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Review

Root System Architecture and Omics Approaches for Belowground Abiotic Stress Tolerance in Plants

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Abstract: Plant growth and productivity is negatively affected by several abiotic stresses. To overcome the antagonistic effect of a changing environment, plants have evolved several modifications at the physiological as well as molecular levels. Besides being a vital organ for a plant's nutrient uptake, roots also plays a significant role in abiotic stress regulation. This review provides insight into changing Root System Architecture (RSA) under varying environmental stimuli using high-throughput omics technologies. Several next-generation and high-throughput omics technologies, such as phenomics, genomics, transcriptomics, proteomics, and metabolomics, will help in the analysis of the response of root architectural traits under climatic vagaries and their impact on crop yield. Various phenotypic technologies have been implied for the identification of diverse root traits in the field as well as laboratory conditions, such as root-box pinboards, rhizotrons, shovelomics, ground-penetrating radar, etc. These phenotypic analyses also help in identifying the genetic regulation of root-related traits in different crops. High-throughput genomic as well as transcriptome analysis has led researchers to unravel the role of the root system in response to these environmental cues, even at the single-cell level. Detailed analysis at the protein and metabolite levels can provide a better understanding of the response of roots under different abiotic stresses. These technologies will help in the improvement of crop productivity and development of resistant varieties.

Keywords: differentially expressed genes; phenotyping; genomics; nutrient stress; transcriptomics; proteomics; metabolomics

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1. Introduction

Plants, during their life cycle, are exposed to various environmental vagaries, such as drought, salinity, temperature, and nutrient deficiency, which contribute to 50% crop losses worldwide [1]. In order to overcome the accelerating global climate change, climate-change-resistant crops must be developed for sustainable agricultural practices and crop production [2]. However, to overcome environmental changes, the adaptive ability of plants has developed refined mechanisms, comprising of transcriptional and proteomic modulations [3]. In plants, the uptake and transport of mineral nutrients is accomplished by its roots, which is the key organ for this function. Environmental adaptability, through genetic enhancement, of plant roots is as essential as for the aboveground parts [4]. Besides releasing several metabolic exudates, roots provide physical support to the plants [5]. Root architectural traits consist of root surface area, length, and lateral root number, which improves abiotic stress tolerance; e.g., water uptake during water-limited conditions [6]. Quite a few anatomical traits, i.e., cell size, number, configuration, density, and cell wall thickness, determine the nutrient uptake and transport pathways and provide mechanical strength to the roots [7]. Several crop species with a vigorous RSA can efficiently uptake mineral nutrients from the soil [8]. Through the modification of root system architecture, plants exploit rigorous nutrient reserves, such as nitrate and inorganic phosphate, heterogeneously dispersed in the soil. Dynamic changes during root development are shown

by cell cycle regulatory genes and starch metabolism genes. In addition, aerenchyma formation in root cells during water stress store energy for deep soil penetration [9,10]. Moreover, root cortical cell size, number, and aerenchyma help in dropping the energy cost for soil exploration, by changing the root cortex to air spaces [11,12]. Regulating the root apical hydraulic conductivity, size, and number of xylem vessels help during changing environmental conditions [13].

Molecular breeding is a more powerful tool than conventional breeding for root system modifications. However, for molecular breeding, chromosomal mapping of the target genes and their expected phenotypic behaviour are essential. Omics technologies, such as genomics, transcriptomics, proteomics, metabolomics, and phenomics, can deepen our understanding of root behaviour. Precise identification of the concealed root system variation traits has been allowed by next-generation sequencing (NGS) and high-throughput genotyping [14]. However, root transcriptional responses vary drastically, depending on the type of stress. In recent years, consideration of the physiological and molecular categorization of composite root traits has been given by physiologists and breeders for developing climate-smart crops.

2. Phenomics Underlying Abiotic Stress Tolerance in Root

Phenotypic analysis is a usual practice for the representation of root growth and genetic analysis of root development. For field as well as lab conditions, several advanced phenotyping methods have been developed in the past years. However, a deep root is still a major limitation in the high-throughput phenotyping of root system architecture. Various software are now available for precise analysis of phenotypic data of roots [15]. At present, high-throughput phenomics are also used for genetic examination, to identify the QTLs for a number of root traits in several crops.

2.1. Growth and Development of Root

Under variable field conditions, researchers usually face difficulty to obtain information regarding genetic regulation of RSA. Recently, in situ, non-destructive methods have been used to simplify the spatial and temporal behaviour of root grown in soil, which include magnetic resonance, computed tomography, and rhizotrons [16]. It was observed that shoot-borne crown roots near the soil surface help in plant water and nutrient uptake, get concealed, and availability of water induces new crown roots under water-deficit conditions. *Zea mays* mutants lacking crown roots showed that under dehydration, crown roots suppression may enhance crop productivity [5]. During water scarcity, roots penetrate deep into the soil, and a key character of their drought resistance is a widely spread and branched rooting system [17]. Root angle depicts the horizontal and vertical spreading of roots into the soil, which is considered an important stress-responsive characteristic [18]. As compared to a profuse root system, deep, thin roots have high potential to regulate soil components during drought. However, during high salinity, root cell wall composition, such as enhanced lignin and suberin deposition, changes drastically, which hampers water and ion transport [19,20].

2.2. Root Phenotyping in Field/Laboratory

For the phenotypic study of roots under field conditions, several tools are being used, such as root-box pinboards, soil-filled grass rhizotrons, polyvinyl chloride (PVC) tubes, and the trench method [21]. Several models for root phenotyping are also being developed, such as 3D and 4D root architecture models, allometric models, R-SWMS-based model, response surface models, etc. [22]. These models predict the changes in root system architecture due to external stresses by coupling with different high-throughput imaging techniques (Figure 1). Further, to reduce the difficulty in sampling, a method has been developed by entrenching PVC tubes in the field for roots before sowing or sampling. For the quantitative analysis of different root traits, rather than qualitative, the basket method, coring, trenching, and shovelomics are being used [23]. Moreover, for

measuring root biomass and thickness in trees, ground-penetrating radar (GPR) techniques are being applied. Recently, allosteric models were used to predict root biomass changes in field crops [24]. Apart from GPR, X-ray computed tomography is also being established for the visualization of roots under field conditions. Gel medium, being transparent, is functional for both 2D and 3D root imaging, while MRI and X-ray CT are broadly used for 3D visualization of roots. In rice, X-ray CT is used to examine 3D imaging of root growth in auxin-related mutants, nutrient uptake models of root hairs, and interactions among RSA, genotype, and the growth environment. Recently, 3D root imaging of wheat RSA growth around an obstacle was simulated using a model coupled with R-SWMS software [25]. In addition, a semi-field root facility for deep-root phenotyping using the RadiMax platform was developed by University of Copenhagen, Højbakkegaard, Taastrup, Denmark, with 150 minirhizotrons, which allow root screening up to a depth of 3 m. Roots are observed using multispectral imaging, and a high-performance computer system for root quantification has been developed to analyse 80 different root traits at different growth stages along with DNA profiling [26]. At the time of anthesis, roots are exposed to ^{15}N, and mature ears and root depths can be analysed to predict ^{15}N uptake [27].

Figure 1. Schematic diagram representing the different root models used to predict root system architecture in response to various abiotic stresses. Spatial and temporal changes can be predicted through 3D/4D root models. Changes in root biomass can be predicted through allosteric models. Terrestrial biogeochemical and response surface models can be used to predict nutrient acquisition.

2.3. Phenotyping for Root Traits

High-throughput phenotyping (HTP) offers a non-destructive sampling method for the analysis of correlations among different root traits and crop adaptability under different environmental conditions. These HTP methods use advanced optical recording tools, including rhizotrons, for screening soil-grown roots or soil-free transparent media [28,29]. In common bean, the gravitropism-related traits of basal roots during phosphorus acquisition have been studied with the help of hydroponic growth pouches [30]. Under water-deficit conditions, to study the aerenchyma of the root cortex and to follow root growth, minirhizotrons can be used; however, they are limited to a small surface area [31] (Figure 2). Moreover, to maximize the uptake of nutrients by roots, high-nutrient-containing regions promote branching. In response to water and nitrogen availability, activity of nodule

formation in roots is being studied by rhizotubes [32]. Using the HTP platform, canopy temperature (CT) and normalized difference vegetation index (NDVI) can be measured to develop unbiased models for yield prediction [33]. Similarly, for rapid and reliable screening, CT and NDVI can provide an indirect method for deep-root screening [34]. CT values are directly corelated to transpiration, stomatal conductance, and vapour pressure deficit, and is associated indirectly with higher root depth and root dry weight [35]. Hand-held thermometers are useful only to measure CT values in small areas. However, to measure large canopy areas, airborne thermography offers a cost-effective and less laborious option [36]. Similarly, spectral reflectance indices of NDVI were reported to be directly corelated with chlorophyll content, photosynthetic capacity, abiotic stresses, and deep root trait such as root length densities (RLD) and root dry weight (RDW) [34,35]. In contrast, root diameter was found to be negatively corelated with NDVI [35].

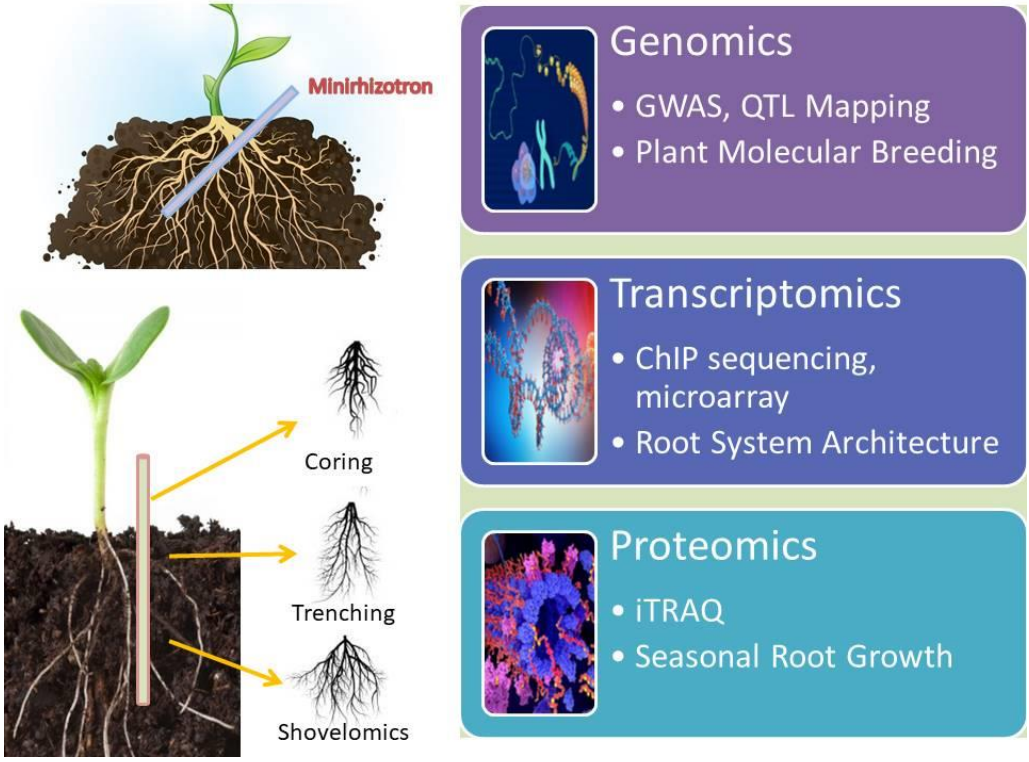

Figure 2. Overview of the plant root phenotyping and genomics tools to measure root system architecture. Root phenomics (**left**) include invasive sampling techniques, such as coring, trenching, and shovelomics, and non-destructive sampling techniques, such as minirhizotron. To analyse the effect of various abiotic stresses on root system architecture, different genomics tools, such as GWAS, QTL mapping, RILs, transcriptomics, and proteomics, such as iTRAQ, are used (**right**).

3. Root Genomics Underlying Abiotic Stress Tolerance

The study of genomics under various abiotic stress conditions comprises various high-throughput sequencing, genome-wide association studies (GWAS), recombinant inbred lines (RILs), and quantitative trait loci (QTL) mapping (Figure 2).

3.1. Nutrient Stress

For the identification of the root growth rate's responsive genomic loci, GWAS was performed under nutrient deficiency. GWAS analysis during normal root growth expressed no relationship with non-normalized root growth rates. GWAS analysis under nutrient deficiency identified the candidate genes causing the natural variation in root growth rate and also found the effect of a single stress and their combinations in various genetic manners. Certainly, in a population of natural accession under nutrient stress, the root

growth rate trait has not been evaluated. However, natural accession from the RegMap population has been used to study the variation in the *Arabidopsis* root growth rate [37]. By recognizing the rapid deterioration in linkage disequilibrium in *Arabidopsis*, 145 genes equivalent to 87 SNPs located in 32 different genomic regions were identified. GWAS analysis was performed to identify loci associated with varying RGR in single and combined stresses; which specifies the genetic architecture, mitigating Fe, Zn, or P deficiency in *Arabidopsis*. Deficiency in P or Fe alone caused a reduced primary root length, whereas deficiency in both did not show these symptoms. Similar results were also observed in the combined effect of P and Zn deficiency. The root growth rate (RGR) of the control declined in the P or Fe deficiency samples, but not in the Zn, P–Fe, or P–Zn deficient conditions, as compared to the control. For the determination of genetic variation in the root growth rate, heritability (part of phenotypic variation caused by related genes) was analysed by the mixed model [38]. Results showed that the root growth rate was an inherited trait exhibiting extensive heritability, from 10% (Fe deficient) to 80% (control). Under P deficiency, *CLV2* initiate root meristem differentiation, which was confirmed by GWAS [39]. A reduced RGR was detected in P deficiency in Col-0, whereas other accessions behaved in a conflicting manner. Phosphorus deficiency promotes early primary root growth; however, it promotes a decline in the root growth rate caused by Fe or Zn deficiency. Combined deficiency in P and Fe causes long primary roots as compared to P or Fe alone in Col-0. Reduced root growth rate under Fe deficiency, enhanced under the combined effect of P–Fe deficiency. Zn deficiency caused reduced primary root growth, which is reversed by combined P–Zn deficiency. Heritability of RGR in P–Fe and Fe deficiency was found to be significant; in contrast, non-significant variations were observed during P–Zn and Zn deficiency. Using a genome-scale gene co-function network, AraNetv2 and all GWAS candidate genes for P–Fe, the Fe deficiency trait, and three improved modules were identified. Furthermore, one module was identified in P–Zn and the Zn-deficient trait, with substantial gene ontology enrichment for the regulation of cell cycle and cell proliferation. VARIANT IN METHYLATION 1 (*VIM1*) was identified in s GWAS of the root growth rate under combined P–Zn deficiency. The BRASSINAZOLE-RESISTANT 1 (*BZR1*) gene was found to be associated with root growth under Zn deficiency. Knock-out mutations of the VOLTAGE-DEPENDENT ANION-SELECTIVE CHANNEL PROTEIN 3 (*VDAC3*) lead to increased primary root growth (PRG) under P–Fe deficiency [40] (Table 1).

Table 1. Root-responsive genes/gene products confer tolerance against various abiotic stresses.

	Stress Responsive Genes/QTLs	Gene Names	Function	Reference
Genomics	*AtBZR1*	*Brassinazole-Resistant 1*	RGR regulation under Zn deficiency	[40]
	AtPHR1	*Phosphare Response 1*	Responsible for crosstalk among Fe and P signalling to control root growth	
	AtVIM1	*Variant in Methylation 1*	RGR regulation under P–Zn deficiency	
	AtVDAC3	*Voltage-Dependent Anion-Selective Channel Protein 3*	Primary root growth control under P–Fe deficiency	
	OsDRO1	*Deep Rooting 1*	Deep rooting under drought stress	[41]
	OsDRO2	*Deep Rooting 2*	Root angle maintenance under drought stress	[42]
	CaLG04	*QTLs*	Root length maintenance under drought stress	[43]
	CaLG06		Root surface area maintenance under drought stress	
	OsqDTY3.2		Maintain whole plant water level under drought stress	[44]

Table 1. *Cont.*

	Stress Responsive Genes/QTLs	Gene Names	Function	Reference
Transcriptomics	*SlPIP1;7*	*Plasma membrane Intrinsic Protein 1;7*	Promotes root growth along with tolerance to drought	[45]
	CaTIP2/3	*Tonoplast Intrinsic Protein 2/3*	Drought tolerance	[46]
	CaNIP6;3	*NOD26 Like Protein 6;3*	Drought tolerance	
	TaPSTOL1	*Phosphorus Starvation Tolerance*	Early root growth under phosphorus deficiency	[47]
	AtNTR1.1	*Nitrate Transporter 1.1*	Gets slightly reduced in roots under high nitrate condition	[48]
	Ci1-FFT	*fructan 1-fructosyltransferase*	Freezing tolerance in roots	[49]
Proteomics	*TaRab24*	*RAS oncogene family protein 24*	Drought-stress tolerance and root growth improvement	[50]
	TaPPDK, TaLEA1 and TaLEA2	*Pyruvate phosphate dikinase, Late Embryogenesis abundant 1&2*	Increase root depth, root biomass as well as tolerance to salinity stress	[50]
	GmRACK1	*Receptor for Activated C Kinase 1*	Regulation of flooding stress	[51]

3.2. Drought Stress

The natural environment and breeding results in a modified root system, which differentially regulates RSA in a spatio-temporal manner. For the identification of novel genetic loci for RSA traits, genome-wide mapping is being used for different populations, such as introgression and recombinant inbred lines (RILs), biparental populations, and global core collections. In rice, a cross between IR64 (shallow root), with inactive *DRO1*, and Kinandang Patnog (deep rooting), with active *DRO1*, led to the identification of six QTLs for deep rooting under drought stress [41], of which *DRO2*, which regulates the root growth angle, was found to be localized at chromosome 4 [42]. A cross between winter wheat varieties in a biparental RIL population identified two major QTLs for primary and maximum root length [52]. A total of 29 QTLs were observed under well-watered conditions and 23 QTLs were observed under water-stress conditions; under both these conditions, seven constantly expressed QTLs were found to be co-regulated with key root characteristics, such as root length, number of roots, total surface area of root, and seminal root angle, in a double haploid wheat population. These root trait QTLs were unevenly distributed between chromosomes, among which chromosomal region Xgwm644.2–P6901.2 on chromosome 3B harboured 9 QTLs, affecting major root morphological traits [53]. GWAS analysis of 91 phenotypically diverse genotypes of bread wheat reported two major alleles causing increased root lengths under PEG-induced dehydration stress. In 100 bread wheat genotypes, three drought responsive pleiotropic SNPs were identified after GWAS analysis [54].

Under drought conditions, GWAS analysis found three to four QTLs as major regulators in three consecutive growing seasons for both morphological and anatomical characters of roots in barley [55]. A cross between a dehydration-tolerant and -sensitive population resulted in a single QTL for root density. Under water-deficit conditions, a cross between two inbred lines, 'DH1M' and 'T877', using an RIL population, identified two QTLs for crown root angle (*CRA2*) and crown root length (*CRL1*) (Table 2). GWAS analysis of maize lines obtained from CIMMYT (International Maize and Wheat Improvement Center) using association mapping identified 18 SNPs for root structural and functional characters [56]. Syntenic regions among cereal genomes identified drought-adaptive QTLs for various RSAs, which revealed conserved genetic regulation on rice chromosome 9, with wheat chromosome 5, barley chromosome 5 and 7, maize chromosome 10, and sorghum chromosome 2. Several root-related traits were found to be useful in a breeding system for the development of new drought-tolerant cultivars for sustainable yield. Evolutionary studies found a network of genes controlling root traits under different environmental conditions via some epistasis effects [57]. Sixteen QTLs have been mapped in common bean for root gravitropic traits out of which three were for basal root angle and were related to deep

rooting. Further, lateral root development plasticity and aerenchyma formation improved rice adaptation under increased soil moisture stress and the QTL for this is *qAER-12*. The QTL for lateral root plasticity is *qTLRN-12* and for L-type lateral root production plasticity is *qLLRN-12*. The deep-rooting cultivar of rice also has a QTL, *qDTY3.2*, which helps in the maintenance of whole-plant water level under drought [44]. Chickpea showed a drought tolerance trait harbouring three different QTLs for root length density (*CaLG04*), root surface area (*CaLG06*), root dry weight, and total plant dry weight (*CaLG04*) [45].

Table 2. Role of different root traits in abiotic stress tolerance.

Abiotic Stress	Morphological and Root Traits	References
Drought stress	Increased crown root angle and length	[56]
	Lateral root development and aerenchyma formation	[44]
	Shallow or deep root	[22]
	Fewer but large size cortical cells	[58]
	Increased root hair length and density	[59]
Salinity stress	Cellular dehydration and ionic imbalance	[60]
	Enhanced lignin and suberin deposition in cell wall	[20]
	Root bending away from saline environment	[61]
	Growth of both primary and lateral root get arrested	[62]
	Decreased root hair length and density	[63]
Temperature stress	Compact roots during cold stress and elongated roots during heat stress	[64]
	Seminal root elongation in warm climates	[65]
	Cell elongation in root elongation zone and reduced meristem size under warm conditions	
Flooding stress	Adventitious root formation	[66]
	Formation of aerenchyma and oxygen loss barriers	[67]
Nutrient stress	Reduced primary root length in Fe and Zn deficiency	[38]
	P deficiency promotes early primary root growth and root hair proliferation	[40]
	Lateral root growth inhibition in nitrate deficiency	[48]

4. Transcriptomics: A Key to Understand Abiotic Stress Tolerance in Root

Transcriptomics is a total set of RNA that portray the physiological and biological behaviour of the cell. In recent years, high-throughput RNA sequencing has become a useful tool for interpreting the spatio-temporal behaviour of transcripts. Technology advancements enable accurate and high-resolution transcriptomes even at the single-cell level. Different abiotic stresses cause a low yield and poor quality of several crops. Regarding abiotic stress-tolerance mechanisms, several stress regulatory genes are responsible. Certainly, many transcripts underlying abiotic stress are expressed in roots as compared to shoots and leaves (Table 1).

4.1. Root Architectural Traits

Plasticity is an exceptional form of genetic variation, confirmed by root phenotype regulatory genomic loci, and can be an approach for stress adaption through the root system [68]. In the roots of *Arabidopsis*, transition from proliferation to differentiation is regulated by *AtMYB36* while *MYB56* negatively regulates lateral root development. In tea roots, MYB is responsible for the biosynthetic regulation of tea via *MYB-CsTS1* transcrip-

tional regulation, which then gets transported to the leaves. Tuberous root development is regulated by complex hormones, as revealed through the cassava transcriptome [69].

4.2. Drought Stress

Transcriptomic changes during drought stress were analysed in several drought-tolerant/sensitive genotypes, RILs, and near isogenic lines. Water scarcity leads to the variation in different metabolic, translational, and defence-related pathways. In drought-tolerant species, cell growth and cell wall biosynthesis genes are less affected under severe drought, while in drought-sensitive species they get repressed. Likewise, in drought-tolerant species, carbohydrate metabolism genes were upregulated, while they were found to be downregulated in drought-sensitive genotypes under severe drought [70]. Autophagy-associated genes were found to be upregulated only in drought-sensitive species under drought stress [71]. Drought-tolerant varieties have a distinct RSA, including a shallow or deep root, compared to sensitive genotypes, but they do not have a significant difference in physiological mechanism [22]. In drought-tolerant species under drought-stress conditions, hormone signalling genes, such as *ERFs*, *AUX/IAA*, and *GA2ox*, as well as ABA and brassinosteroid biosynthesis play important roles. Ethylene response factors in crosstalk with other phytohormones regulate the abiotic stress response, as ethylene is responsible for root elongation [72]. As an adaptive response, root development responsive genes under drought stress might be accountable for RSA plasticity. In the root transcriptome of chickpea during drought stress, there is upregulation of stress responsive TFs, kinases, ROS scavengers, root nodulation-specific genes, and oxylipin biosynthesis genes [73]. Overexpression of a plasma membrane-specific protein, *SlPIP1; 7*, was found to promote root growth along with drought-stress tolerance in transgenic tomato (*Solanum lycopersicum*) [45]. Under water-scarce conditions, novel dehydration responsive genes were acknowledged in roots of common bean through differential display RT-PCR analysis. Further studies demonstrated that a dehydration-responsive gene, *OCT1*, gets upregulated in the roots of common bean after 1 h of dehydration and further gets depleted after de novo synthesis of ABA [74]. Differential regulation of aquaporin and vacuolar-specific transcripts were observed under drought stress in *Cicer arientum* L. [46]. In a transcriptome analysis of rice roots using k-means clustering analysis, under control conditions, 339 outside mesodermis-specific transcripts and 290 inside mesodermis-specific transcripts were observed. However, under drought-stress conditions, 8 inside mesodermis-specific, 14 outside mesodermis-specific, and 7 root-preferred genes were found to be upregulated. Besides this, 59 outside mesodermis-specific, 12 inside mesodermis-specific, and 231 whole root-specific transcripts were found to be downregulated [75].

4.3. Salinity Stress

Increased salt concentration directly affects root cells, which affect crop yield and improvement in semi-arid as well as lowland areas of coastal regions. Carbohydrate metabolism, transport, and cytoskeleton-responsive genes are upregulated in salt-tolerant rice roots as compared to the salt-sensitive variety [76]. In the case of high soil salinity, uptake of Na^+ is facilitated by voltage-dependent NSCC (non-selective cation channels) through the roots [77]. Salt-tolerant varieties reduce the ion concentration in the cytosol by cumulative water uptake and sodium translocation via upregulating aquaporins and cation transporters. Secreted CRPs and Rapid alkalization factor 23 (*RAF23*) upregulation in *Arabidopsis* contribute to salinity tolerance via root elongation. During salinity, ABA gets accumulated in the roots of plant species, and then distributed in different plants on the basis of the pH gradient [77]. Different ABA-responsive TFs, such as bZIP, DREB2, MYC, and MYB, which activate salinity as well as drought-stress-tolerance genes, show the presence of common regulatory pathways between these two stresses [78]. In alfalfa, NGS analysis shows that *miR156* overexpression modified the nodulation response, root development, and phytohormone biosynthesis genes [79]. Transcriptome analysis of mannitol

and NaCl-treated root tips results in differential expression of genes involved in signalling and signal transduction, transcriptional regulation, and anti-oxidative defence [29].

4.4. Temperature Stress

Differently expressed genes were also reported under cold stress as well as heat stress in roots, similar to the shoots. Heat stress has become one of the biggest problems nowadays, and it is necessary to know the underlying tolerance mechanism through the root system. During high temperature stress in rice, small-RNA transcriptome analysis shows that heat-stress-responsive miRNAs were expressed only in the heat-tolerant variety [80]. Some of the target genes showed a negative correlation with miRNAs, which confers that these target genes and miRNAs might be responsible for heat tolerance. Interestingly, a higher number of differentially expressed miRNAs were reported in roots as compared to shoots, signifying that the roots are highly prone to heat stress. Similar to high-temperature stress, low temperatures also cause harmful effects on several temporal and non-temporal species. In various plant species, cold is sensed through the shoots; however, some plants also sense a decrease in temperature through their belowground parts. Recently, a tissue-specific, genome-wide analysis of *CBL* and *CIPK* was conducted in cassava in response to cold stress, which showed root-specific expression of *CBL4*, *CBL10*, *CIPK7*, and *CIPK13*, while leaf tissue-specific expression of *CBL5* and *CIPK14*. This clarifies that *CBLs* and *CIPKs* function during stress tolerance in plants, in a tissue-specific manner [81]. The transcriptome of wildtype sugarcane roots under low-temperature (10°C) stress reveals that signal transduction initiates through transcription factor ERF, DREB, CAMTA, MYB, and C2H2, which results in upregulation of cold-responsive genes, namely, *LEA*, dehydrins, and *COR*, thus providing cold-stress tolerance [82].

4.5. Nutrient Stress

During evolution, plants have developed mechanisms to sense nutrient scarcity. Deficiencies in essential nutrients, such as NPK, affect plant growth and development. Deficiencies in nitrogen activate several genes involved in phytohormone biosynthesis (abscisic acid and jasmonic acid), amino acid metabolism, and the phenylpropanoid pathway. Under nitrate deficiency, lateral root growth gets inhibited in *Arabidopsis*, as revealed by studies on nitrate transporter NTR1.1 [48]. Under nitrate starvation, NTR1.1 moves auxin basipetally to avoid its accretion in the lateral root tip and inhibit lateral root growth [83]. Genes responsible for the phenylpropanoid metabolism pathway were also induced during phosphorus deficiency. Phosphocholine phosphatase, a high-affinity phosphate transporter and glycolipid biosynthesis encoding gene, gets upregulated during phosphorus deficiency. Early root growth in a wheat variety depicted phosphorus-deficiency tolerance, which was conferred by phosphorus-deficiency tolerance (*PSTOL1*) protein kinase [47]. A deficiency in potassium also induces the expression of protein kinases, transporters, and phytohormones such as jasmonic acid, auxin, and ethylene [84]. Mutation analysis of low phosphate root 1 (*lpr1*) maintained primary root growth under phosphorus deficiency, while phosphate deficiency response (*pdr2*) and hypersensitive to pi starvation 7 (*hps7*) shows primary root growth inhibition. Sensitive to protein rhizotoxicity (*STOP1*) and aluminium-activated malate transporter 1 (*ALMT1*) were also found to be accountable for primary root growth (PRG) reduction [85]. The improved root growth results in better uptake of Zn and Fe, which enhances their content in plants. Deficiency in Fe negatively affects root length, whereas a Zn deficiency endorses early root growth. Under an Fe-deficient condition, a mutant of bHLH TF POPEYE, or a bHLH34 and bHLH104 interaction, restricts primary root growth [86]. PRG reduction in Col-0 under phosphorus deficiency is due to the toxicity of Fe. Under phosphorus deficiency, *ALMT1* promotes Fe accumulation in the root meristem and resulted in a reduction in cell expansion. Under P deficiency, Fe gets accumulated in root tips that lead to root apical meristem differentiation, through callose deposition in the symplastic pathway. Callose deposition and Fe accumulation in the root meristem and elongation zone is determined by the *PDR2-LPR1* module under P starvation. It

was reported that *CLE14* is responsible for root meristem diversity through *CLV2/PEPR2* receptors under P deficiency [39].

4.6. Heavy Metal Stress

Heavy metal contamination of soil is due to industrialization, which hampers the productivity of several crop plants. Many heavy metals, such as cadmium, arsenic, and chromium, are toxic to plants as well as other organisms [87]. An increased concentration of these metals in soil causes lateral root inhibition [88]. The serine acetyltransferase level also gets elevated in *Arabidopsis* roots under Cd stress. Furthermore, under heavy metal stress, plants activate the MAPK pathway and roots activate cellular signalling mechanisms. In response to heavy metal toxicity, the genes responsible for oxidative stress response and glutathione metabolism gets upregulated in rice roots [89]. It was reported earlier that *OsMT1e-P* gets expressed in roots of rice under heavy metal stress [90]. Tobacco plants ectopically expressing *OsMT1e-P* accumulate Na^+ and Cu^{2+} in roots and restricts their mobilization to vegetative parts, thus improving heavy metal stress tolerance [90].

4.7. Applications of Transcriptomics in Roots

The response to flooding by soybean was observed by HiCEP and microarray techniques [91,92]. As a response to flooding, the genes responsible for carbohydrate and lipid metabolism, cell wall synthesis/degradation, protein biosynthesis, photosynthesis, and secondary metabolism regulation were reduced slightly in roots [93]. To identify the transcription factors, targeted transcripts in a genome-wide manner, ChIP sequencing can be used. Recently, another high-throughput sequencing method, named DNA affinity purification (DAP seq), has been used for this [94]. In addition to this, P and N starvation enhance root length through the strigolactone signalling pathway [95]. This leads to a conclusion that root system architecture plasticity is vital in yield enhancement and nutrient uptake under abiotic stress. Several transcription factors, such as AP2/ERF, LOB/ASL, bHLH, and GRAS, were also reported in root development, and modification of these transcription factors as well as the responsive genes for root development were shown to help in the improvement of climate-resilient crops.

5. Proteomics of Roots in Response to Abiotic Stress

Proteomics can be defined as the identification and interaction of structural and functional proteins in a particular time interval. Proteins are primarily involved in most of the cellular events; as a result of this, proteomics has an advantage over other omics techniques. Proteomics can identify translational and posttranslational modifications, thus improving our understanding of critical biological phenomena in roots under various abiotic stresses.

5.1. Temperature Stress

A quantitative proteomic method, iTRAQ, has been used to compare self-grafted and root-grafted watermelon in cold stress [96], and found that cold resistance is enhanced by root grafting (Figure 2). Root-grafted watermelon reduced energy toward photosynthesis and carbon metabolism and enhanced ROS scavenging activity and arginine biosynthesis under cold stress. Several other cold-regulatory proteins, such as dehydrins, 25 KDa dehydrin-like protein, ERD14, and cold acclimation-specific protein, were abundant in chicory roots [97]. A novel cold regulatory protein, 1-FFT, has been identified in the root of chicory, which confer freezing tolerance in this plant [49]. Other than some metabolic and energy-related proteins, few folding, proteolysis, and stability related proteins were observed during cold stress. Upon cold stress, CYP2 and cysteine protease gets accumulated in the roots. Quantitative proteome assessment under chilling stress found that membrane transport and signal transduction-related proteins were present abundantly in the plasma membrane of rice roots. To overcome chilling stress in the roots of rice oxalyl-CoA decarboxylase, a ROS scavenger gets elevated [98]. Detoxification of methylglyoxal was also

observed via the gradual increase in glyoxalase I protein level during cold stress. Several HSPs, such as HSP70, were found to be most abundant in the roots of several crops as a response to cold stress [99]. At the phase of recovery after chilling, accumulation of cellulose synthesis proteins gets elevated, showing that cell wall synthesis confers stress recovery (Table 1).

5.2. Drought Stress

In the roots of soybean, watermelon, and rapeseed during drought stress, several proteins related to carbon/nitrogen metabolism have been observed [100]. Concurrently, several root growth-related small G-proteins, such as Ran GTPase, also have been observed. In the roots of watermelon under drought stress, various proteolytic enzymes, such as leucine amino peptidase, enable the degradation of irreversibly impaired proteins [101]. In wheat, Rab24 protein accumulation was found to increase drought tolerance and root growth enhancement under drought-stress conditions [50]. These studies supported the fact that during drought stress in roots, defence-related proteins and PCD regulatory proteins are involved. During the recovery period after drought stress, there is an enhancement of actin isoform B in the roots of soybean seedlings, which defined the role of actin during repair of injured membranes. Lignin deposition also gets enhanced in the cell wall of the root, which provides mechanical strength during water scarcity.

5.3. Salinity Stress

Investigation at the proteomic level found the involvement of plasma membrane receptors, G protein, Ca^{2+} signalling proteins, phosphoproteins, and ethylene receptors to overcome salinity. In the roots of various crops, Receptor protein kinases (RPKs), transforming GF β receptor-interacting protein, and small GTP-binding proteins get enhanced under high salinity [102]. Likewise, 14-3-3 family proteins, such as GF14a and GF14b, were also highly abundant in roots of various crops during salinity. During enhanced salinity, root activates various events, such as modification in carbohydrate metabolism, ion homeostasis and membrane trafficking, antioxidant activity, cytoskeleton reorganisation, and cell wall components redistribution. Salinity causes enhancement of NADH dehydrogenases, cytochrome C oxidases, and ATP synthase in roots of various plants. Some photosynthesis regulatory proteins, such as PPDK, increased the salinity-stress tolerance and root biomass in wheat under salt-stress conditions [50]. Enzymes related to glycolysis were also upregulated in the roots of various crops as a response to salinity [102]. Salinity enhanced the Na^+/K^+ ratio in the roots, causing cellular dehydration and ionic imbalance. To balance Na^+/K^+ ratio in roots, voltage-gated potassium channels gets activated, and cyclic nucleotide-gated channels gets reduced. Additionally, numerous ABC transporters also get enhanced in roots of wheat to overcome salinity stress [103]. ROS-foraging enzymes, such as peroxiredoxin and thioredoxin, also get enhanced in the roots of various crops during salinity [104]. In the roots of various species, to overcome the effect of salinity, the ascorbate glutathione pathway plays an important role. In the roots of *Arabidopsis*, salt-regulating peroxidase initially gets depleted and gets enhanced after further exposure to salinity [105].

5.4. Flooding Stress

As an early response to flooding, several primary metabolism regulatory proteins get activated in the roots as well as the whole plant. Expression of various cell wall-regulatory proteins, such as methionine synthase, β-1, 3-glucanases, and β-glucosidase, gets depleted in the roots under waterlogging stress, resulting in impaired growth [106,107]. For the recovery of roots after flooding stress, cytoskeleton reorganisation, cell wall alteration, and de novo protein synthesis are vital cellular processes. In post-flood roots, actin isoform B gets elevated for the expansion of the cell wall. Under the initial stages of flooding stress in soybean root tip, eukaryotic translation initiation factor 4G gets dephosphorylated [107]. RNA metabolism and poly-ADP-ribosylation of proteins also get enhanced in soybean root

during flooding stress [108]. RACK1 was found to play an important role under flooding stress in soybean, though the mRNA level of *RACK1* gets downregulated, whereas its protein gets accumulated in the nucleus of root tips [51].

6. Metabolomics of Roots in Response to Abiotic Stress

Plant root metabolites are essential components of cellular metabolism due to their impact on root growth, biomass, and architecture. Recently, metabolomics has recognized itself as one of the major innovations in science, flagging the way for precise metabolite outlining in plant roots. Metabolomics has the capability to identify an enormous range of metabolites from a solitary root extract under different environmental stimuli, consequently allowing speedy and thorough investigation of metabolites.

6.1. Metabolites in Root Development

During cassava tuberous root development, the concentration of UDP-glucose and NADH increased in parenchyma and pre-tuberous roots. In the cortex and pre-tuberous roots, cell membrane organization components, such as guanosine, cytidine, and choline and glycine betain, were detected. Sugar metabolism or starch biosynthesis increased considerably from pre-tuberous to mature roots, which showed a correlation with nucleotides, sugar phosphates, and UDP-glucose. As compared to pre fibrous root sucrose, the G1P, G6P, UDP-glucose, and amino acids (glutamine, glutamic acid, serine, tyrosine, phenylalanine, and tryptophan) levels increased, and the cysteine, homoserine, threonine, raffinose, and oxaloacetic acid levels decreased in developing tuberous roots, necessary for carbon supply for starch biosynthesis. The level of cytokinin was considerably higher in pre-tuberous to mature roots as compared with fibrous roots. The MEP pathway-derived tZ and iP cytokinins were higher in tuberous roots, whereas the MVP pathway-derived cZ cytokinins were abundant in pre-tuberous root samples. Further, the IAA levels progressively declined in pre-tuberous root as well as the cortex and parenchyma of intermediate-stage roots. The gibberellic acid and jasmonic acid level changed slightly in tuberous roots, whereas salicylic acid and abscisic acid were higher in pre-tuberous root as compared to fibrous roots [109]. Similar to the changes in mRNA and protein levels during tuberous root development, metabolites also exhibit developmental stage-specific patterns in cassava. This shows that there might be a connection between transcript expression and metabolite changes [20]. Root length and number gets affected by phytohormones, and they are also responsible for adequate RSA [110]. For example, in lateral and crown root development, auxins have a specific role. In rice, *CRL4/OsGNOM1* controls crown-root development via auxin transport. For the development of lateral roots in rice, *OsCYP2/LRL2* plays a critical role, besides degradation of the auxin-responsive proteins [60]. Auxin negatively regulates *DRO1*, which initiates asymmetric root growth and trigger downward bending of the root in response to gravity [22]. In the root tip and root cap cells, flavonoid gets accumulated, which is released in the rhizosphere from the root [111]. Flavonoids inhibit auxin transport and modify the cell morphology, root morphology, and gravitropism [7]. Equilibrium of ROS between the zone of cell proliferation and zone of elongation is modulated by UPBEAT1 (UPB1) TF, which also controls the activity of peroxidase genes. *Ubp1-1* helps develop longer and mature lateral roots as compared to the wild type, whereas overexpression of *UBP1* reduces lateral roots [10]. In a genome-wide analysis of rice roots, nine glutathione S-transferase and 32 peroxidase genes were found to be root specific, which shows the significant role of these genes in root ROS processing [112]. Auxin plays a vital role in root morphogenesis, and it positively regulates the number and length of the lateral roots, the length of the root hairs, the primary root hair length, and the gravity response. Ethylene modulates the auxin signalling machinery and affects root growth by regulating auxin biosynthesis [79].

6.2. Abiotic Stress Tolerance

Lan and co-workers found multiple levels of gene regulation in phosphate-deficient *Arabidopsis* roots, and suggested that the integrated measurement and changes in tran-

script and protein is enough for generating components essential for stress responses [113]. During flooding, the concentration of NADH and NAD^+ is increased and the ATP level decreased, which indicates impairment of the electron transport chain, while the amount of mitochondrial NADH gets increased. Flooding stress modulates the urea cycle and enhances the synthesis of PEP through oxaloacetate produced in the TCA cycle [114]. The intermediate or end product of the metabolic pathways play a vital role in several biochemical processes and phenotypic traits, including root traits [115]. In response to various phytohormones, several genetic variations have been observed for different root traits [116]. Under drought stress, the auxin and sugar metabolic pathway produces various metabolites to control the metabolism of root traits. In *Medicago*, for the development of root architecture, the lignin biosynthesis pathway plays a crucial role, and in mutant plants, caffeic acid O-methyl transferase under the control of the *CRA1* gene affects the lignin concentration of roots, causes short and thick roots, and also recognises polar auxins and specific flavonoids for root improvement [117]. Contrasting accumulation of root metabolites under drought stress between leguminous and non-leguminous crops suggested that 4-hydroxy-2-oxoglutaric acid is highly tissue specific in non-leguminous crops root and coumestrol is specific to the roots of leguminous crops [118]. Transcriptomic and metabolomic analysis for roots and shoots of *Medicago* under several situations found different components that regulate different levels of drought-tolerance mechanisms, such as the role of myoinositol and proline [47]. Under water scarcity, root nodules uptake adequate amounts of nitrogen for plant growth and development. To determine the alteration in primary metabolites and lipids in roots of barley under salinity stress, four MS-based metabolomics and lipidomics analyses quantified 154 metabolite accumulations [119].

7. Conclusions and Future Prospects

Various environmental factors, such as salinity, drought, temperature, nutrients, etc., affect plant roots, ultimately hampering plant growth and development. Several omics-based techniques have been developed to understand the underlying mechanism of roots under these harsh conditions. During these unfavourable conditions, roots adapt themselves by modulating their phenotype, transcripts, proteins, and metabolites. To identify these modulations under field as well as lab conditions, phenomics, genomics, transcriptomics, proteomics, and metabolomics techniques have been developed. The current review summarizes the role of RSA under varying climatic conditions through multi-omics technologies. Interdisciplinary programmes between breeders, physiologists, and bioinformatics can provide a major breakthrough in understanding root developmental traits in a changing environment, subsequently leading to development of resilient crops without disturbing the overall crop yield. Recent phenomics techniques, such as thermal imaging and ultrasound, needs further exploration in combination with molecular techniques such as CRISPR/Cas9, single-cell omics, and tissue-specific promoter studies, to provide a better understanding of the RSA under changing environments. Several GWAS studies are confined only to model organisms; however, other agronomically important crops still need further research for the development of RSA to make it abiotic-stress resilient. Further research can be carried out on the impact of combined and sequential abiotic stresses, and various root exudates, on the soil microbiome and RSA. However, challenges associated with complex cross-talks at various morphological, physiological, anatomical, and molecular levels need to be addressed for a complete exploration of the adaptation mechanisms during abiotic stress tolerance and RSA development. Moreover, QTL mapping could further shed light to better understand the RSA regulation at the chromosomal level under abiotic stress, which may help to develop climate-smart crop varieties.

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