Root Anatomical and Structural Responses to Drought

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In response to drought, roots adjust their traits, improving plant adaptation, survival, and yield. Among these traits, root system architecture (RSA) is essential in increasing water uptake, therefore, much of the research has focused on understanding RSA. Phenotyping systems, such as X-ray computed tomography, magnetic resonance imaging, ground-penetrating radar, shovelomics, rhizotrons, and transparent soils, were developed to study RSA. These phenotyping systems identified several root architectural traits that increased water uptake and drought resistance and were utilized in developing drought-resilient plants. Plants also invest a large portion of their photosynthetic carbon (C) as exudates to build root–microbe symbiosis for drought adaptation. Roots adapt their structure in response to drought to increase penetration, distribution, and contact with the soil for improved water and nutrient uptake. These structural adaptations ensure necessary nutrition and water acquisition, maintaining plant physiological activities and productivity during drought. Roots also adapt their anatomical characteristics in response to drought. Roots increase penetration in soil, reduce metabolic cost, regulate hydraulic conductivity, and facilitate microbial symbiosis to increase resource acquisition.

Keywords: drought resilience ; root exudates ; root hydraulics

1. Roots’ Structural Response to Drought

Several studies which reported correlations between root structural traits and plant performance under drought are summarized and presented in **Table 1** and **Figure 1**a,b. Identifying these drought-responsive structural traits in different crops will facilitate plant breeders to utilize these traits for screening drought tolerant genotypes.

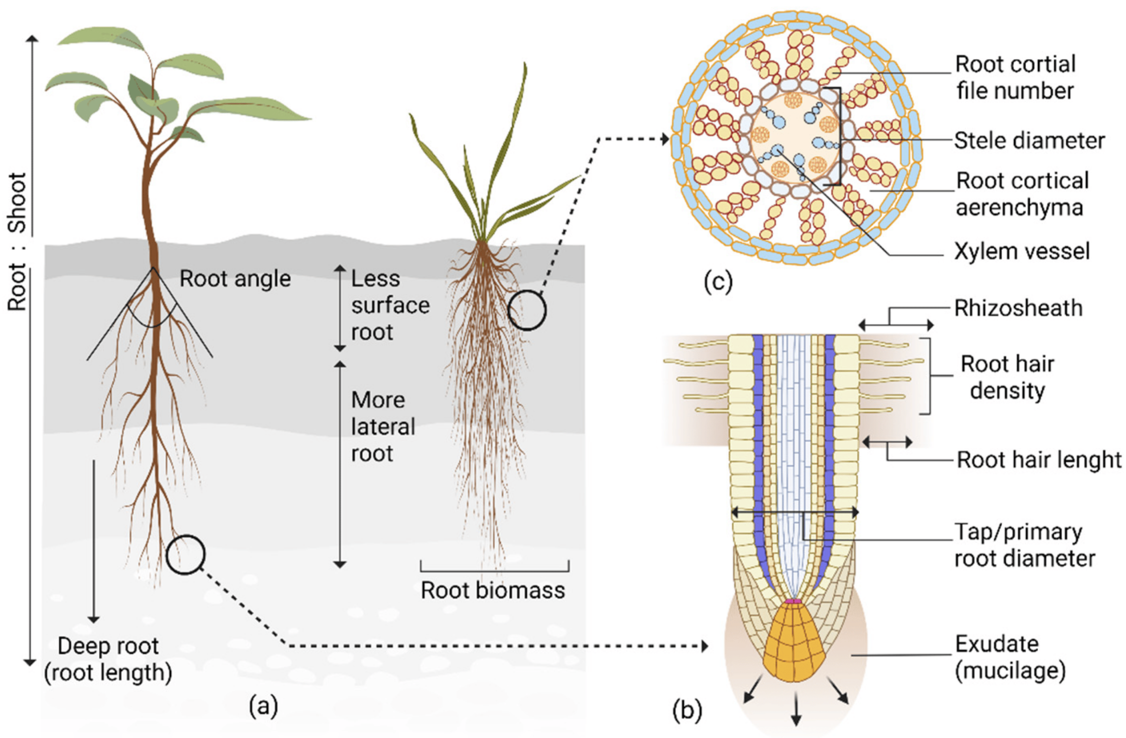

Figure 1. Drought adaptive root traits. (**a**) Changes in root angle, length, and biomass; the ratio with the shoot, and increased lateral branching facilitate plant adaptation to drought; (**b**) Root hair length and density, rhizosheath size, taproot diameter, and exudates are crucial drought-responsive traits. (**c**) Plants adapt their anatomical traits such as root cortical file number, cortical aerenchyma, stele diameter, and xylem vessel in response to drought.

Table 1. Root structural traits and their adaptive response to drought.

Structural Root Traits	Drought Adaptive Responses	Crop	Reference
Taproot diameter	Large taproot diameter genotypes had increased yield and drought resistance.	White clover (*Trifolium repens* L.), Soybean (*Glycine max* L.), Chickpea (*Cicer arietinum* L.)	Caradus and Woodfield [1], Fenta et al. [2], Rabbi et al. [3]
Taproot length	Long taproot genotypes yielded higher.	Soybean (*Glycine max* L.)	Jumrani and Bhatia [4]
Root hair	Reduced root hair genotype had lower water absorption and decreased drought resistance.	Arabidopsis (*Arabidopsis thaliana* L.)	Tanaka et al. [5]
Root hair production time	Drought-resistant genotypes had faster root hair production.	Barley (*Hordeum vulgare* L.)	Carter et al. [6]
Root hair length and number	Longer and higher root hair genotypes had less negative leaf water potential and improved water status under drought.	Barley (*Hordeum vulgare* L.)	Marin et al. [7]
Rhizosheath size	Large rhizosheath genotypes were drought resistant. Longer and denser root hairs contributed to larger rhizosheath formation.	Barley (*Hordeum vulgare* L.), Lotus (*Lotus japonicus* L.), and Maize (*Zea mays* L.)	Liu et al. [8], Rabbi et al. [3].
Root growth angle and rooting depth	Narrow root angles had downward root growth resulting in deep rooting and better yield under drought.	Rice (*Oryza sativa* L.), Soybean (*Glycine max* L.)	Uga et al. [9], Gobu et al. [10], Fenta et al. [2]
Seminal and nodal root angle	Steeper seminal and nodal root angle genotypes had a higher yield.	Maize (*Zea mays* L.)	Ali et al. [11]
Tap and lateral root branching intensity	Drought-resistance genotypes had more tap and lateral root branches.	Soybean *Glycine max* L.)	Fenta et al. [2]
Number of crown root	Low crown root number genotypes had better water status and yield.	Maize (*Zea mays* L.)	Gao and Lynch [12]
Quantity of fine-diameter roots	Drought-resistant genotypes had substantial amounts of small-diameter roots in deep soil.	Wheat (*Triticum aestivum*)	Becker et al. [13]
Lateral root branching density	Genotypes with fewer but longer lateral roots had better water status, biomass, and yield.	Maize (*Zea mays* L.)	Zhan et al. [14]
Root length, branching rate and surface area	Drought-resistant genotypes had increased root length, branching rate, larger root surface, and decreased coarse to fine root ratio.	Oat (*Avena sativa* L.)	Canales et al. [15]
Root volume and dry matter	Drought-resistant genotypes had larger root volumes and more root dry weight.	Sorghum (*Sorghum bicolor* L. Moench)	Kiran et al. [16]

Root drought-responsive structural traits are not static but fluctuate readily in conjunction with the environment, management practice, soil microbes, and genotype. Moreover, different root traits interact, sometimes synergistically or antagonistically, affecting drought adaptation. Thus, careful consideration is needed when planning drought-resistant crops based on structural traits only. However, crop-specific drought-responsive structural traits (**Table 1**) are easy to phenotype and implement for screening genotypes. Therefore, it has importance in terms of ease of applicability and achieving fast results in developing drought-resistant crops.

2. Root Anatomical Responses to Drought

2.1. Anatomical Adaptation in Reducing Metabolic Cost

Plants invest photosynthates in establishing root systems for exploring water and nutrients needed for metabolic processes. During drought, the expenditure of photosynthates is high, firstly to invest more in root growth to increase water uptake, and secondly to increase respiration to maintain roots in drying soil, thus, compromising plant productivity [8][10]. Anatomical adaptation during drought reduces metabolic costs and allows plants to distribute resources for further resource acquisition, growth, and essential physiological activities, resulting in improved yield. Chimungu et al. [11] reported cortical tissue with fewer but larger cell sizes, and low cortical cell file numbers in maize reduced metabolic cost by decreasing respiration rates during drought. Large cortical genotypes had increased root growth and water acquisition, deeper roots, better stomatal conductance and leaf CO_2 assimilation, and greater shoot biomass and grain yield. Colombi et al. [8] reported a similar result in wheat, where a genotype with a large root cortical cell diameter significantly reduced root penetration metabolic cost. During drought, root cortical tissue lysed and creates an intercellular vacuum space, cortical aerenchyma [15] (**Figure 1**c), the formation of which can reduce metabolic costs. This mostly occurs in older roots that no longer take up water efficiently [15], thus having minimal negative impact on water uptake. Instead, it reduces soil exploration metabolic costs [10][17], permits root growth, and improves soil resource acquisition in dry conditions [10]. Under water stress, maize genotypes with high root cortical aerenchyma had 30% more shoot biomass [18].

2.2. Anatomical Response Improving Root Penetration

Water deficit in the soil increases mechanical impedance, thus restricting root penetration into deep soil, which hinders resource capture, consequently reducing crop productivity [19]. Anatomical adaptation facilitates improving root penetration in drying soil. For example, smaller outer cortical cells stabilize the root against ovalization, prevent collapsing, and allow the root to penetrate soil. In contrast, large mesodermis cortical cells and thick axial roots with more aerenchyma reduce the metabolic cost of soil exploration and allow root growth in hard soils [20]. In deep rooting maize genotypes, the roots generated from node three had a reduced cell file number and increased middle cortical area; while the roots generated from node four had increased aerenchyma [17]. Maize and wheat genotypes with multiseriate cortical sclerenchyma had a 22% increase in deep soil penetration and a 49% increase in shoot biomass compared to genotypes that lacked it [7]. These genotypes also had small cells with thick walls in outer cortical tissue, increased root lignin concentration, tensile strength, and root tip bending force.

2.3. Anatomical Attributes Facilitating Microbial Symbiosis

Roots absorb water and nutrients through the root epidermis, hairs, and avascular mycorrhizal (AM) hyphae. The AM colonize in root cortical cells and extend their hyphae into the soil, sometimes expanding soil volume exploration at least 15 cm beyond the root surface [21]. The AM receives organic C from the root and, in return, delivers nutrients to the root [22]. This mutual relationship increases drought resistance and reduces yield loss [23][24][25][26]. Root anatomical traits play an essential role in microbial symbiosis. In maize, larger root diameters and larger aerenchyma lacunae increase mycorrhizal colonization, whereas increased aerenchyma and decreased living cortical area reduce mycorrhizal colonization [5]. Cortex thickness is also crucial for AM colonization in woody species [27][28]. Dreyer et al. [29] reported that a continuous sclerenchymatic ring in the outer cortex and aerenchyma in the inner cortex decrease AM colonization in three palm species. They suggested that the sclerenchymatic ring acts as a physical barrier preventing penetration of AM fungal, while the empty aerenchyma area reduces the available tissue in the root for AM colonization.

2.4. Anatomical Adaptation in Regulating Water Transport

Root anatomical traits have a substantial influence on water uptake. Through concentric layers of root cells, water first enters from the soil to the root stele, then into the xylem, and finally into the shoot [30]. Transportation in the xylem is vertical, as casparian strips limit radial movement, with the size and number of xylem vessels affecting the water transportation rate [31][32]. During root development, two types of xylem vessels are formed, the narrow protoxylem vessels and larger metaxylem vessels, through which the majority of the water is transported [31]. Prince et al. [4] reported soybean genotypes with large xylem vessels, increased xylem diameter, and metaxylem numbers performed well in water-limited environments. Large xylem vessels in olive (*Olea eurpaea*) increased root conductivity during drought stress, allowing deep rooting and extended water acquisition [33].

Phenotyping root anatomical traits is still low throughout, therefore, less research has focused on drought adaptive root anatomical traits. Further research in this area will improve phenotypic efficiency, accelerate the discovery of additional anatomical traits that assist directly in drought adaptation or indirectly through the facilitation of AM colonization, and ultimately contribute to developing drought-resilient crops.

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