Y. Yang et al., 2020). Abirad et al., (2022) reported 288 DEGs belonging to families of NAC, AUX/IAA, WRKY, AP2/ERF, MYB and EXPANSIN that are being produced under drought stress in roots of rice.

Genes involved in transport of nutrients including *nia2*, *nrt1.2*, *nrt3.2*, *gln1.3* and *glt* are also upregulated under water deficit situations (Martinez et al., 2020), for example, Qi et al. (2019) reported upregulation of genes responsible for potassium transport including *MdHKT1*, *MdHAK3.2* and *MdCHX4.11* under water stress.

Quantitative Trait Loci (QTL) involved

Studies have been conducted in different plants such as rice (Y. Kim et al., 2020), grain legumes (Ye et al., 2018) and wheat (C. Li et al., 2021) where they have reported different QTL and genes produced in drought stress. Ranjan et al., (2022) has reported QTL, mRNAs, genes and transcription factors that actively take part in response of RSA to water stress. Among these various root traits, dry weight of root and root length harbors maximum gene number that are expressed in response to drought. For example, under drought QTL such as PRL3, PRL2, CRL1, SRL2, SRL7, SRL9, and QTRL.cgb-3B are associated with root length in maize (T. Li et al., 2017) and wheat (X. Liu et al., 2013) respectively. Likewise in wheat, Qrdws.uwa-4AL and Qrdws.uwa-5AL are known to be associated with root dry weight in wheat (Ayalew et al., 2017) and in sorghum QTLs qRDW1_2, qRDW1_5, and qRDW1_8 are linked to root dry weight (Mace et al., 2012). In rice, overexpression of OsNAC5 (Jeong et al., 2013) and OsNAC10 (Jeong et al., 2010) were reported to enhance the root diameter in drought stress. Kawai et al., (2022) has recently reported that under mild drought conditions, QHB and OsWOX10 are responsible for regulating diameter of lateral roots in rice. In *Brassica napus*, a gene BnaC03g45915D (ortholog of *A. thaliana* gene RD29B) is found to be present within QTL qR/S-13-1 and showed increased expression in dry conditions configuring plants to adapt to drought conditions more efficiently (Prerostova et al., 2018). Analysis of QTL that are associated with physiological and morphological traits w.r.t drought tolerance helps to develop understanding about the genetic architecture involved in drought responses and how it can be utilized to produce crops that are well adapted to drought.

ROOT PHENOTYPING METHODS

Phenotyping presents many challenges in front of plant breeders for enhancing stress tolerance in crop plants as screening roots for complex genetic traits is extremely difficult under field conditions (Sharma et al 2016). Root phenotyping methods involves combination of imaging and image processing with automation. Image-based phenotyping is a non-destructive method involving optical analysis of plant traits (Furbank et al 2011; Fiorani and Schurr 2013), and it mainly involves characterization of biochemical, physiological and anatomical properties of roots (Guo and Zhu 2014).

Minirhizotrons involves non-destructive analysis in which a clear tube is positioned in ground and root growth adjoining the tube is detected and image is captured using camera which is installed down the tube (Smit et al., 2000). However, it has certain limitations, as tube and soil interface provides an unnatural environment for the growth of roots, which results in false assessments of characteristics of growth in plants (Wasson et al., 2012). Electrical resistance tomography (ERT) is another approach used for analyzing physical properties of soil (Basso et al., 2010) and how soil water is being exploited by roots in different crops (Srayeddin and Doussan, 2009) both are the measures to detect root behavioral patterns indirectly. Various software such as WinRhizo, Image J, EZ-Rhizo, Root system analyzer, Smart Root, Optimas analysis, Root trace, and Root Nav are popular for image-based analysis of root phenotyping (Sharma et al., 2016). For measuring growth kinetics and branching angles Smart Root software can be used. DART is another software that can be used for studying root structure. It is a manual software coded in JAVA (Bot et al., 2010) and produces flexible datasets of individual parameters of root. Manual softwares like WinRHIZOTM, DART etc., helps to study root lifespan by monitoring color of roots manually (Li et al., 2022). X-ray computed tomography (CT) can be used for assessment of roots within soil profile and for visualizing 3D configuration of roots which helps to decide which character of roots is useful under drought conditions for obtaining high crop yield (Wasaya et al. 2018). The 3D magnetic resonance imaging (MRI) is a non-destructive method that is being practised commonly as a 3D root phenotyping process (Metzner et al., 2014). Image quality of MRI is known to be influenced by substrate type and water content (Rogers & Bottomley 1962). Daniel et al. (2022) has recently used this method for phenotyping roots of 288 wheat seedlings using a new pipeline which is designated as medium-throughput phenotyping. Electrical capacitance (EC) is another 3D root phenotyping method used in the field, which analyzes alternating current of low frequency (less than 1kHz) between the soil and base of stem and then evaluate the dielectric properties for re-establishing root architecture (Dalton, 1995). This method has been used for phenotyping roots of different crops, including maize (Imre et al., 2018), soybean (Cseresnyés et al., 2017) and wheat (Cseresnyés et al., 2021). Ground-penetrating radar (GPR) is another non-destructive geophysical device which uses electromagnetic waves for detecting surfaces which is based on physical and dielectric properties of materials. It is used for analyzing features of RSA and estimation of its biomass (Lorenzo et al 2010). When compared to soil, roots have distinct dielectric permittivity thereby, GPR is useful to detect number, diameter and depth of coarse roots by measuring the reflected signals produced by hyperbolic reflections on radargrams (Wu et al. 2014; Lombardi et al., 2021). For example, GPR was used to measure coarse roots in plants, including, cassava (Delgado et al., 2017), citrus (Zhang et al., 2019) and willow (Li et al., 2015).

For observing roots in controlled environment, various soil-less growth media are being employed, such as gels, paper rolls, and aerated aqueous solutions. Hydroponics techniques are practiced commonly for growing plants using transparent plexiglass nail board sandwiches packed with glass beads of about 1.5 mm size for maintaining proper flow of nutrients (Zhu et al 2005). These systems help to measure total root length, root traits, root branching angles through imaging technique or manually.

CONCLUSIONS

With changing climate and global warming, drought and associated stress are going to be of prime importance in agriculture as developing drought resistant cultivars is central to achieving Zero Hunger, one of the 17 goals proposed in the 2030 Agenda for Sustainable Development (FAO, 2020). Root is the first organ that senses the changes in soil moisture and sends signal to adapt at morphological, anatomical, and molecular scales. These changes are accompanied with changes in root encompassing the first response from plant to counter water scarcity. Plant breeding focusing on modifying the RSA for drought avoidance mechanisms

such as root specific suberin deposition, ABA, various phytohormones such as auxin, phenolics, along with crop management practices such as timely supply of micro and macro nutrients might result in drought resilient crops.

Hence, understanding of the RSA is necessary to produce high-yielding crops under water-limiting conditions, particularly in the dryland agricultural system, for ensuring global food security. This goal requires an overall understanding of plant response to drought and related stresses including the response from root which is often difficult to decipher due to lack of direct access to roots for analysis. Newer technologies and methods to analyze root response are coming forth and are bound to evolve with fast changing technologies like imaging technology and artificial intelligence. Nevertheless, understanding root is of prime importance to create high-yielding crops under water stress and RSA is going to be among the important breeding traits in near future.

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REFERENCES

- Abdel, C.G., Al-Rawi, I.M.T., 2011. "Anatomical alteration in response to irrigation and water stress in some legume crops." *Am. J. Exp. Agric.* 1, 231–264.
- Abdirad, S., Ghaffari, M. R., Majd, A., Irian, S., Soleymaniniya, A., Daryani, P., ... & Salekdeh, G. H. (2022). Genome-wide expression analysis of root tips in contrasting rice genotypes revealed novel candidate genes for water stress adaptation. *Frontiers in plant science* , 13 .
- Anderegg, W. R. (2012). Complex aspen forest carbon and root dynamics during drought. *Climatic Change* , 111 (3), 983-991.
- Aslam, M., Maqbool, M. A., & Cengiz, R. (2015). Drought stress in maize (zea maysl.) Effects, resistance mechanisms, global achievements and. *Cham: Springer* .
- Abd Allah, A. A., Badawy, S. A., Zayed, B. A., & El-Gohary, A. A. (2010). THE ROLE OF ROOT SYSTEM TRAITS IN THE DROUGHT TOLERANCE OF RICE (*Oryza sativa* L.). *Journal of Plant Production* , 1 (4), 621–631. <https://doi.org/10.21608/jpp.2010.86384>
- Abdel, C.G., Al-Rawi, I.M.T., 2011. "Anatomical alteration in response to irrigation and water stress in some legume crops." *Am. J. Exp. Agric.* 1, 231–264.
- Ahmed, M., Khan, S., Irfan, M., Aslam, M. A., Shabbir, G., & Ahmad, S. (2018). Effect of Phosphorus on Root Signaling of Wheat under Different Water Regimes. In S. Fahad, A. Basir, & M. Adnan (Eds.), *Global Wheat Production* . InTech. <https://doi.org/10.5772/intechopen.75806>
- Alam, S. M. (1999). Nutrient uptake by plants under stress conditions. *Handbook of plant and crop stress* , 2 , 285-313.
- Al-Ghzawi, A. A.-M., Zaitoun, S., Gosheh, H., & Alqudah, A. (2009). Impacts of drought on pollination of *Trigonella moabitica*(Fabaceae) via bee visitations. *Archives of Agronomy and Soil Science* , 55 (6), 683–692. <https://doi.org/10.1080/03650340902821666>
- Alvarez, J., Rocha, J., & Machado, S. (2008). Bulliform cells in *Loudetiopsis chrysothrix* (Nees) Conert and *Tristachya leiostachya* Nees (Poaceae): Structure in relation to function. *Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL* , 51 . <https://doi.org/10.1590/S1516-89132008000100014>
- Andersen, M. N., Asch, F., Wu, Y., Jensen, C. R., Næsted, H., Mogensen, V. O., & Koch, K. E. (2002). Soluble Invertase Expression Is an Early Target of Drought Stress during the Critical, Abortion-Sensitive Phase of Young Ovary Development in Maize. *Plant Physiology* , 130 (2), 591–604. <https://doi.org/10.1104/pp.005637>

- Awasthi, R., Kaushal, N., Vadez, V., Turner, N. C., Berger, J., Siddique, K. H. M., & Nayyar, H. (2014). Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. *Functional Plant Biology* ,41 (11), 1148. <https://doi.org/10.1071/FP13340>
- Ayalew, H., Liu, H., & Yan, G. (2017). Identification and validation of root length QTLs for water stress resistance in hexaploid wheat (*Triticum aestivum* L.). *Euphytica* , 213 (6), 126. <https://doi.org/10.1007/s10681-017-1914-4>
- Balsamo, R. A., Willigen, C. Vander, Bauer, A. M., & Farrant, J. (2006). Drought tolerance of selected *Eragrostis* species correlates with leaf tensile properties. *Annals of Botany* , 97 (6), 985–991. <https://doi.org/10.1093/aob/mcl068>
- Bareke, T. (2018). Biology of seed development and germination physiology. *Advances in Plants & Agriculture Research* , Volume 8 (Issue 4). <https://doi.org/10.15406/apar.2018.08.00335>
- Bari, Rajendra, and Jonathan D G Jones. 2009. “Role of Plant Hormones in Plant Defence Responses.” *Plant Molecular Biology* 69(4): 473–88. <https://doi.org/10.1007/s11103-008-9435-0>.
- Barnabás, B., Jäger, K., & Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell & Environment* , 31 (1), 11–38. <https://doi.org/10.1111/j.1365-3040.2007.01727.x>
- Basso, B., Amato, M., Bitella, G., Rossi, R., Kravchenko, A., Sartori, L., ... & Gomes, J. (2010). Two-dimensional spatial and temporal variation of soil physical properties in tillage systems using electrical resistivity tomography. *Agronomy Journal* , 102 (2), 440–449.
- Bates, T. R., & Lynch, J. P. (2000). The efficiency of *Arabidopsis thaliana* (Brassicaceae) root hairs in phosphorus acquisition. *American Journal of Botany* , 87 (7), 964–970.
- Bidinger, F., Musgrave, R. B., & Fischer, R. A. (1977). Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. *Nature* , 270 (5636), Article 5636. <https://doi.org/10.1038/270431a0>
- Bista, D. R., Heckathorn, S. A., Jayawardena, D. M., Mishra, S., & Boldt, J. K. (2018). Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and-tolerant grasses. *Plants* , 7 (2), 28.
- Borrell, A. K., Mullet, J. E., George-Jaeggli, B., van Oosterom, E. J., Hammer, G. L., Klein, P. E., & Jordan, D. R. (2014). Drought adaptation of stay-green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. *Journal of Experimental Botany* , 65 (21), 6251–6263. <https://doi.org/10.1093/jxb/eru232>
- Borrell, A. K., van Oosterom, E. J., Mullet, J. E., George-Jaeggli, B., Jordan, D. R., Klein, P. E., & Hammer, G. L. (2014). Stay-green alleles individually enhance grain yield in sorghum under drought by modifying canopy development and water uptake patterns. *The New Phytologist* , 203 (3), 817–830. <https://doi.org/10.1111/nph.12869>
- Boulard, T., Roy, J.-C., Pouillard, J.-B., Fatnassi, H., & Grisey, A. (2017). Modelling of micrometeorology, canopy transpiration and photosynthesis in a closed greenhouse using computational fluid dynamics. *Biosystems Engineering* , 158 , 110–133. <https://doi.org/10.1016/j.biosystemseng.2017.04.001>
- Channaoui, S., El Idrissi, I. S., Mazouz, H., & Nabloussi, A. (2019). Reaction of some rapeseed (*Brassica napus* L.) genotypes to different drought stress levels during germination and seedling growth stages. *OCL* , 26 , 23.
- Chapman, N., Miller, A. J., Lindsey, K., & Whalley, W. R. (2012). Roots, water, and nutrient acquisition: Let’s get physical. *Trends in Plant Science* , 17 (12), 701–710. <https://doi.org/10.1016/j.tplants.2012.08.001>
- Chen, S., Cui, X., Chen, Y., Gu, C., Miao, H., Gao, H., Chen, F., Liu, Z., Guan, Z., & Fang, W. (2011). Cg-DREBa transgenic chrysanthemum confers drought and salinity tolerance. *Environmental and Experimental Botany* , 74 , 255–260. <https://doi.org/10.1016/j.envexpbot.2011.06.007>

- Chen, Y., Xie, Y., Song, C., Zheng, L., Rong, X., Jia, L., ... & Xuan, W. (2018). A comparison of lateral root patterning among dicot and monocot plants. *Plant Science* , 274 , 201-211.
- Chimungu, J. G., Brown, K. M., & Lynch, J. P. (2014). Reduced Root Cortical Cell File Number Improves Drought Tolerance in Maize. *Plant Physiology* , 166 (4), 1943–1955. <https://doi.org/10.1104/pp.114.249037>
- Choi, H., Park, H.-J., Park, J. H., Kim, S., Im, M.-Y., Seo, H.-H., Kim, Y.-W., Hwang, I., & Kim, S. Y. (2005). Arabidopsis calcium-dependent protein kinase AtCPK32 interacts with ABF4, a transcriptional regulator of abscisic acid-responsive gene expression, and modulates its activity. *Plant Physiology* , 139 (4), 1750–1761. <https://doi.org/10.1104/pp.105.069757>
- Christmann, Alexander, Erwin Grill, and Jin Huang. 2013. “Hydraulic Signals in Long-Distance Signaling.” *Current opinion in plant biology* 16(3): 293–300.
- Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. *Frontiers in Plant Science* , 4 (NOV), 1–16. <https://doi.org/10.3389/fpls.2013.00442>
- Cseresnyes, I., Kabos, S., Takacs, T., Vegh, K. R., Vozary, E., & Rajkai, K. (2017). An improved formula for evaluating electrical capacitance using the dissipation factor. *Plant and Soil* , 419 (1), 237-256.
- Cseresnyes, I., Kelemen, B., Takacs, T., Fuzy, A., Kovacs, R., Megyeri, M., ... & Miko, P. (2021). Electrical Capacitance versus Minirhizotron Technique: A Study of Root Dynamics in Wheat–Pea Intercrops. *Plants* , 10 (10), 1991.
- Cuneo, I. F., Barrios-Masias, F., Knipfer, T., Uretsky, J., Reyes, C., Lenain, P., ... & McElrone, A. J. (2021). Differences in grapevine rootstock sensitivity and recovery from drought are linked to fine root cortical lacunae and root tip function. *New Phytologist* , 229 (1), 272-283.
- Dalton, F. N. (1995). In-situ root extent measurements by electrical capacitance methods. *Plant and soil* , 173 (1), 157-165.
- Dash, M., Yordanov, Y. S., Georgieva, T., Tschaplinski, T. J., Yordanova, E., & Busov, V. (2017). Poplar Ptab ZIP 1-like enhances lateral root formation and biomass growth under drought stress. *The Plant Journal* , 89 (4), 692-705.
- De Bauw, P., Vandamme, E., Lupembe, A., Mwakasege, L., Senthilkumar, K., & Merckx, R. (2019). Architectural Root Responses of Rice to Reduced Water Availability Can Overcome Phosphorus Stress. *Agronomy* , 9 (1), Article 1. <https://doi.org/10.3390/agronomy9010011>
- De Smet, I., Vassileva, V., De Rybel, B., Levesque, M. P., Grunewald, W., Van Damme, D., ... & Beeckman, T. (2008). Receptor-like kinase ACR4 restricts formative cell divisions in the Arabidopsis root. *science* , 322 (5901), 594-597.
- Delgado, A., Hays, D. B., Bruton, R. K., Ceballos, H., Novo, A., Boi, E., & Selvaraj, M. G. (2017). Ground penetrating radar: a case study for estimating root bulking rate in cassava (*Manihot esculenta* Crantz). *Plant methods* , 13 (1), 1-11.
- Dhanda, S. S., & Sethi, G. S. (2002). Tolerance to drought stress among selected Indian wheat cultivars. *The Journal of Agricultural Science* , 139 (3), 319–326. <https://doi.org/10.1017/S0021859602002526>
- Dietrich, D., Pang, L., Kobayashi, A., Fozard, J. A., Boudolf, V., Bhosale, R., ... & Bennett, M. J. (2017). Root hydrotropism is controlled via a cortex-specific growth mechanism. *Nature plants* , 3 (6), 1-8.
- Edmeades, G. O. (2013). Progress in achieving and delivering drought tolerance in maize-an update. *ISAAA: Ithaca, NY* , 130 .
- Esau, K. *Plant Anatomy*, 2nd ed.; JohnWiley and Sons: New York, NY, USA, 1965.

- FAO (2020). *The state of food and agriculture 2020*. (Rome: Overcoming water challenges in agriculture). doi: 10.4060/cb1447en
- FAO (2021). *The Impact of Disasters and Crises on Agriculture and Food Security*. Rome: Food and agriculture organization of the United Nations
- Fang, Q., Ma, L., Yu, Q., Ahuja, L. R., Malone, R. W., & Hoogenboom, G. (2010). Irrigation strategies to improve the water use efficiency of wheat–maize double cropping systems in North China Plain. *Agricultural Water Management* , 97 (8), 1165–1174. <https://doi.org/10.1016/j.agwat.2009.02.012>
- Fang, Y., Du, Y., Wang, J., Wu, A., Qiao, S., Xu, B., Zhang, S., Siddique, K. H. M., & Chen, Y. (2017). Moderate Drought Stress Affected Root Growth and Grain Yield in Old, Modern and Newly Released Cultivars of Winter Wheat. *Frontiers in Plant Science* , 8 . <https://www.frontiersin.org/articles/10.3389/fpls.2017.00672>
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development* , 29 (1), 185–212. <https://doi.org/10.1051/agro:2008021>
- Farooq, M., Hussain, M., & Siddique, K. H. (2014). Drought stress in wheat during flowering and grain-filling periods. *Critical reviews in plant sciences* , 33 (4), 331-349.
- Fiorani, F., & Schurr, U. (2013). Future scenarios for plant phenotyping. *Annu. Rev. Plant Biol* , 64 (1), 267-291.
- Fitter, A. (2002). Characteristics and functions of root systems. In *Plant roots* (pp. 49-78). CRC Press.
- Fonta, J. E., Giri, J., Vejchasarn, P., Lynch, J. P., & Brown, K. M. (2022). Spatiotemporal responses of rice root architecture and anatomy to drought. *Plant and Soil* , 479 (1–2), 443–464. <https://doi.org/10.1007/s11104-022-05527-w>
- Franco, J. A., Banon, S., Vicente, M. J., Miralles, J., & Martinez-Sanchez, J. J. (2011). Root development in horticultural plants grown under abiotic stress conditions—a review. *The Journal of Horticultural Science and Biotechnology* , 86 (6), 543-556.
- Fuentealba, M. P., Zhang, J., Kenworthy, K. E., Erickson, J. E., Kruse, J., & Trenholm, L. E. (2015). Root development and profile characteristics of bermudagrass and zoysiagrass. *HortScience* , 50 (10), 1429-1434.
- Furbank, R. T., & Tester, M. (2011). Phenomics—technologies to relieve the phenotyping bottleneck. *Trends in plant science* , 16 (12), 635-644.
- Gaballah, M. M., Ghoneim, A. M., Rehman, H. U., Shehab, M. M., Ghazy, M. I., El-Iraqi, A. S., Mohamed, A. E., Waqas, M., Shamsudin, N. A. A., & Chen, Y. (2022). Evaluation of Morpho-Physiological Traits in Rice Genotypes for Adaptation under Irrigated and Water-Limited Environments. *Agronomy* , 12 (8), 1–14. <https://doi.org/10.3390/agronomy12081868>
- Galindo-Castaneda, T., Brown, K. M., & Lynch, J. P. (2018). Reduced root cortical burden improves growth and grain yield under low phosphorus availability in maize. *Plant, Cell & Environment* , 41 (7), 1579–1592. <https://doi.org/10.1111/pce.13197>
- Gao, R., Yang, X., Liu, G., Huang, Z., & Walck, J. L. (2015). Effects of rainfall pattern on the growth and fecundity of a dominant dune annual in a semi-arid ecosystem. *Plant and Soil* , 389 (1), 335–347. <https://doi.org/10.1007/s11104-014-2366-4>
- Ge, L., & Chen, R. (2019). Negative gravitropic response of roots directs auxin flow to control root gravitropism. *Plant, Cell & Environment* , 42 (8), 2372-2383.
- Gessler, A., Schaub, M., & McDowell, N. G. (2017). The role of nutrients in drought-induced tree mortality and recovery. *New Phytologist* , 214 (2), 513-520.

- Gebbing, T., & Schnyder, H. (1999). Pre-Anthesis Reserve Utilization for Protein and Carbohydrate Synthesis in Grains of Wheat1. *Plant Physiology* , 121 (3), 871–878. <https://doi.org/10.1104/pp.121.3.871>
- Ghoneim, A. M., E.e, G., & Osman, M. M. A. (2018). Effects of Nitrogen Levels on Growth, Yield And Nitrogen use Efficiency Of Some Newly Released Egyptian Rice Genotypes. *Open Agriculture* , 3 (1), 310–318. <https://doi.org/10.1515/opag-2018-0034>
- Ghoneim, A. M. (2020). Soil Nutrients Availability, Rice Productivity and Water Saving under Deficit Irrigation Conditions. *Journal of Plant Production* , 11 (1), 7–16. <https://doi.org/10.21608/jpp.2020.77983>
- Gonzalez, E., Galvez, L., Royuela, M., Aparicio-Tejo, P., & Arrese-Igor, C. (2001). Insights into the regulation of nitrogen fixation in pea nodules: lessons from drought, abscisic acid and increased photoassimilate availability. *Agronomie* , 21 (6-7), 607-613.
- Granier, C., Inze, D., & Tardieu, F. (2000). Spatial distribution of cell division rate can be deduced from that of p34(cdc2) kinase activity in maize leaves grown at contrasting temperatures and soil water conditions. *Plant Physiology* , 124 (3), 1393–1402. <https://doi.org/10.1104/pp.124.3.1393>
- Gu, H., Yang, Y., Xing, M., Yue, C., Wei, F., Zhang, Y., ... & Huang, J. (2019). Physiological and transcriptome analyses of *Opisthoppappus taihangensis* in response to drought stress. *Cell & bioscience* , 9 (1), 1-12.
- Gubiš, J., Vaňková, R., Červená, V., Dragúňová, M., Hudcovicová, M., Lichtnerová, H., ... & Jureková, Z. (2007). Transformed tobacco plants with increased tolerance to drought. *South African Journal of Botany* , 73 (4), 505-511.
- Guet, J., Fichot, R., Lédée, C., Laurans, F., Cochard, H., Delzon, S., Bastien, C., & Brignolas, F. (2015). Stem xylem resistance to cavitation is related to xylem structure but not to growth and water-use efficiency at the within-population level in *Populus nigra* L. *Journal of Experimental Botany* , 66 (15), 4643–4652. <https://doi.org/10.1093/jxb/erv232>
- Gunes, A., Cicek, N., Inal, A., Alpaslan, M., Eraslan, F., Guneri, E., & Guzelordu, T. (2011). Genotypic response of chickpea (*Cicer arietinum* L.) cultivars to drought stress implemented at pre- and post-anthesis stages and its relations with nutrient uptake and efficiency *Plant, Soil and Environment* , 52 (No. 8), 368–376. <https://doi.org/10.17221/3454-PSE>
- Guo, Q., & Zhu, Z. (2006). Phenotyping of plants. *Encyclopedia of Analytical Chemistry: Applications, Theory and Instrumentation* , 1-15.
- Guo, L., Wu, Y., Chen, J., Hirano, Y., Tanikawa, T., Li, W., & Cui, X. (2015). Calibrating the impact of root orientation on root quantification using ground-penetrating radar. *Plant and soil* , 395 (1), 289-305.
- Guseman, J. M., Webb, K., Srinivasan, C., & Dardick, C. (2017). DRO 1 influences root system architecture in *Arabidopsis* and *Prunus* species. *The Plant Journal* , 89 (6), 1093-1105.
- Gusmao, M., Siddique, K. H. M., Flower, K., Nesbitt, H., & Veneklaas, E. J. (2012). Water Deficit during the Reproductive Period of Grass Pea (*Lathyrus sativus* L.) Reduced Grain Yield but Maintained Seed Size: Water Deficit during the Reproductive Period of Grass Pea. *Journal of Agronomy and Crop Science* , 198 (6), 430–441. <https://doi.org/10.1111/j.1439-037X.2012.00513.x>
- Hachez, C., Zelazny, E., & Chaumont, F. (2006). Modulating the expression of aquaporin genes in planta: a key to understand their physiological functions?. *Biochimica et Biophysica Acta (BBA)-Biomembranes* , 1758 (8), 1142-1156.
- Hameed, M., Basra, S., & Naz, N. (2009). Anatomical adaptations to salinity in cogon grass [*Imperata cylindrica* (L.) Raeuschel] from the Salt Range, Pakistan. *Plant and Soil* , 322 , 229–238. <https://doi.org/10.1007/s11104-009-9911-6>

- Harris, D., Rashid, A., Arif, M., & Yunas, M. (2005). Alleviating micronutrient deficiencies in alkaline soils of the North-West Frontier Province of Pakistan: on-farm seed priming with zinc in wheat and chickpea. *Micronutrients in South and South East Asia* , 143 , 151.
- Hazman, M., & Brown, K. M. (2018). Progressive drought alters architectural and anatomical traits of rice roots. *Rice* , 11 (1), 62. <https://doi.org/10.1186/s12284-018-0252-z>
- He, M., & Dijkstra, F. A. (2014). Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist* , 204 (4), 924-931.
- Henry, A., Gowda, V. R., Torres, R. O., McNally, K. L., & Serraj, R. (2011). Variation in root system architecture and drought response in rice (*Oryza sativa*): phenotyping of the OryzaSNP panel in rainfed lowland fields. *Field Crops Research* , 120 (2), 205-214.
- Herrbach, V., Rembliere, C., Gough, C., & Bensmihen, S. (2014). Lateral root formation and patterning in *Medicago truncatula*. *Journal of plant physiology* , 171 (3-4), 301-310.
- Hessini, K., Wasli, H., Al-Yasi, H. M., Ali, E. F., Issa, A. A., Hassan, F. A., & Siddique, K. H. (2022). Graded moisture deficit effect on secondary metabolites, antioxidant, and inhibitory enzyme activities in leaf extracts of *Rosa damascena* Mill. var. *trigentipetala*. *Horticulturae* , 8 (2), 177.
- Hu, Y., & Schmidhalter, U. (2005). Drought and salinity: a comparison of their effects on mineral nutrition of plants. *Journal of Plant Nutrition and Soil Science* , 168 (4), 541-549.
- Hu, Ling et al. 2018. “Comparative Analysis of Root Transcriptome Profiles between Drought-Tolerant and Susceptible Wheat Genotypes in Response to Water Stress.” *Plant Science* 272: 276–93. <https://www.sciencedirect.com/science/article/pii/S0168945217308543>.
- Hura, T., Hura, K., Dziurka, K., Ostrowska, A., Bączek-Kwinta, R., & Grzesiak, M. (2012). An increase in the content of cell wall-bound phenolics correlates with the productivity of triticale under soil drought. *Journal of Plant Physiology* , 169 (17), 1728–1736. <https://doi.org/10.1016/j.jplph.2012.07.012>
- Hussain, M. Iftikhar et al. 2016. “Salt and Drought Stresses in Safflower: A Review.” *Agronomy for Sustainable Development* 36(1): 1–31. <http://dx.doi.org/10.1007/s13593-015-0344-8>.
- 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>
- Islam, M. M., Kayesh, E., Zaman, E., Urmi, T. A., & Haque, M. M. (2018). Evaluation of rice (*Oryza sativa* L.) genotypes for drought tolerance at germination and early seedling stage. *The Agriculturists* , 16 (1), 44-54.
- Imre C, Katalin S, Kálmán R, Anna F, Péter M, Ramóna K, Tünde T. (2018). Application of electrical capacitance method for prediction of plant root mass and activity in field-grown crops. *Frontiers in Plant Science* 9:93
- Ishimaru, T., Sasaki, K., Lumanglas, P. D., Leo U. Cabral, C., Ye, C., Yoshimoto, M., Kumar, A., & Henry, A. (2022). Effect of drought stress on flowering characteristics in rice (*Oryza sativa* L.): A study using genotypes contrasting in drought tolerance and flower opening time. *Plant Production Science* , 25 (3), 359–370. <https://doi.org/10.1080/1343943X.2022.2085589>
- Iwata, S., Miyazawa, Y., Fujii, N., & Takahashi, H. (2013). MIZ1-regulated hydrotropism functions in the growth and survival of *Arabidopsis thaliana* under natural conditions. *Annals of botany* , 112 (1), 103-114.
- Janiak, A., Kwaśniewski, M., & Szarejko, I. (2016). Gene expression regulation in roots under drought. *Journal of Experimental Botany* , 67 (4), 1003–1014. <https://doi.org/10.1093/jxb/erv512>

- Jeong, J. S., Kim, Y. S., Baek, K. H., Jung, H., Ha, S.-H., Do Choi, Y., Kim, M., Reuzeau, C., & Kim, J.-K. (2010). Root-Specific Expression of OsNAC10 Improves Drought Tolerance and Grain Yield in Rice under Field Drought Conditions. *Plant Physiology* , 153 (1), 185–197. <https://doi.org/10.1104/pp.110.154773>
- Jeong, J. S., Kim, Y. S., Redillas, M. C. F. R., Jang, G., Jung, H., Bang, S. W., Choi, Y. D., Ha, S.-H., Reuzeau, C., & Kim, J.-K. (2013). OsNAC5 overexpression enlarges root diameter in rice plants leading to enhanced drought tolerance and increased grain yield in the field. *Plant Biotechnology Journal* , 11 (1), 101–114. <https://doi.org/10.1111/pbi.12011>
- Jiang, C., Belfield, E. J., Cao, Y., Smith, J. A. C., & Harberd, N. P. (2013). An Arabidopsis soil-salinity-tolerance mutation confers ethylene-mediated enhancement of sodium/potassium homeostasis. *The Plant Cell* , 25 (9), 3535–3552.
- Ji, X., Dong, B., Shiran, B., Talbot, M. J., Edlington, J. E., Hughes, T., White, R. G., Gubler, F., & Dolferus, R. (2011). Control of Abscisic Acid Catabolism and Abscisic Acid Homeostasis Is Important for Reproductive Stage Stress Tolerance in Cereals1. *Plant Physiology* , 156 (2), 647–662. <https://doi.org/10.1104/pp.111.176164>
- Jordan, D. R., Hunt, C. H., Cruickshank, A. W., Borrell, A. K., & Henzell, R. g. (2012). The Relationship Between the Stay-Green Trait and Grain Yield in Elite Sorghum Hybrids Grown in a Range of Environments. *Crop Science* , 52 (3), 1153–1161. <https://doi.org/10.2135/cropsci2011.06.0326>
- Jovanovic, M., Lefebvre, V., Laporte, P., Gonzalez-Rizzo, S., Lelandais-Brière, C., Frugier, F., ... & Crespi, M. (2007). How the environment regulates root architecture in dicots. *Advances in Botanical Research* , 46 , 35–74.
- Kachout, S. S., BenYoussef, S., Ennajah, A., Abidi, S., & Zoghalmi, A. (2021). Physiological and morphological traits associated with germinative and reproductive stage of garden orache (*A. hortensis* L. var. *Rubra*) under water stress. *Chemical and Biological Technologies in Agriculture* , 8 (1), 1–16. <https://doi.org/10.1186/s40538-021-00218-7>
- Kadam, N. N., Yin, X., Bindrabab, P. S., Struik, P. C., & Jagadish, K. S. V. (2015). Does Morphological and Anatomical Plasticity during the Vegetative Stage Make Wheat More Tolerant of Water Deficit Stress Than Rice? *Plant Physiology* , 167 (4), 1389–1401. <https://doi.org/10.1104/pp.114.253328>
- Karlova, R., Boer, D., Hayes, S., & Testerink, C. (2021). Root plasticity under abiotic stress. *Plant Physiology* , 187 (3), 1057–1070. <https://doi.org/10.1093/plphys/kiab392>
- Kawai, T., Shibata, K., Akahoshi, R., Nishiuchi, S., Takahashi, H., Nakazono, M., Kojima, T., Nosaka-Takahashi, M., Sato, Y., Toyoda, A., Lucob-Agustin, N., Kano-Nakata, M., Suralta, R. R., Niones, J. M., Chen, Y., Siddique, K. H. M., Yamauchi, A., & Inukai, Y. (2022). WUSCHEL-related homeobox family genes in rice control lateral root primordium size. *Proceedings of the National Academy of Sciences* , 119 (1), e2101846119. <https://doi.org/10.1073/pnas.2101846119>
- Ketring, D. L. (1991). Physiology of Oil Seeds: IX. Effects of Water Deficit on Peanut Seed Quality. *Crop Science* , 31 (2), crops1991.0011183X003100020047x. <https://doi.org/10.2135/cropsci1991.0011183X003100020047x>
- Khan, H. R., McDonald, G. K., & Rengel, Z. (2003). Zn fertilization improves water use efficiency, grain yield and seed Zn content in chickpea. *Plant and Soil* , 249 (2), 389–400. <https://doi.org/10.1023/A:1022808323744>
- Kim, J.-Y., Mahé, A., Brangeon, J., & Prioul, J.-L. (2000). A Maize Vacuolar Invertase, *IVR 2* , Is Induced by Water Stress. Organ/Tissue Specificity and Diurnal Modulation of Expression. *Plant Physiology* , 124 (1), 71–84. <https://doi.org/10.1104/pp.124.1.71>
- Kim, Y., Chung, Y. S., Lee, E., Tripathi, P., Heo, S., & Kim, K.-H. (2020). Root Response to Drought Stress in Rice (*Oryza sativa* L.). *International Journal of Molecular Sciences* , 21 (4), Article 4. <https://doi.org/10.3390/ijms21041513>

- Kitomi, Y., Kanno, N., Kawai, S., Mizubayashi, T., Fukuoka, S., & Uga, Y. (2015). QTLs underlying natural variation of root growth angle among rice cultivars with the same functional allele of DEEPER ROOTING 1. *Rice* , 8 (1), 1-12.
- Kızılgöçü, F., Tazebay, N., Namlı, M., Albayrak, Ö., & Yıldırım, M. (2017). The Drought Effect on Seed Germination and Seedling Growth in Bread Wheat (*Triticum aestivum* L.). *International Journal of Agriculture, Environment and Food Sciences* , 1 (1), 33–37. <https://doi.org/10.31015/jaefs.17005>
- Klein, S. P., Schneider, H. M., Perkins, A. C., Brown, K. M., & Lynch, J. P. (2020). Multiple Integrated Root Phenotypes Are Associated with Improved Drought Tolerance1 [OPEN]. *Plant Physiology* ,183 (3), 1011–1025. <https://doi.org/10.1104/pp.20.00211>
- Kosma, Dylan K. et al. 2014. “AtMYB41 Activates Ectopic Suberin Synthesis and Assembly in Multiple Plant Species and Cell Types.” *Plant Journal* 80(2): 216–29.
- Kooyers, N. J. (2015). The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science: An International Journal of Experimental Plant Biology* , 234 , 155–162. <https://doi.org/10.1016/j.plantsci.2015.02.012>
- Kou, X., Han, W., & Kang, J. (2022). *Responses of root system architecture to water stress at multiple levels: A meta-analysis of trials under controlled conditions* . December , 1–16. <https://doi.org/10.3389/fpls.2022.1085409>
- Krasensky, Julia, and Claudia Jonak. 2012. “Drought, Salt, and Temperature Stress-Induced Metabolic Rearrangements and Regulatory Networks.” *Journal of Experimental Botany* 63(4): 1593–1608. <https://doi.org/10.1093/jxb/err460>.
- Kreszies, T., Eggels, S., Kreszies, V., Osthoff, A., Shellakkutti, N., Baldauf, J. A., ... & Schreiber, L. (2020). Seminal roots of wild and cultivated barley differentially respond to osmotic stress in gene expression, suberization, and hydraulic conductivity. *Plant, Cell & Environment* , 43 (2), 344-357.
- Kumari, V. V., Banerjee, P., Verma, V. C., Sukumaran, S., Chandran, M. A. S., Gopinath, K. A., Venkatesh, G., Yadav, S. K., Singh, V. K., & Awasthi, N. K. (2022). Plant Nutrition: An Effective Way to Alleviate Abiotic Stress in Agricultural Crops. *International Journal of Molecular Sciences* , 23 (15). <https://doi.org/10.3390/ijms23158519>
- Le Bot, J., Serra, V., Fabre, J., Draye, X., & Adamowicz, S. (2010). DART: a software to analyse root system architecture and development from captured images. *Plant and Soil* , 326 (1), 261-273.
- Lee, Jae-Hoon, and Woo Taek Kim. 2011. “Regulation of Abiotic Stress Signal Transduction by E3 Ubiquitin Ligases in Arabidopsis.” *Molecules and Cells* 31(3): 201–8. <https://doi.org/10.1007/s10059-011-0031-9>.
- Lee, S. B., & Suh, M. C. (2013). Recent advances in cuticular wax biosynthesis and its regulation in Arabidopsis. *Molecular Plant* ,6 (2), 246–249. <https://doi.org/10.1093/mp/sss159>
- Li, G., Santoni, V., & Maurel, C. (2014). Plant aquaporins: roles in plant physiology. *Biochimica et Biophysica Acta (BBA)-General Subjects* , 1840 (5), 1574-1582.
- Li, T., Yang, H., Zhang, W., Xu, D., Dong, Q., Wang, F., Lei, Y., Liu, G., Zhou, Y., Chen, H., & Li, C. (2017). Comparative transcriptome analysis of root hairs proliferation induced by water deficiency in maize. *Journal of Plant Biology* , 60 (1), 26–34. <https://doi.org/10.1007/s12374-016-0412-x>
- Li, H., Mo, Y., Cui, Q., Yang, X., Guo, Y., Wei, C., ... & Zhang, X. (2019). Transcriptomic and physiological analyses reveal drought adaptation strategies in drought-tolerant and-susceptible watermelon genotypes. *Plant Science* , 278 , 32-43.
- Li, C., Li, L., Reynolds, M. P., Wang, J., Chang, X., Mao, X., & Jing, R. (2021). Recognizing the hidden half in wheat: Root system attributes associated with drought tolerance. *Journal of Experimental Botany* , 72 (14), 5117–5133. <https://doi.org/10.1093/jxb/erab124>

- Li, A., Zhu, L., Xu, W., Liu, L., & Teng, G. (2022). Recent advances in methods for in situ root phenotyping. *PeerJ* , 10 , e13638.
- Liang, C., Wang, W., Wang, J., Ma, J., Li, C., Zhou, F., ... & Huang, X. (2017). Identification of differentially expressed genes in sunflower (*Helianthus annuus*) leaves and roots under drought stress by RNA sequencing. *Botanical studies* , 58 (1), 1-11.
- Liu, X., Li, R., Chang, X., & Jing, R. (2013). Mapping QTLs for seedling root traits in a doubled haploid wheat population under different water regimes. *Euphytica* , 189 (1), 51–66. <https://doi.org/10.1007/s10681-012-0690-4>
- Liu, Y., Li, P., Xu, G. C., Xiao, L., Ren, Z. P., & Li, Z. B. (2017). Growth, Morphological, and Physiological Responses to Drought Stress in *Bothriochloa ischaemum*. *Frontiers in Plant Science* , 8 , 230. <https://doi.org/10.3389/fpls.2017.00230>
- Liu, Q., Luo, L., & Zheng, L. (2018). Lignins: biosynthesis and biological functions in plants. *International journal of molecular sciences* , 19 (2), 335.
- Liu, J., Hasanuzzaman, M., Wen, H., Zhang, J., Peng, T., Sun, H., & Zhao, Q. (2019). High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice. *Protoplasma* , 256 (5), 1217-1227.
- Lombardi, E., Ferrio, J. P., Rodríguez-Robles, U., Resco de Dios, V., & Voltas, J. (2021). Ground-Penetrating Radar as phenotyping tool for characterizing intraspecific variability in root traits of a widespread conifer. *Plant and Soil* , 468 (1), 319-336.
- Lorenzo Cimadevila, H., Pérez Gracia, M. D. L. V., Novo, A., & Armesto, J. (2010). Forestry applications of ground-penetrating radar. *Forest Systems (formerly: Investigación agraria: sistemas y recursos forestales)* , 19 (1), 5-17.
- Lu, Y., Hao, Z., Xie, C., Crossa, J., Araus, J.-L., Gao, S., Vivek, B. S., Magorokosho, C., Mugo, S., Makumbi, D., Taba, S., Pan, G., Li, X., Rong, T., Zhang, S., & Xu, Y. (2011). Large-scale screening for maize drought resistance using multiple selection criteria evaluated under water-stressed and well-watered environments. *Field Crops Research* , 124 (1), 37–45. <https://doi.org/10.1016/j.fcr.2011.06.003>
- Luo, W., Xu, C., Ma, W., Yue, X., Liang, X., Zuo, X., ... & Han, X. (2018). Effects of extreme drought on plant nutrient uptake and resorption in rhizomatous vs bunchgrass-dominated grasslands. *Oecologia* , 188 (2), 633-643.
- Lynch, J. P. (2011). Root Phenotypes for Enhanced Soil Exploration and Phosphorus Acquisition: Tools for Future Crops. *Plant Physiology* , 156 (3), 1041–1049. <https://doi.org/10.1104/pp.111.175414>
- Lynch, J. (2013). Steep, cheap and deep: An ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* , 112 . <https://doi.org/10.1093/aob/mcs293>
- Lynch, J. P., Chimungu, J. G., & Brown, K. M. (2014). Root anatomical phenotypes associated with water acquisition from drying soil: Targets for crop improvement. *Journal of Experimental Botany* , 65 (21), 6155–6166. <https://doi.org/10.1093/jxb/eru162>
- Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R. D., Eissenstat, D. M., McCormack, M. L., & Hedin, L. O. (2018). Evolutionary history resolves global organization of root functional traits. *Nature* , 555 (7694), 94–97. <https://doi.org/10.1038/nature25783>
- Mace, E. S., Singh, V., Van Oosterom, E. J., Hammer, G. L., Hunt, C. H., & Jordan, D. R. (2012). QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. *Theoretical and Applied Genetics* , 124 (1), 97–109. <https://doi.org/10.1007/s00122-011-1690-9>

- Mahmood, T., Iqbal, M. S., Li, H., Nazir, M. F., Khalid, S., Sarfraz, Z., Hu, D., Baojun, C., Geng, X., Tajo, S. M., Dev, W., Iqbal, Z., Zhao, P., Hu, G., & Du, X. (2022). Differential seedling growth and tolerance indices reflect drought tolerance in cotton. *BMC Plant Biology* ,*22* (1), 1–11. <https://doi.org/10.1186/s12870-022-03724-4>
- Mahouachi, J. (2009). Changes in nutrient concentrations and leaf gas exchange parameters in banana plantlets under gradual soil moisture depletion. *Scientia Horticulturae* , *120* (4), 460–466. <https://doi.org/10.1016/j.scienta.2008.12.002>
- Malamy, J. E., & Benfey, P. N. (1997). Organization and cell differentiation in lateral roots of *Arabidopsis thaliana*. *Development* , *124* (1), 33–44.
- Manickavelu, A., Nadarajan, N., Ganesh, S. K., Gnanamalar, R. P., & Chandra Babu, R. (2006). Drought tolerance in rice: morphological and molecular genetic consideration. *Plant Growth Regulation* , *50* (2), 121–138.
- Manske, G. G., & Vlek, P. L. (2002). Root architecture—wheat as a model plant. In *Plant Roots* (pp. 410–426). CRC Press.
- Mansoor, U., Fatima, S., Hameed, M., Naseer, M., Ahmad, M. S. A., Ashraf, M., Ahmad, F., & Waseem, M. (2019). Structural modifications for drought tolerance in stem and leaves of *Cenchrus ciliaris* L. ecotypes from the Cholistan Desert. *Flora: Morphology, Distribution, Functional Ecology of Plants* , *261* , 151485. <https://doi.org/10.1016/j.flora.2019.151485>
- Manzi, Matías, Marta Pitarch-Bielsa, Vicent Arbona, and Aurelio Gómez-Cadenas. 2017. “Leaf Dehydration Is Needed to Induce Abscisic Acid Accumulation in Roots of Citrus Plants.” *Environmental and Experimental Botany* 139: 116–26. <https://www.sciencedirect.com/science/article/pii/S0098847217301089>.
- Maqbool, S., Hassan, M. A., Xia, X., York, L. M., Rasheed, A., & He, Z. (2022). Root system architecture in cereals: Progress, challenges and perspective. *Plant Journal* , *110* (1), 23–42. <https://doi.org/10.1111/tpj.15669>
- Marthandan, V., Geetha, R., Kumutha, K., Renganathan, V. G., Karthikeyan, A., & Ramalingam, J. (2020). Seed priming: A feasible strategy to enhance drought tolerance in crop plants. *International Journal of Molecular Sciences* , *21* (21), 1–23. <https://doi.org/10.3390/ijms21218258>
- Martinez, H. E., de Souza, B. P., Caixeta, E. T., de Carvalho, F. P., & Clemente, J. M. (2020). Water deficit changes nitrate uptake and expression of some nitrogen related genes in coffee-plants (*Coffea arabica* L.). *Scientia Horticulturae* , *267* , 109254.
- Metzner, R., van Dusschoten, D., Bühler, J., Schurr, U., & Jahnke, S. (2014). Belowground plant development measured with magnetic resonance imaging (MRI): exploiting the potential for non-invasive trait quantification using sugar beet as a proxy. *Frontiers in plant science* , *5* , 469.
- Mouliá, B., Coutand, C., & Lenne, C. (2006). Posture control and skeletal mechanical acclimation in terrestrial plants: Implications for mechanical modeling of plant architecture. *American Journal of Botany* , *93* (10), 1477–1489. <https://doi.org/10.3732/ajb.93.10.1477>
- Nadeem, M., Li, J., Yahya, M., Sher, A., Ma, C., Wang, X., & Qiu, L. (2019). Research Progress and Perspective on Drought Stress in Legumes: A Review. *International Journal of Molecular Sciences* ,*20* (10), 2541. <https://doi.org/10.3390/ijms20102541>
- Nonami, Hiroshi. 1998. “Plant Water Relations and Control of Cell Elongation at Low Water Potentials.” *Journal of Plant Research* 111(3): 373–82. <https://doi.org/10.1007/BF02507801>.
- Nosalewicz, A., Siecińska, J., Śmiech, M., Nosalewicz, M., Wiącek, D., Pecio, A., & Wach, D. (2016). Trans-generational effects of temporal drought stress on spring barley morphology and functioning. *Environmental and Experimental Botany* , *131* , 120–127.

- Ochatt, S. J. (2015). Agroecological impact of an in vitro biotechnology approach of embryo development and seed filling in legumes. *Agronomy for Sustainable Development* , 35 (2), 535–552. <https://doi.org/10.1007/s13593-014-0276-8>
- Ogura, T., Goeschl, C., Filiault, D., Mirea, M., Slovak, R., Wolhrab, B., Satbhai, S. B., & Busch, W. (2019). Root System Depth in Arabidopsis Is Shaped by EXOCYST70A3 via the Dynamic Modulation of Auxin Transport. *Cell* , 178 (2), 400–412.e16. <https://doi.org/10.1016/j.cell.2019.06.021>
- Okçu, G., Kaya, M. D., & Atak, M. (2005). Effects of salt and drought stresses on germination and seedling growth of pea (*Pisum sativum* L.). *Turkish journal of agriculture and forestry* , 29 (4), 237–242.
- Onyemaobi, O., Sangma, H., Garg, G., Wallace, X., Kleven, S., Suwanchaikasem, P., Roessner, U., & Dolferus, R. (2021). Reproductive stage drought tolerance in wheat: Importance of stomatal conductance and plant growth regulators. *Genes* , 12 (11). <https://doi.org/10.3390/genes12111742>
- Opitz, N., Marcon, C., Paschold, A., Malik, W. A., Lithio, A., Brandt, R., Piepho, H.-P., Nettleton, D., & Hochholdinger, F. (2016). Extensive tissue-specific transcriptomic plasticity in maize primary roots upon water deficit. *Journal of Experimental Botany* , 67 (4), 1095–1107. <https://doi.org/10.1093/jxb/erv453>
- Osakabe, Y., Arinaga, N., Umezawa, T., Katsura, S., Nagamachi, K., Tanaka, H., . . . & Yamaguchi-Shinozaki, K. (2013). Osmotic stress responses and plant growth controlled by potassium transporters in Arabidopsis. *The Plant Cell* , 25 (2), 609–624.
- Pace, P. F., Cralle, H. T., El-Halawany, S. H., Cothren, J. T., & Senseman, S. A. (1999). Drought-induced changes in shoot and root growth of young cotton plants. *J. Cotton Sci* , 3 (4), 183–187.
- Peng, Y., Lin, W., & Cai, W. (2007). *Overexpression of a Panax ginseng tonoplast aquaporin alters salt tolerance , drought tolerance and cold acclimation ability in transgenic Arabidopsis plants* . 729–740. <https://doi.org/10.1007/s00425-007-0520-4>
- Péret, B., Li, G., Zhao, J., Band, L. R., Voß, U., Postaire, O., . . . & Bennett, M. J. (2012). Auxin regulates aquaporin function to facilitate lateral root emergence. *Nature cell biology* , 14 (10), 991–998.
- Pflugfelder, D., Kochs, J., Koller, R., Jahnke, S., Mohl, C., Pariyar, S., . . . & van Dusschoten, D. (2022). The root system architecture of wheat establishing in soil is associated with varying elongation rates of seminal roots: quantification using 4D magnetic resonance imaging. *Journal of experimental botany* , 73 (7), 2050–2060.
- Pierik, R., & Testerink, C. (2014). *The Art of Being Flexible: How to Escape from Shade , Salt , and Drought 1 . 166* (September), 5–22. <https://doi.org/10.1104/pp.114.239160>
- Pockman, W. T., & Sperry, J. S. (2000). Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* , 87 (9), 1287–1299.
- Prasad, P. V. V., Pisipati, S. R., Ristic, Z., Bukovnik, U., & Fritz, A. K. (2008). Impact of Nighttime Temperature on Physiology and Growth of Spring Wheat. *Crop Science* , 48 (6), 2372–2380. <https://doi.org/10.2135/cropsci2007.12.0717>
- Prerostova, S., Dobrev, P. I., Gaudinova, A., Knirsch, V., Körber, N., Pieruschka, R., . . . & Vankova, R. (2018). Cytokinins: Their impact on molecular and growth responses to drought stress and recovery in Arabidopsis. *Frontiers in plant science* , 9 , 655.
- Priestley, D. A. (1986). *Seed aging: implications for seed storage and persistence in the soil* . Comstock Associates.
- Pushpavalli, R., Zaman-Allah, M., Turner, N. C., Baddam, R., Rao, M. V., & Vadez, V. (2014). Higher flower and seed number leads to higher yield under water stress conditions imposed during reproduction in chickpea. *Functional Plant Biology* , 42 (2), 162–174.

- Qi, J., Sun, S., Yang, L., Li, M., Ma, F., & Zou, Y. (2019). Potassium uptake and transport in apple roots under drought stress. *Horticultural plant journal* , 5 (1), 10-16.
- Qi, F., & Zhang, F. (2020). Cell Cycle Regulation in the Plant Response to Stress. *Frontiers in Plant Science* , 10 . <https://www.frontiersin.org/articles/10.3389/fpls.2019.01765>
- Quan, R., Shang, M., Zhang, H., Zhao, Y., & Zhang, J. (2004). Engineering of enhanced glycine betaine synthesis improves drought tolerance in maize. *Plant Biotechnology Journal* , 2 (6), 477-486.
- Raja, V., Qadir, S. U., Alyemini, M. N., & Ahmad, P. (2020). Impact of drought and heat stress individually and in combination on physio-biochemical parameters, antioxidant responses, and gene expression in *Solanum lycopersicum*. *3 Biotech* , 10 (5), 208. <https://doi.org/10.1007/s13205-020-02206-4>
- Ramachandran, P., Wang, G., Augstein, F., de Vries, J., & Carlsbecker, A. (2018). Continuous root xylem formation and vascular acclimation to water deficit involves endodermal ABA signalling via miR165. *Development* , 145 (3), dev159202.
- Ranjan, A., Sinha, R., Singla-Pareek, S. L., Pareek, A., & Singh, A. K. (2022). Shaping the root system architecture in plants for adaptation to drought stress. *Physiologia Plantarum* , 174 (2), e13651. <https://doi.org/10.1111/ppl.13651>
- Rehman, T., Tabassum, B., Yousaf, S., Sarwar, G., & Qaisar, U. (2022). Consequences of drought stress encountered during seedling stage on physiology and yield of cultivated cotton. *Frontiers in Plant Science* , 13 .
- Rewald, B., Ephrath, J. E., & Rachmilevitch, S. (2011). A root is a root is a root? Water uptake rates of Citrus root orders. *Plant, Cell & Environment* , 34 (1), 33–42. <https://doi.org/10.1111/j.1365-3040.2010.02223.x>
- Richards, R. A., & Passioura, J. B. (1989). A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. *Australian Journal of Agricultural Research* , 40 (5), 943-950.
- Rogers, H. H., & Bottomley, P. A. (1962). In situ nuclear magnetic resonance imaging of roots: influence of soil type, ferromagnetic particle content, and soil water 1. *Agronomy Journal* , 79 (6), 957-965.
- Robbins, N. E., & Dinney, J. R. (2018). Growth is required for perception of water availability to pattern root branches in plants. *Proceedings of the National Academy of Sciences of the United States of America* , 115 (4), E822–E831. <https://doi.org/10.1073/pnas.1710709115>
- Roche, J., Hewezi, T., Bouniols, A., & Gentzbittel, L. (2007). Transcriptional profiles of primary metabolism and signal transduction-related genes in response to water stress in field-grown sunflower genotypes using a thematic cDNA microarray. *Planta* , 226 (3), 601-617.
- Ronde, J. A., Cress, W. A., Krüger, G. H. J., Strasser, R. J., & Van Staden, J. (2004). Photosynthetic response of transgenic soybean plants, containing an Arabidopsis P5CR gene, during heat and drought stress. *Journal of plant physiology* , 161 (11), 1211-1224.
- Roohi, E., Tahmasebi Sarvestani, Z., Modarres-Sanavy, S. a. M., & Siosemardeh, A. (2013). Comparative Study on the Effect of Soil Water Stress on Photosynthetic Function of Triticale, Bread Wheat, and Barley. *Journal of Agricultural Science and Technology* , 15 (2), 215–225.
- Rowse, H. R., & Goodman, D. (1981). Axial Resistance to Water Movement in Broad Bean (*Vicia faba*) Roots. *Journal of Experimental Botany* , 32 (3), 591–598. <https://doi.org/10.1093/jxb/32.3.591>
- Sah, R. P., Chakraborty, M., Prasad, K., Pandit, M., Tudu, V. K., Chakravarty, M. K., Narayan, S. C., Rana, M., & Moharana, D. (2020). Impact of water deficit stress in maize: Phenology and yield components. *Scientific Reports* , 10 (1), Article 1. <https://doi.org/10.1038/s41598-020-59689-7>

- Samarah, N., Mullen, R., & Cianzio, S. (2004). Size Distribution and Mineral Nutrients of Soybean Seeds in Response to Drought Stress. *Journal of Plant Nutrition* , 27 (5), 815–835. <https://doi.org/10.1081/PLN-120030673>
- Sandhu, N., Raman, K. A., Torres, R. O., Audebert, A., Dardou, A., Kumar, A., & Henry, A. (2016). Rice Root Architectural Plasticity Traits and Genetic Regions for Adaptability to Variable Cultivation and Stress Conditions. *Plant Physiology* , 171 (4), 2562–2576. <https://doi.org/10.1104/pp.16.00705>
- Schneider, H. M., Wojciechowski, T., Postma, J. A., Brown, K. M., Lücke, A., Zeisler, V., Schreiber, L., & Lynch, J. P. (2017). Root cortical senescence decreases root respiration, nutrient content and radial water and nutrient transport in barley. *Plant, Cell & Environment* , 40 (8), 1392–1408. <https://doi.org/10.1111/pce.12933>
- Segal, E., Kushnir, T., Mualem, Y., & Shani, U. (2008). Water uptake and hydraulics of the root hair rhizosphere. *Vadose Zone Journal* , 7 (3), 1027–1034.
- Segura, F., Vicente, M. J., Franco, J. A., & Martínez-Sánchez, J. J. (2015). Effects of maternal environmental factors on physical dormancy of *Astragalus nitidiflorus* seeds (Fabaceae), a critically endangered species of SE Spain. *Flora - Morphology, Distribution, Functional Ecology of Plants* , 216 , 71–76. <https://doi.org/10.1016/j.flora.2015.09.001>
- Seghatoleslami, M. J., Kafi, M., & Majidi, E. (2008). Effect of drought stress at different growth stages on yield and water use efficiency of five proso millet (*Panicum miliaceum* L.) genotypes. *Pak. J. Bot* , 40 (4), 1427–1432.
- Sehgal, A., Sita, K., Kumar, J., Kumar, S., Singh, S., Siddique, K. H. M., & Nayyar, H. (2017). Effects of Drought, Heat and Their Interaction on the Growth, Yield and Photosynthetic Function of Lentil (*Lens culinaris* Medikus) Genotypes Varying in Heat and Drought Sensitivity. *Frontiers in Plant Science* , 8 , 1776. <https://doi.org/10.3389/fpls.2017.01776>
- Sehgal, A., Sita, K., Siddique, K. H. M., Kumar, R., Bhogireddy, S., Varshney, R. K., HanumanthaRao, B., Nair, R. M., Prasad, P. V. V., & Nayyar, H. (2018). Drought or/and heat-stress effects on seed filling in food crops: Impacts on functional biochemistry, seed yields, and nutritional quality. *Frontiers in Plant Science* , 871 (November), 1–19. <https://doi.org/10.3389/fpls.2018.01705>
- Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H. H., & Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* , 10 (2), 1–25. <https://doi.org/10.3390/plants10020259>
- Sengupta, D., Kannan, M., & Reddy, A. R. (2011). A root proteomics-based insight reveals dynamic regulation of root proteins under progressive drought stress and recovery in *Vigna radiata* (L.) Wilczek. *Planta* , 233 (6), 1111–1127. <https://doi.org/10.1007/s00425-011-1365-4>
- Serraj, R. (2003). Effects of drought stress on legume symbiotic nitrogen fixation: physiological mechanisms.
- Sevanto, S. (2014). Phloem transport and drought. *Journal of Experimental Botany* , 65 (7), 1751–1759. <https://doi.org/10.1093/jxb/ert467>
- Shan, H., Chen, S., Jiang, J., Chen, F., Chen, Y., Gu, C., . . . & Yang, X. (2012). Heterologous expression of the chrysanthemum R2R3-MYB transcription factor CmMYB2 enhances drought and salinity tolerance, increases hypersensitivity to ABA and delays flowering in *Arabidopsis thaliana*. *Molecular biotechnology* , 51 (2), 160–173.
- Sharma, S.; Carena, M.J. BRACE: A Method for High Throughput Maize Phenotyping of Root Traits for Short-Season Drought Tolerance. *Crop Sci.* 2016 , 56, 2996–3004. [CrossRef]
- Sharma, A., Shahzad, B., Kumar, V., Kohli, S. K., Sidhu, G. P. S., Bali, A. S., Handa, N., Kapoor, D., Bhardwaj, R., & Zheng, B. (2019). Phytohormones Regulate Accumulation of Osmolytes Under Abiotic

Stress. *Biomolecules* , 9 (7), Article 7. <https://doi.org/10.3390/biom9070285>

Sharma, N. K., Gupta, S. K., Dwivedi, V., & Chattopadhyay, D. (2020). Lignin deposition in chickpea root xylem under drought. *Plant Signaling & Behavior* , 15 (6), 1754621.

Sheoran, S., Kaur, Y., Kumar, S., Shukla, S., Rakshit, S., & Kumar, R. (2022). Recent Advances for Drought Stress Tolerance in Maize (*Zea mays* L.): Present Status and Future Prospects. *Frontiers in Plant Science* , 13 , 872566. <https://doi.org/10.3389/fpls.2022.872566>

Shinozaki, Kazuo, and Kazuko Yamaguchi-Shinozaki. 2007. “Gene Networks Involved in Drought Stress Response and Tolerance.” *Journal of Experimental Botany* 58(2): 221–27. <https://doi.org/10.1093/jxb/erl164>.

Singh, V., van Oosterom, E. J., Jordan, D. R., Messina, C. D., Cooper, M., & Hammer, G. L. (2010). Morphological and architectural development of root systems in sorghum and maize. *Plant and Soil* , 333 (1–2), 287–299. <https://doi.org/10.1007/s11104-010-0343-0>

Singh, B., Norvell, E., Wijewardana, C., Wallace, T., Chastain, D., & Reddy, K. R. (2018). Assessing morphological characteristics of elite cotton lines from different breeding programmes for low temperature and drought tolerance. *Journal of Agronomy and Crop Science* , 204 (5), 467–476. <https://doi.org/10.1111/jac.12276>

Sita, K., Sehgal, A., Kumar, J., Kumar, S., Singh, S., Siddique, K. H. M., & Nayyar, H. (2017). Identification of High-Temperature Tolerant Lentil (*Lens culinaris* Medik.) Genotypes through Leaf and Pollen Traits. *Frontiers in Plant Science* , 8 , 744. <https://doi.org/10.3389/fpls.2017.00744>

Smiciklas, K. d., Mullen, R. e., Carlson, R. e., & Knapp, A. d. (1992). Soybean Seed Quality Response to Drought Stress and Pod Position. *Agronomy Journal* , 84 (2), 166–170. <https://doi.org/10.2134/agronj1992.00021962008400020008x>

Smit, A. L., George, E., & Groenwold, J. (2000). Root observations and measurements at (transparent) interfaces with soil. In *Root methods* (pp. 235–271). Springer, Berlin, Heidelberg.

Smith, S., & De Smet, I. (2012). Root system architecture: Insights from *Arabidopsis* and cereal crops. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 367 (1595), 1441–1452. <https://doi.org/10.1098/rstb.2011.0234>

Sperry, J. S., & Saliendra, N. Z. (1994). Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell & Environment* , 17 (11), 1233–1241. <https://doi.org/10.1111/j.1365-3040.1994.tb02021.x>

Sperry, J., Stiller, V., & Hacke, U. (2003). Xylem Hydraulics and the Soil–Plant–Atmosphere Continuum. *Agronomy Journal - AGRON J* , 95 . <https://doi.org/10.2134/agronj2003.1362>

Sperry, J. (2011). *Hydraulics of Vascular Water Transport* (Vol. 9, pp. 303–327). https://doi.org/10.1007/978-3-642-19091-9_12

Srayeddin, I., & Doussan, C. (2009). Estimation of the spatial variability of root water uptake of maize and sorghum at the field scale by electrical resistivity tomography. *Plant and soil* , 319 (1), 185–207.

Sun, L., Song, L., Zhang, Y., Zheng, Z., & Liu, D. (2016). *Arabidopsis* PHL2 and PHR1 Act Redundantly as the Key Components of the Central Regulatory System Controlling Transcriptional Responses to Phosphate Starvation. *Plant Physiology* , 170 (1), 499–514. <https://doi.org/10.1104/pp.15.01336>

Suseela, V., Tharayil, N., Orr, G., & Hu, D. (2020). Chemical plasticity in the fine root construct of *Quercus* spp. Varies with root order and drought. *New Phytologist* , 228 (6), 1835–1851. <https://doi.org/10.1111/nph.16841>

Suzuki, N., Taketa, S., & Ichii, M. (2003). Morphological and physiological characteristics of a root-hairless mutant in rice (*Oryza sativa* L.). *Plant and Soil* , 255 (1), 9–17.

- Swarup, R., Kramer, E. M., Perry, P., Knox, K., Leyser, H. M. O., Haseloff, J., Beemster, G. T. S., Bhalerao, R., & Bennett, M. J. (2005). Root gravitropism requires lateral root cap and epidermal cells for transport and response to a mobile auxin signal. *Nature Cell Biology* , 7 (11), 1057–1065. <https://doi.org/10.1038/ncb1316>
- Takahashi, F., Suzuki, T., Osakabe, Y., Betsuyaku, S., Kondo, Y., Dohmae, N., Fukuda, H., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* , 556 (7700), 235–238. <https://doi.org/10.1038/s41586-018-0009-2>
- Takahashi, F., & Shinozaki, K. (2019). Long-distance signaling in plant stress response. *Current opinion in plant biology* , 47 , 106–111.
- Takahashi, F., Kuromori, T., Urano, K., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2020). Drought stress responses and resistance in plants: From cellular responses to long-distance intercellular communication. *Frontiers in plant science* , 11 , 556972.
- Tanaka-Takada, N., Kobayashi, A., Takahashi, H., Kamiya, T., Kinoshita, T., & Maeshima, M. (2019). Plasma membrane-associated Ca²⁺-binding protein PCaP1 is involved in root hydrotropism of Arabidopsis thaliana. *Plant and Cell Physiology* , 60 (6), 1331–1341.
- Tardieu, F., Simonneau, T., & Muller, B. (2018). The Physiological Basis of Drought Tolerance in Crop Plants: A Scenario-Dependent Probabilistic Approach. *Annual Review of Plant Biology* , 69 , 733–759. <https://doi.org/10.1146/annurev-arplant-042817-040218>
- Tariq, A., Pan, K., Olatunji, O. A., Graciano, C., Li, Z., Sun, F., Sun, X., Song, D., Chen, W., Zhang, A., Wu, X., Zhang, L., Mingrui, D., Xiong, Q., & Liu, C. (2017). Phosphorous Application Improves Drought Tolerance of Phoebe zhenan. *Frontiers in Plant Science* , 8 . <https://www.frontiersin.org/articles/10.3389/fpls.2017.01561>
- Thakur, P., Kumar, S., Malik, J. A., Berger, J. D., & Nayyar, H. (2010). Cold stress effects on reproductive development in grain crops: An overview. *Environmental and Experimental Botany* , 67 (3), 429–443. <https://doi.org/10.1016/j.envexpbot.2009.09.004>
- Tiwari, P., Srivastava, D., Chauhan, A. S., Indoliya, Y., Singh, P. K., Tiwari, S., Fatima, T., Mishra, S. K., Dwivedi, S., Agarwal, L., Singh, P. C., Asif, M. H., Tripathi, R. D., Shirke, P. A., Chakrabarty, D., Chauhan, P. S., & Nautiyal, C. S. (2021). Root system architecture, physiological analysis and dynamic transcriptomics unravel the drought-responsive traits in rice genotypes. *Ecotoxicology and Environmental Safety* , 207 , 111252. <https://doi.org/10.1016/j.ecoenv.2020.111252>
- Tran, T. T., Kano-Nakata, M., Takeda, M., Menge, D., Mitsuya, S., Inukai, Y., & Yamauchi, A. (2014). Nitrogen application enhanced the expression of developmental plasticity of root systems triggered by mild drought stress in rice. *Plant and Soil* , 378 (1), 139–152. <https://doi.org/10.1007/s11104-013-2013-5>
- Turner, I. M. (1994). Sclerophylly: Primarily protective? *Functional Ecology* , 8 , 669–675.
- Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, H., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J., Matsumoto, T., Takai, T., Okuno, K., & Yano, M. (2013). Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. *Nature Genetics* , 45 (9), Article 9. <https://doi.org/10.1038/ng.2725>
- Ullah, A., Tian, Z., Xu, L., Abid, M., Lei, K., Khanzada, A., Zeeshan, M., Sun, C., Yu, J., & Dai, T. (2022). Improving the effects of drought priming against post-anthesis drought stress in wheat (*Triticum aestivum* L.) using nitrogen. *Frontiers in Plant Science* , 13 (August), 1–17. <https://doi.org/10.3389/fpls.2022.965996>
- Varshney, R. K., Barmukh, R., Roorkiwal, M., Qi, Y., Kholova, J., Tuberosa, R., Reynolds, M. P., Tardieu, F., & Siddique, K. H. M. (2021). Breeding custom-designed crops for improved drought adaptation. *Advanced Genetics* , 2 (3), 1–15. <https://doi.org/10.1002/ggn2.202100017>

Vejchasarn, P., Lynch, J. P., & Brown, K. M. (2016). Genetic Variability in Phosphorus Responses of Rice Root Phenotypes. *Rice* , 9 (1), 29. <https://doi.org/10.1186/s12284-016-0102-9>

Vendramini, F., Diaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K., & Hodgson, J. G. (2002). Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* , 154 (1), 147–157. <https://doi.org/10.1046/j.1469-8137.2002.00357.x>

Venugopalan, V. K., Nath, R., Sengupta, K., Nalia, A., Banerjee, S., Chandran, M. A. S., Ibrahimova, U., Dessoky, E. S., Attia, A. O., Hassan, M. M., & Hossain, A. (2021). The Response of Lentil (*Lens culinaris* Medik.) to Soil Moisture and Heat Stress Under Different Dates of Sowing and Foliar Application of Micronutrients. *Frontiers in Plant Science* , 12 , 679469. <https://doi.org/10.3389/fpls.2021.679469>

Vierstra, Richard D. 2009. “The Ubiquitin–26S Proteasome System at the Nexus of Plant Biology.” *Nature Reviews Molecular Cell Biology* 10(6): 385–97. <https://doi.org/10.1038/nrm2688>.

Vivek, B. S., Krishna, G. K., Vengadessan, V., Babu, R., Zaidi, P. H., Kha, L. Q., Mandal, S. S., Grudloyma, P., Takalkar, S., Krothapalli, K., Singh, I. S., Ocampo, E. T. M., Xingming, F., Burgueno, J., Azrai, M., Singh, R. P., & Crossa, J. (2017). Use of Genomic Estimated Breeding Values Results in Rapid Genetic Gains for Drought Tolerance in Maize. *The Plant Genome* , 10 (1). <https://doi.org/10.3835/plantgenome2016.07.0070>

Wang, X., Vignjevic, M., Jiang, D., Jacobsen, S., & Wollenweber, B. (2014). Improved tolerance to drought stress after anthesis due to priming before anthesis in wheat (*Triticum aestivum* L.) var. Vinjett. *Journal of Experimental Botany* , 65 (22), 6441–6456. <https://doi.org/10.1093/jxb/eru362>

Wang, X., Vignjevic, M., Liu, F., Jacobsen, S., Jiang, D., & Wollenweber, B. (2015). Drought priming at vegetative growth stages improves tolerance to drought and heat stresses occurring during grain filling in spring wheat. *Plant Growth Regulation* , 75 (3), 677–687. <https://doi.org/10.1007/s10725-014-9969-x>

Wang, L. Q., Li, Z., Wen, S. S., Wang, J. N., Zhao, S. T., & Lu, M. Z. (2020). WUSCHEL-related homeobox gene PagWOX11/12a responds to drought stress by enhancing root elongation and biomass growth in poplar. *Journal of Experimental Botany* , 71 (4), 1503–1513.

Wasaya, A., Zhang, X., Fang, Q., & Yan, Z. (2018). *Root Phenotyping for Drought Tolerance: A Review* . 1–19. <https://doi.org/10.3390/agronomy8110241>

Wasson, A. P., Richards, R. A., Chatrath, R., Misra, S. C., Prasad, S. V. S., Rebetzke, G. J., Kirkegaard, J. A., Christopher, J., & Watt, M. (2012). Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *Journal of Experimental Botany* , 63 (9), 3485–3498. <https://doi.org/10.1093/jxb/ers111>

Weinhold, L. Histogenetische Studien zum Grenzwurzelproblem. *Beitr. Biol. Pfl.* **1967** , 43, 367–454.

Wery, J et al. 1993. “Screening Techniques and Sources of Tolerance to Extremes of Moisture and Air Temperature in Cool Season Food Legumes.” *Euphytica* 73(1): 73–83. <https://doi.org/10.1007/BF00027184>.

Wu, Y., Guo, L., Cui, X., Chen, J., Cao, X., & Lin, H. (2014). Ground-penetrating radar-based automatic reconstruction of three-dimensional coarse root system architecture. *Plant and soil* , 383 (1), 155–172.

Xu, C., Fu, X., Liu, R., Guo, L., Ran, L., Li, C., . . . & Luo, K. (2017). PtoMYB170 positively regulates lignin deposition during wood formation in poplar and confers drought tolerance in transgenic Arabidopsis. *Tree physiology* , 37 (12), 1713–1726.

Xu, Q., Chen, S., Yunjuan, R., Chen, S., & Liesche, J. (2018). Regulation of Sucrose Transporters and Phloem Loading in Response to Environmental Cues. *Plant Physiology* , 176 (1), 930–945. <https://doi.org/10.1104/pp.17.01088>

Xu, W., Tang, W., Wang, C., Ge, L., Sun, J., Qi, X., . . . & Chen, M. (2020). SiMYB56 confers drought stress tolerance in transgenic rice by regulating lignin biosynthesis and ABA signaling pathway. *Frontiers in*

plant science , 11 , 785.

Xue, L.-J., Frost, C. J., Tsai, C.-J., & Harding, S. A. (2016). Drought response transcriptomes are altered in poplar with reduced tonoplast sucrose transporter expression. *Scientific Reports* , 6 (1), Article 1. <https://doi.org/10.1038/srep33655>

Yadav, G. S., Devi, A. G., Das, A., Kandpal, B., Babu, S., Das, R. C., & Nath, M. (2019). Foliar application of urea and potassium chloride minimizes terminal moisture stress in lentil (*Lens culinaris* L.) crop. *LEGUME RESEARCH-AN INTERNATIONAL JOURNAL* , of . <https://doi.org/10.18805/LR-4148>

Yang, J. C., Zhang, J. H., Wang, Z. Q., Zhu, Q. S., & Liu, L. J. (2003). Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. *Plant, Cell & Environment* , 26 (10), 1621–1631. <https://doi.org/10.1046/j.1365-3040.2003.01081.x>

Yang, J., & Zhang, J. (2006). Grain filling of cereals under soil drying. *New Phytologist* , 169 (2), 223–236. <https://doi.org/10.1111/j.1469-8137.2005.01597.x>

Yang, X., Li, Y., Ren, B., Ding, L., Gao, C., Shen, Q., & Guo, S. (2012). Drought-induced root aerenchyma formation restricts water uptake in rice seedlings supplied with nitrate. *Plant & Cell Physiology* , 53 (3), 495–504. <https://doi.org/10.1093/pcp/pcs003>

Yang, Y., Guo, Y., Zhong, J., Zhang, T., Li, D., Ba, T., Xu, T., Chang, L., Zhang, Q., & Sun, M. (2020). Root Physiological Traits and Transcriptome Analyses Reveal that Root Zone Water Retention Confers Drought Tolerance to *Opisthospappus taihangensis*. *Scientific Reports* , 10 (1), 2627. <https://doi.org/10.1038/s41598-020-59399-0>

Yavas, I., & Unay, A. (2016). Effects of zinc and salicylic acid on wheat under drought stress. *Journal of Animal and Plant Sciences* , 26 (4), 1012–1018.

Ye, H., Roorkiwal, M., Valliyodan, B., Zhou, L., Chen, P., Varshney, R. K., & Nguyen, H. T. (2018). Genetic diversity of root system architecture in response to drought stress in grain legumes. *Journal of Experimental Botany* , 69 (13), 3267–3277. <https://doi.org/10.1093/jxb/ery082>

Yu, X.-C., Zhu, S.-Y., Gao, G.-F., Wang, X.-J., Zhao, R., Zou, K.-Q., Wang, X.-F., Zhang, X.-Y., Wu, F.-Q., Peng, C.-C., & Zhang, D.-P. (2007). Expression of a grape calcium-dependent protein kinase ACPK1 in *Arabidopsis thaliana* promotes plant growth and confers abscisic acid-hypersensitivity in germination, postgermination growth, and stomatal movement. *Plant Molecular Biology* , 64 (5), 531–538. <https://doi.org/10.1007/s11103-007-9172-9>

Yu, P., Gutjahr, C., Li, C., & Hochholdinger, F. (2016). Genetic control of lateral root formation in cereals. *Trends in plant science* , 21 (11), 951–961.

Zare, M., Nejad, M. G., & Bazrafshan, F. (2012). Influence of drought stress on some traits in five mung bean (*Vigna radiata* (L.) R. Wilczek) genotypes. *International Journal of Agronomy and Plant Production* , 3 (7), 234–240.

Zeid, I. M., & Shedeed, Z. A. (2006). Response of alfalfa to putrescine treatment under drought stress. *Biologia plantarum* , 50 (4), 635–640.

Zhang, G. H., Su, Q., An, L. J., & Wu, S. (2008). Characterization and expression of a vacuolar Na⁺/H⁺ antiporter gene from the monocot halophyte *Aeluropus littoralis*. *Plant Physiology and Biochemistry* , 46 (2), 117–126.

Zhang, X., Derival, M., Albrecht, U., & Ampatzidis, Y. (2019). Evaluation of a ground penetrating radar to map the root architecture of HLB-infected citrus trees. *Agronomy* , 9 (7), 354.

Zhang, Q., Yuan, W., Wang, Q., Cao, Y., Xu, F., Dodd, I. C., & Xu, W. (2022). ABA regulation of root growth during soil drying and recovery can involve auxin response. *Plant, Cell & Environment* , 45 (3),

871-883.

Zhao, P., Hou, S., Guo, X., Jia, J., Yang, W., Liu, Z., . . . & Cheng, L. (2019). A MYB-related transcription factor from sheepgrass, LcMYB2, promotes seed germination and root growth under drought stress. *BMC plant biology* , 19 (1), 1-15.

Zhou, G., Zhou, X., Zhou, L., Shao, J., Fu, Y., Nie, Y., Hosseini, S., Cheng, W., Wang, J., & Hu, F. (2018). *Drought - induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials* . October 2017 , 2589–2599. <https://doi.org/10.1111/pce.13356>

Zhu, Jian-Kang. 2002. “SALT AND DROUGHT STRESS SIGNAL TRANSDUCTION IN PLANTS.” *Annual Review of Plant Biology* 53(1): 247–73. <https://doi.org/10.1146/annurev.arplant.53.091401.143329>.

Zhu, J., Kaeppeler, S. M., & Lynch, J. P. (2005). Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theoretical and Applied Genetics* , 111 (4), 688-695.

Zhu, J., Brown, K. M., & Lynch, J. P. (2010). Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant, Cell & Environment* , 33 (5), 740–749. <https://doi.org/10.1111/j.1365-3040.2009.02099.x>