agronomy

MDPI

Review

Root Phenotyping for Drought Tolerance: A Review

Allah Wasaya [1,2], Xiying Zhang [1,*], Qin Fang [1] and Zongzheng Yan [1]

1 Key Laboratory of Agricultural Water Resources, The Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, The Chinese Academy of Sciences, 286 Huaizhong Road, Shijiazhuang 050021, China; wasayauaf@gmail.com or allah.wasaya@bzu.edu.pk (A.W.); fangqinhebei@163.com (Q.F.); yanzongzheng15@mails.ucas.ac.cn (Z.Y.)

2 College of Agriculture, Bahauddin Zakariya University, Bahadur Sub-Campus, Layyah 31200, Pakistan

* Correspondence: xyzhang@sjziam.ac.cn; Tel.: +86-311-8587-1762

Received: 16 August 2018; Accepted: 29 October 2018; Published: 31 October 2018

check for updates

Abstract: Plant roots play a significant role in plant growth by exploiting soil resources via the uptake of water and nutrients. Root traits such as fine root diameter, specific root length, specific root area, root angle, and root length density are considered useful traits for improving plant productivity under drought conditions. Therefore, understanding interactions between roots and their surrounding soil environment is important, which can be improved through root phenotyping. With the advancement in technologies, many tools have been developed for root phenotyping. Canopy temperature depression (CTD) has been considered a good technique for field phenotyping of crops under drought and is used to estimate crop yield as well as root traits in relation to drought tolerance. Both laboratory and field-based methods for phenotyping root traits have been developed including soil sampling, mini-rhizotron, rhizotrons, thermography and non-soil techniques. Recently, a non-invasive approach of X-ray computed tomography (CT) has provided a break-through to study the root architecture in three dimensions (3-D). This review summarizes methods for root phenotyping. On the basis of this review, it can be concluded that root traits are useful characters to be included in future breeding programs and for selecting better cultivars to increase crop yield under water-limited environments.

Keywords: root phenotyping; drought tolerance; root traits; X-ray chromatography; canopy temperature depression

1. Introduction

Drought is a major yield-limiting factor throughout the world [1,2], and is a widespread limitation for cereals production especially under dry land conditions [3–6]. Periods of water deficit during critical stages of crop development such as booting and/or grain filling, can greatly impact the yield stability and productivity [7]. Under drought stress, water and nutrient absorption may be reduced in crop plants [8]. Variation in climate alters the hydrologic cycle, and eventually reduces the availability of water due to a change in rainfall patterns, reduction in available water resources and reduction in water supply [9]. Contribution of albedo deserts increases temperature which reduces rainfall. This decrease in rainfall causes soil dryness and reduces vegetation cover [10]. Due to climatic variability, changes in temperature and rainfall patterns affect soil moisture availability. Roots are the main organs to respond, perceive and maintain crop yield under drought conditions. Plants with deeper root systems extract water from deeper soil layers and help the plants to avoid drought stress [11,12].

Plant root systems are essential for adaptation against different types of biotic and abiotic stresses. Apart from genotyping quantitative traits, phenotyping has been a major challenge for plant breeders to improve abiotic stress tolerance in crop plants. It includes genetically complex traits that are extremely difficult to measure, and would be ideal to assist plant breeders for using in breeding program [13]. Roots have been evolved to be responsive and extremely adaptive to the local environment, their morphology, growth and physiology are closely related with plant genotype and growth medium properties. For example, elongation rate and number of lateral roots can be decreased by high soil water content or soil density and this can also be associated with shoot growth reduction [14]. The type of root distribution required for different crops depends on the target environment, as abiotic stresses experienced by roots have a significant effect on the crop yield [15,16]. Strong root development is essential for survival of seedlings in soils which undergo rapid surface drying, while sufficient moisture remains available in deeper soil layers. Therefore, good understanding about plant responses to abiotic stresses might be helpful in the selection of more resistant crop varieties [17].

The root system architecture (RSA) is affected by various factors such as soil temperature, moisture, nutrients and soil pH [18,19] which greatly affects crop growth and yield [20,21]. Several root characters such as morphological plasticity [22,23], root tip diameter [24], gravitropism [25], and rhizosheaths [26] allow the plants to adapt and respond to various environmental factors and they might be quite useful for improving water use efficiency in crop species [27]. Therefore, it is very important to understand the RSA regulating mechanisms for crop improvement [17,22]. Different types of roots have special features such as primary root length [28,29], length and number of lateral roots [30,31], crown root number [32,33] and cortical cell file number and cell size [34], which help in determining water absorption/uptake ability among various root types as an adaptation strategy under dry conditions [35,36].

Image-based phenotyping of plant roots is based on the non-destructive (where possible) optical analyses of plant traits [37,38], and its main objective is to characterize the plant's anatomical, biochemical and physiological properties [39]. Root traits are more related to drought tolerance compared with above ground plant parts [20,40] and are key factors to maintain crop yield [4] under drought [41,42]. Root phenotyping is as important as shoot phenotyping, because plant's ability to uptake moisture and nutrients mainly depends on root architecture and function [43,44]. Therefore, root phenotyping is important for crop breeding, although under field conditions, screening roots by phenotyping is a very difficult task [27].

This review mainly focuses on root traits which are useful for improving crop productivity under drought situation and their phenotyping through non-invasive techniques to save time. Out of the different root phenotyping techniques, X-Ray tomography is a non-invasive and time saving technique to obtain 3-D images of roots to decide which root trait might be useful for obtaining the high crop yield under drought. As single root morphology has scarcely been considered for plant's adaptation strategy to drought conditions, different types of roots can be characterized by various traits [35] to determine the ability of various root classes for water uptake [36]. It is observed from previous studies that different root traits such as fine root diameter, specific root length and area, root angle, and root length density are useful for improving plant's productivity under drought conditions. It is, therefore, suggested that all these root traits may be included in breeding programs to improve crop productivity under drought conditions.

2. Root Traits Related to Water and Nutrient Uptake and Drought Tolerance

Plant root systems consist of four different types of roots, i.e., (1) coarse or tap roots (first root to emerge from the seed) [45]; (2) lateral roots (any root branching from another root) [45]; (3) shoot-borne roots (roots which arise from shoot tissues) [45]; and (4) basal roots (roots which develop from the hypocotyl) [46]. Coarse or tap roots give anchorage to plants and establish root system architecture, control root system depth, and thus, determines a plant's ability to grow under a compacted soil profile [47]. While lateral/fine roots are more active, they constitute a major part of a root system [36,48]. Different types of roots are present in different crop plants. For instance, wheat (*Triticum aestivum* L.) crop has mainly two types of roots; seminal roots arising from the embryonic seed part and nodal roots arising from the basal part of the tiller [49]. A more vertical angle and higher number of seminal roots in wheat seedlings have been associated with more compact and deeper roots in wheat [50]. Different root traits have different function/s which are presented in Table 1.

Table 1. Root traits and their role for improving crop productivity under drought.

Traits	Role	Reference
Fine roots	Extract water and nutrients from the soil.	[51,52]
Coarse roots	Support plants in soil, constitute root system architecture, control depth of root system and enhances plant's ability to grow in compact soil.	[42,47]
Nodal roots	Harvest late season precipitation.	[42,53]
Root diameter	Regulates root length, surface area, increase water uptake under drought.	[54–56]
Root hairs	Assist in root contact with soil particles for uptake of water and nutrients as soil dries.	[55]
Root angle	Helps in deeper root growth and affects the area from which roots capture water and nutrients.	[45–57]
Root tissue density	Controls specific root length and specific surface area which increases plant's performance and carbon economy under water stress.	[58,59]
Root length density at depth	Involved in efficient extraction of subsoil water.	[60]

Root traits affect the amount of water and nutrient absorption, and are important for maintaining crop yield under water stress conditions [4]. Plants with higher main root diameter have more growth potential as it has direct relation with water absorption [61], and have more ability to explore compact soil [18]. Fine roots are most permeable and thought to have greater ability to absorb water, especially in herbaceous plants [54]. This role becomes even more important in water and nutrient-deficient soils due to an increase in climate variability under current cropping systems [62]. Root architecture also has a significant impact on nitrogen use efficiency [52]. Increased early vigour results in deeper and faster root growth, forming more adventitious roots in the upper soil layer, which increases nutrient and water use and reduces surface soil evaporative losses [63]. In addition to these traits, several morphological root traits such as root tissue density (RTD), specific surface area (SSA) and specific root length (SRL) are correlated with increased crop productivity under drought conditions [64,65]. Root diameter and root tissue density control the root surface area and length; and hence, encapsulate the overall effect in terms of root length per dry biomass allocated to root system [64].

Several studies have reported the significance of a deep root system for uptake of water from deeper soil layers under water-stressed environments in various crops such as sorghum (*Sorghum bicolor* L.) [66], pulses [67,68], rice (*Oryza sativa* L.) [55,69], maize (*Zea mays* L.) [70], and wheat [71,72]. In a study, root length density in the active root zone area (up to 30 cm) improved water and nutrient uptake leading to higher yield of gram (*Cicer arietinum* L.) grown under water deficit conditions [73,74]. Sufficient water could be extracted by plants having root length density >0.5 cm cm^{-3} [75]. Wheat genotypes with deeper roots, higher root density at depth, and less root density at the surface have higher yield under rain-fed conditions [76]. Similarly, fine roots increase nutrient and water absorption through increased root surface area per unit mass [77]. The significance of a vigorous and deeper root system for more yield has been documented in soybean (*Glycine max* L.) [78], bean (*Phaseolus vulgaris* L.) [40], chickpea [5], wheat [72,76], barley (*Hordeum vulgare* L.) [6] and maize [9,10,70].

Under drought conditions, plant's ability to extract water from depth has great relevance in balancing water relation as well as carbon assimilation. It is observed that plants with smaller root diameter and specific root length of fine roots are better adapted to dry conditions [79]. Deep roots are essential for small statured crops, such as wheat, rice and common bean (*Phaseolus vulgaris* L.) to extract water from deeper soil layers [47,80,81]. The root architecture gets revamped under drought conditions and facilitates the production of a large number of long lateral roots and root hairs which may enhance total surface area for water acquisition [82]. Different water conservation approaches, such as leaf rolling, stomatal closure, leaf abscission and increased root mass especially at greater depth raise water status in plants, needed for higher yield and biomass production in crop plants. Superior root phenotypes are considered key components for improving drought tolerance characteristics which offer better performance under drought by efficient uptake and utilization of water in crops such as soybean [83,84]. Deep root systems with higher rooting density are better considered to extract soil water mainly from deeper soil layers [85,86].

Plants may increase root length either by root fineness (RF) or reducing root tissue density (RTD), and/or increasing biomass allocation. For example, in sugar beet, changes in the RTD showed a strong relation to drought tolerance under conditions of drought stress [87]. Similarly, in herbaceous tall grass prairie species, root fineness (RF) is considered a functional trait for drought tolerance [88]. Root architecture as well as root size within the plant community depend on the level of competition for water, and its distribution in soil, which greatly affects the final crop yield [89]. However, selection for deep and fast growing roots may enhance soil water harvesting and help in yield stabilization under water stress conditions.

3. Techniques Used for Root Phenotyping under Controlled and Field Conditions

Roots are an important plant organ and its phenotyping is as important as shoot phenotyping, because plant's performance mainly depends on the root system [43,44]. For root phenotyping, different techniques are used under laboratory as well as field conditions. The advantages and limitations for growth conditions (Laboratory/field) are presented in Table 2. For ease in the methodology, root phenotyping was first developed in the laboratory and then demonstrated in field to check its applicability [90]. Root phenotyping methodologies typically combine some degree of automation with imaging and image processing. Image analysis approaches have been broadly used as reliable and fast root phenotyping techniques and have become available through different softwares, such as EZ-Rhizo [91], Smart Root [92], WinRhizo [93], Optimas analysis software, Image J [94], Root Nav [95], IJ_Rhizo [96], Root System Analyzer [97] and Root Trace [98]. Commonly-used systems for root observation are based on soil-less growth media. For this purpose, different techniques are used to grow plants, e.g., growing plants in paper rolls [99–101], gels [50,102,103], in air regularly sprayed with nutrient solution [104] or in aerated aqueous solutions [105]. Plants are also grown in hydroponics by using transparent plexiglas nail board sandwiches with mechanical resistance. These sandwiches were filled with glass beads of 1.5 mm in size for the circulation of nutrient solution [106]. These systems measure root branching angles, total root length and related root traits manually or through imaging or visual rating. For image processing, high resolution cameras and/or scanners are used for resolving lateral roots, and mostly individual root diameter is used for decision criteria to differentiate between the main and lateral roots [99] by using WinRhizo software [107,108]. RSA can be analyzed through Smart Root software [92] for the measurement of growth kinematics and branching angles of individual roots of a root system [101]. These systems require some manual input for such analyses [101].

Image processing becomes a more challenging task when soil is used as a growth medium. To make the medium a more natural system or closer to it, soil-filled rhizotrons/columns are used to study soil-root interaction as it is difficult or even impossible to develop soil compaction or drying effects in soil-free systems. For this purpose, soil or any other growth substrate is used for filling of columns or Rhizotrons. Then root assessment along a transparent wall [109] or within a soil column is performed by using X-ray–based computed tomography (CT) [110,111] to visualize 3-D root configuration.

Due to the hidden nature of roots, there are certain limitations for the effective application of current phenomic technologies to assess root system architecture under field conditions for developed root system traits in marker-assisted selection [112]. It is very difficult to assess roots optically in the field, unless ones need to dig them out or approach them by making a tunnel. The most widely-used conventional methodology for field root study is the trench profile technique, in which soil is removed from the sides of the plant carefully using fine brushes then roots get drawn layer-wise from successive soil profiles [113]. Among the different phenotyping techniques being used in the field, the soil core method and standard excavation method are considered as the best techniques to explore density, depth and angle of root [112,114]. Soil cores are taken for the measurement of vertical root length densities or weights by using excavation techniques [115]. The core break method proposed by Reference [109] is the quickest method used to assess the maximum depth of roots in soil samples, in which about 2 m length soil cores are divided into different portions of 10 cm each for the determination of maximum root depth [100].

Several methodologies/techniques are used for the assessment of root mass as well as root distribution in different soil layers. These methodologies need labor and may cause some destruction to crops during sample collection, as plants are uprooted for the measurement of root architecture and root mass which need vertical pulling strength [110]. Out of these, Shovelomics is a technique widely used for root system analysis for field studies [111,112,116]. In this method, soil is excavated in such a way that one plant should remain in the center of the surface. Then roots are gently washed and the main root branches are analyzed for different root traits like root density and root angles. Different techniques are used to determine the basic root traits such as root dimensions, structure and root branching from simple counting [112] to imaging along with custom image analysis software [116,117].

Mini-rhizotron systems consisting of Plexiglas tubes containing small camera or scanner inserted in the soil to assess the surroundings of the root soil are also used in field studies [118]. Through mini-rhizotrons, limited genotypes may be monitored [119]. Different indirect methods are also used for analyzing RSA, such as root pulling resistance [110] or analysis of abscisic acid (ABA) content in the leaf [120].

An electrical capacitance measurement technique is also used for the measurement of total root mass which inspects the applied current response. One electrode inserted at the stem base and the other inserted in the rooting medium [121]. This technique has been used in the field for high throughput analysis of root mass [122]. However, recent studies have shown that root capacitance may be more associated with root circumference or its cross-sectional area at the soil [123] or solution surface [124]. These observations raised some doubt on its reliability, otherwise it is a good technique to find out the soil-root interactions and root phenotypes based on electrical properties. However, such techniques do not provide detail of root function, architecture, as well root anatomy, e.g., root hair densities under field conditions [27].

The development in non-invasive approaches such as X-ray computed tomography (CT), provides an excellent opportunity to determine 3-D root architecture in undisturbed soil cores in detail. It may be considered as an excellent tool for root phenotyping when compared to other destructive methods. In this method, roots are excavated first from the soil and then washed, imaged and finally analyzed with commercially available softwares [112,117]. CT has various advantages over other destructive methods. Though other different non-invasive 3-D visualization procedures exist, X-ray computed tomography (CT) is considered a good technique for soil-root interaction studies [125]. Different image-based softwares are used for the analysis of root traits, which have some advantages and limitations (Table 3).

Table 2. Advantages/disadvantages of methods used for growing plants for root phenotyping.

Growth Environment	Advantages	Disadvantages	Examples	References
Laboratory	It allows for easy and non-destructive visualization of RSA; Easy to assess root growth; Non-destructive as it does not require any washing of roots; Time saving as it does not require soil excavation as in the field; Easily repeated under controlled conditions; Requires less resources; It is non-destructive method and gives clear picture of all root types and RSA.	The root system architecture in laboratory-grown plants does not accurately reflect what it is like in the field; Controlled conditions also eliminate possible interaction with beneficial microbes due use of growth media other than soil as in field conditions; As plants are grown in controlled conditions which prevents their exposure to environmental conditions, therefore, physiological relevance of roots need further evaluation.	EZ-Rhizo; RootNav; Root Reader 3D; X-ray computed tomography; SmartRoot.	[18,44,95,126–128]
Green house/Glass house	Close to the field conditions as the medium used may be soil or sand filled pots; Large number of varieties can be evaluated in a shorter period of time; Easy to handle the experiments compared with the field; Less time is required for root washing as compared to the field.	Some roots may be destroyed during washing; RSA may be affected by the growth container; As plants are grown in controlled conditions which prevents their exposure to environmental conditions, therefore, the physiological relevance of roots need further evaluation.	Root Reader 2D; WinRhizo.	[127,129]
Field	Give true picture or presentation of root structure; It gives clear physiological and practical picture as plants grow by facing all the environmental factors.	Roots form an extensive network which is difficult to excavate all the roots; Labor intensive and time consuming; Root excavation is very tedious and intensive work; Washing of roots is also time consuming; Destructive method as roots may be destroyed during excavation and washing. Problems may occur due to variability in the field or soil conditions.	Shovelomics; DIRT; WinRhizo; X-ray computed tomography.	[44,48,112,127,130]

Note: RSA—root system architecture.

Table 3. Techniques/softwares used for image analysis for root phenotyping under controlled/field conditions.

Software/Imaging Technique	Growth Environment/Application	Image Type	Medium	Crop	Parameters to be Observed	Advantages	Limitations	Reference
EZ-Rhizo	Laboratory	2-D	Agar plates containing MS medium	*Arabidopsis thaliana*	Main root (length, vector length, angle, number); Lateral roots (position, length, vector length, angle and number); Higher order lateral roots (order, position, length, vector length, angle and lateral root number).	Non-invasive image procurement with a newly developed program for root exposure, measures multiple root system parameters. Under different nutritional and environmental conditions phenotypic explanation of each plant species is analysed.	Due to the complexity of the root system roots growing too close to each other may not be correctly analysed; analyse images in 2-D.	[91,131]
RootNav	laboratory	2-D	natural sandy loam soil	Wheat, rice, *Arabidopsis*, canola	Total length; Tip angle; Emergence angle; Start distance; Convex hull area.	An innovative, semi-automated method used for root architectural information. Faster and easier to use than manual methods Length results are reliable with manual measures, and RootNav has been found to be also.	It has only been written in C# using the NET framework libraries. The tool runs under Windows XP, Vista 7 and 8. Database access is achieved only using the MySQL Connector library.	[95]
Root Reader 3D	Laboratory (transparent gellan gum system) Hydroponics and sand culture	3-D	hydroponic and sand culture gellen gum	Rice	Primary and total root length; Number of crown and lateral roots; Root initiation angle; Exploitation volume; Exploitation index; Surface area; Convex hull volume; Gravitropic response and narrowness index.	It provides a flexible foundation for more extensive root trait analysis, uses a silhouette-based back-projection algorithm combined with cross-sectional volume; analyse images in 3-D.	Many root traits and quantitative techniques, including advanced dynamic and topological analyses, have not yet been incorporated into the software. It also requires calibration after every reading.	[126,132,133]
X-ray computed tomography	Laboratory/ Field	2-D; 3-D	Gelzan or aluminum soda cans, silica beads, or potting soil	Barley, Wheat, Canola	Individual root angle; Total root angle; Individual root length; Total root length.	Examine the root growth behavior in soil without disruption, capture 3-D root structure and totally non-destructive.	Resolution is limited to 1000–2000 $\times$ and does not clearly analyse the cross-section diameter; as it requires high resolution, calibration of gray levels to attenuate coefficients is complicated.	[130]

Table 3. *Cont.*

SmartRoot	laboratory	2-D	Aeroponic system with Hoagland solution	Lupin, Maize	Growth rates; lateral root density; inter-lateral distances; branching angles.	Provides vectoral representation of roots and gives discrimination between root branching and root overlapping. Initially, this issue attracted attention because overlaps create biases in the estimation of the total root length.	Unable to estimate variables such as total root length, at which most root analysis software are usually very good, analyse images in 2-D.	[92]
Shovelomics	Field	2-D	sandy loam soil	maize	Numbers; angles and branching pattern of crown and brace roots; angles; branching.	Quantify root system architectural traits of mature root systems in relatively high throughputs; Nodal root angles or the number of axial and lateral roots are determined from excavated and washed root systems by rating or counting.	Developed only to automatize the quantification of root architectural traits of maize root crowns.	[112]
DIRT	Field	2-D	gellan gum gel	cowpea	Root top and root tip angle; maximum and median width of root system.	Measures traits of monocot and dicot roots from digital images, automates the extraction of root traits by making a high-throughput grid.	Measurements are inspired by the Shovelomics standard for root excavation.	[134]
WinRhizo	Field	2-D	mesocosms consisting of PVC	Maize	Axil root length; axil diameter; lateral root order; number and length.	It can do morphology (length, area, volume), topology, and architecture, made of a computer program and image acquisition components that can be combined to meet different needs.	Its limitations are that color is used to draw the root; Skelton and root distribution used in this software are the same, so it causes confusion.	[129]

Canopy temperature (CT) is one of the major physiological traits related to plant water status and several metabolic processes such as photosynthesis, respiration and transpiration. Canopy temperature depression (CTD) is also a good technique used for field phenotyping of crop plants under stress environments, especially droughts. Canopy temperature and CTD are considered as good indicators of yield [135,136] and transpiration rate [137] under drought conditions. CTD is the difference between air temperature and CT which is correlated with different physiological processes such as stomatal conductance [138], leaf water potential [139], and grain yield [135,140,141] under stress conditions. Measuring CTD through CT and air temperature is a nondestructive method used to check the plant water status under drought conditions [142,143]. Plant water balance is a direct measure of drought response in crop plants [143]. This is associated with the plant transpiration process which is the main cause of leaf temperature variation and is directly associated with leaf temperature and stomatal conductance [138,144]. Therefore, CTD has been used in breeding programs to screen out stress tolerant or susceptible genotypes especially under drought conditions. The phenomenon behind this is drought avoidance which occurs through cooler canopy temperature [81]. Cooler canopy temperature is involved in up to 60% yield variation [81]. The main processes linked with drought adaptation are increased root dry weight, transpiration rate and decreased CT during grain formation [81]. It is observed that transpiration through stomata results in cooler leaves if water is available for transpiration. When water is limited for transpiration, closing of stomata occurs which rises canopy temperature. This change in stomatal conductance as well as leaf transpiration in response to water stress can be detected through thermal imaging [145] and has the potential for selecting large numbers of plants for CO_2 availability [146] and water uptake capacity [147]. The gaseous exchange of water occurs through stomata due to which leaf surfaces are cooled by evaporation and leaf temperature is reduced. While, contrary to this, stomatal closure and reduced transpiration increases leaf or CT [148]. Cooler CT is linked with higher grain yield because of more stomatal opening, exchange of gases and maximum photosynthetic rates [138,149]. Cooler CT is also linked with deeper roots, [68] and higher grain yield [99]. Wheat varieties with cooler canopy temperature have been shown to produce more yield compared with genotypes having warmer canopies [140,150] and warmer CT is associated with reduced stomatal conductance [151].

Under field conditions, reduction in root growth occurs due to a reduction in below ground carbon partitioning at high temperature which may reduce root number, length and diameter at the reproductive stage [152]. However, root development may be promoted under moderate drought through sending an increased amount of carbon assimilates to roots. Thus, it results in increased primary root development and suppression of lateral roots under moderate drought [153]. CT is also associated with root development and it was observed that wheat genotypes with cooler canopy temperatures resulted in an increase of 40% root dry weight at deeper depth (upto 120 cm) [81]. Under drought stress, cooler genotypes exhibited a deeper root system by extracting 35% more water from the deeper soil layer (upto 90 cm) [154]. It shows that cool canopy temperature has been strongly associated with increased plant access to water due to deeper roots [81]. CT can be used as a phenotypic selection tool for breeder's trials [148]. Therefore, canopy temperature can also be used for root phenotyping in crop plants under water stress. Besides its merits, this technique has some limitations; it does not measure plant temperatures correctly, since it depends strongly on microclimate of the plant stand. Therefore, it is carefully balanced with reference temperatures of transpiring canopies. Secondly, higher variability occurs due to rapid changes in environmental conditions in the field, e.g., on cloudy days [155,156]. Variability also occurs due to differences in canopy densities of different genotypes [157]. Differences in plant density in different varieties might be due to differences in the germination rate. This might be due to variation in soil properties and different sowing densities.

4. Use of Breeding and Molecular Approaches to Exploit Root Traits for Drought Tolerance

Drought tolerance through conventional breeding has been achieved in different cereals like wheat [158], rice [159] and maize [160]. However, the breeding approaches for improving crop productivity under drought stress situations are laborious and time consuming as it requires careful management under field conditions [161].

Plant responses to stress conditions occur through various changes at developmental and physiological stages, brought about by altering the expression of stress inducible genes [162]. Root traits are considered to be complex, which is controlled by polygenes having a quantitative effect and are difficult to quantify under field conditions and highly prone to environmental effects. Genetic loci controlling such traits are called quantitative trait loci (QTL). Identification of drought tolerance-related QTLs is one of the promising approaches, using marker-assisted selection [163]. Lots of efforts have been made to identify genes and QTL controlling root traits. Various researchers have studied the linkage of QTL with those traits responsible for increasing root systems foraging capacity in crop plants. These characters showed a molecular mapping of root traits in wheat [164,165], which exhibits the presence of multiple QTLs for different root traits; for instance, root number, length, seminal root number and angle, total root biomass, root system depth, lateral root number and length, and root surface area. It is observed that the productivity, and nutrient and water use efficiency (WUE) of crops could be enhanced by genetic improvement of root system architecture under drought conditions.

The root traits are difficult to phenotype and its QTL mapping is an alternative technique used in breeding programs [166]. Rapid screenings at the seedling stage on the basis of root traits helped in identifying the contrasting lines for mapping QTLs in soybean [20]. To ensure crop productivity under a stressful environment, different alleles may be incorporated into elite cultivars to produce desired root phenotypes through molecular breeding. Different QTLs have been identified for major cereals and legumes such as wheat, rice, maize, barley, pearl millet, sorghum, chickpea and soybean for drought tolerance [167,168]. Identification of genes or molecular markers linked with root architecture and root growth is useful to improve root traits through breeding and molecular selection and are also used to identify QTLs for agronomic traits for drought tolerance [169]. Wild species may have one or more positive alleles at major gene loci that affect agronomic traits [170]. Gene mining from wild species in different plants like tomato [171], soybean [172,173], and rice [174] has proved to be successful for drought tolerance.

Different QTLs have been identified for both biotic and abiotic stress parameters along with physiological, agronomic and seed composition traits in soybean [175]. Several researchers have identified QTLs for RSA in maize and rice and evaluated their effects under different moisture levels on yield [176,177]. For instance, in rice, for greater root length, marker-assisted backcross was used to introgress alleles following four major QTLs affecting root traits [178–180]. Likewise, a major QTL for leaf ABA concentration was also found effective for root architecture as well as grain yield in maize [120,177,181]. Similarly, four major QTLs controlling grain yield and stay-green (Stg1–Stg4) character have also been identified in sorghum [182]

5. Conclusions

Among various environmental stresses, drought is one of the serious stresses which has a significant but negative impact on crop yield. To manage drought, different tools are used to enhance crop yield under drought scenarios. Phenotyping root is one of the drought management tools as roots are more prone to drought conditions and play a significant role in the plant's life by extracting soil resources from deeper soil layers to carry on several metabolic functions in the plant's body and its phenotyping helps to understand different root traits. Similarly, different root phenotyping methodologies and platforms are usually used along with some imaging and image analysis softwares to understand root traits and their role during drought conditions in plants. Different 2-D and 3-D techniques are used for root phenotyping and among all these, each has its advantages and drawbacks. X-ray based computed tomography is a non-invasive technique for 3-D visualization of root traits. Besides, this canopy temperature depression (CTD) has also been considered a good technique for phenotyping of crops facing drought under field conditions. On the basis of this review, it is observed that different root traits such as fine root diameter, specific root length, root area, root angle and root length density are useful for improving plant's productivity under drought conditions. It is, therefore, suggested that these all root traits may be included in breeding programs to improve crop production under drought conditions.

Author Contributions: Wrote the manuscript and prepared tables, A.W.; gave the idea about manuscript and revised it critically and contributed for intellectual contents, X.Z.; helped for collection of manuscript literature, Q.F. and Z.Y.

Funding: This work was supported by the National Key R&D Program of China (2016YFD0300401) and Chinese Academy of Sciences as a part of President's International Fellowship Initiative (PIFI) Program for post-doctoral studies.

Acknowledgments: The authors are grateful to the Chinese Academy of Sciences for providing funds to complete this study.

Conflicts of Interest: The authors declare that there is no conflict of interest for this study. The study was conducted in the absence of any commercial or financial relationship that could be constructed as a potential conflict of interest.

References

1. Araus, J.L.; Slafer, G.A.; Royo, C.; Serret, M.D. Breeding for yield potential and stress adaptation in cereals. *Crit. Rev. Plant Sci.* **2008**, *27*, 377–412. [CrossRef]
2. Farooq, M.; Hussain, M.; Wahid, A.; Siddique, K.H.M. Drought stress in plants: An overview. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*; Aroca, R., Ed.; Springer: Berlin, Germany, 2012; pp. 1–36.
3. Farooq, M.; Hussain, M.; Siddique, K.H. Drought stress in wheat during flowering and grain-filling periods. *Crit. Rev. Plant Sci.* **2014**, *33*, 331–349. [CrossRef]
4. Narayanan, S.; Mohan, A.; Gill, K.S.; Prasad, P.V.V. Variability of root traits in spring wheat germplasm. *PLoS ONE* **2014**, *9*, 0100317. [CrossRef] [PubMed]
5. Dilley, M.; Chen, R.S.; Deichmann, U.; Lerner-Lam, A.L.; Arnold, M. *Natural Disaster Hotspots: A Global Risk Analysis*; International Bank for Reconstruction and Development: Washington, DC, USA, 2005.
6. Helmer, M.; Hilhorst, D. Natural disasters and climate change. *Disasters* **2006**, *30*, 1–4. [CrossRef] [PubMed]
7. Richard, C.A.; Hickey, L.T.; Fletcher, S.; Jennings, R.; Chenu, K.; Christopher, J.T. High-throughput phenotyping of seminal root traits in wheat. *Plant Methods* **2015**, *11*, 1. [CrossRef] [PubMed]
8. Stasovsky, E.; Peterson, C.A. The effects of drought and subsequent rehydration on the structure and vitality of *Zea mays* seedling roots. *Can. J. Bot.* **2015**, *69*, 1170–1178. [CrossRef]
9. Prudhomme, C.; Giuntoli, I.; Robinson, E.L.; Douglas, B.; Clark, N.W.; Arnell, R.; Dankers, B.M.; Fekete, W.; Franssen, D.; Gerten, S.N.; et al. Hydrological droughts in the 21st century, hotspots and uncertainties from a global multimodel ensemble experiment. *Proc. Natl Acad. Sci. USA* **2014**, *111*, 3262–3267. [CrossRef] [PubMed]
10. Charney, T.N. Dynamics of deserts and drought in the Sahel. *Quart. J. R. Meteorol. Soc.* **1975**, *101*, 193–202. [CrossRef]
11. Ludlow, M.M.; Muchow, R.C. A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.* **1990**, *43*, 107–153.
12. Boyer, J.S. Advances in drought tolerance in plants. *Adv. Agron.* **1996**, *56*, 187–218.
13. 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]
14. Bengough, A.G.; McKenzie, B.M.; Hallett, P.D.; Valentine, T.A. Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* **2011**, *62*, 59–68. [CrossRef] [PubMed]
15. Batey, T. Soil compaction and soil management–A review. *Soil Use Manag.* **2009**, *25*, 335–345. [CrossRef]
16. Wang, Y.; Frei, M. Stressed food–The impact of abiotic environmental stresses on crop quality. *Agric. Ecosyst. Environ.* **2011**, *141*, 271–286. [CrossRef]
17. Den Herder, G.; Van Isterdael, G.; Beeckman, T.; De Smet, I. The roots of a new green revolution. *Trends Plant Sci.* **2010**, *15*, 600–607. [CrossRef] [PubMed]

18. Bao, Y.; Aggarwal, P.; Robbins, N.E.; Sturrock, C.J.; Thompson, M.C.; Tan, H.Q.; Tham, C.; Duan, L.; Rodriguez, P.L.; Vernoux, T. Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 9319–9324. [CrossRef] [PubMed]
19. Robbins, N.E.; Dinneny, J.R. The divining root: Moisture-driven responses of roots at the micro-and macro-scale. *J. Exp. Bot.* **2015**, *10*, 1–10. [CrossRef] [PubMed]
20. Manavalan, L.P.; Guttikonda, S.K.; Nguyen, V.T.; Shannon, J.G.; Nguyen, H.T. Evaluation of diverse soybean germplasm for root growth and architecture. *Plant Soil* **2010**, *330*, 503–514. [CrossRef]
21. Prince, S.J.; Mutava, R.N.; Pegoraro, C.; Oliveira, A.C.D.; Nguyen, H.T. Root characters. In *Genomics and Breeding for Climate Resilient Crops*; Kole, C., Ed.; Springer: Berlin, Germany, 2013; pp. 67–131.
22. Lynch, J.P. Roots of the second green revolution. *Aust. J. Bot.* **2007**, *55*, 493–512. [CrossRef]
23. Forde, B.G. Is it good noise? The role of developmental instability in the shaping of a root system. *J. Exp. Bot.* **2009**, *60*, 3989–4002. [PubMed]
24. Haling, R.E.; Brown, L.K.; Bengough, A.G.; Young, I.M.; Hallett, P.D.; White, P.J.; George, T.S. Root hairs improve root penetration, root-soil contact, and phosphorus acquisition in soils of different strength. *J. Exp. Bot.* **2013**, *64*, 3711–3721. [CrossRef] [PubMed]
25. Uga, Y.; Sugimoto, K.; Ogawa, S.; Rane, J.; Ishitani, M.; Hara, N.; Kitomi, Y.; Inukai, Y.; Ono, K.; Kanno, N. Control of root system architecture by *DEEPER ROOTING 1* increases rice yield under drought conditions. *Nat. Genet.* **2013**, *45*, 1097–1102. [CrossRef] [PubMed]
26. Delhaize, E.; Ma, J.F.; Ryan, P.R. Transcriptional regulation of aluminium tolerance genes. *Trends Plant Sci.* **2012**, *17*, 341–348. [CrossRef] [PubMed]
27. Fenta, B.A.; Beebe, S.E.; Kunert, K.J.; Burridge, J.D.; Barlow, K.M.; Lynch, J.P.; Foyer, C.H. Field phenotyping of soybean roots for drought stress tolerance. *Agronomy* **2014**, *4*, 418–435. [CrossRef]
28. Forde, B.G. Nitrogen signalling pathways shaping root system architecture: An update. *Curr. Opin. Plant Biol.* **2014**, *21*, 30–36. [CrossRef] [PubMed]
29. López-Bucio, J.; Cruz-Ramırez, A.; Herrera-Estrella, L. The role of nutrient availability in regulating root architecture. *Curr. Opin. Plant Biol.* **2003**, *6*, 280–287. [CrossRef]
30. Walch-Liu, P.; Ivanov, I.I.; Filleur, S.; Gan, Y.; Remans, T.; Forde, B.G. Nitrogen regulation of root branching. *Ann. Bot.* **2006**, *97*, 875–881. [CrossRef] [PubMed]
31. Zhan, A.; Lynch, J.P. Reduced frequency of lateral root branching improves N capture from low-N soils in maize. *J. Exp. Bot.* **2015**, *66*, 2055–2065. [CrossRef] [PubMed]
32. Lynch, J.P. Root phenes that reduce the metabolic costs of soil exploration: Opportunities for 21st century agriculture. *Plant Cell Environ.* **2014**, *14*, 1–10. [CrossRef] [PubMed]
33. Saengwilai, P.; Tian, X.; Lynch, J.P. Low crown root number enhances nitrogen acquisition from low-nitrogen soils in maize. *Plant Physiol.* **2014**, *166*, 581–589. [CrossRef] [PubMed]
34. Chimungu, J.G.; Brown, K.M.; Lynch, J.P. Large root cortical cell size improves drought tolerance in maize. *Plant Physiol.* **2014**, *166*, 2166–2178. [CrossRef] [PubMed]
35. Waisel, Y.; Eshel, A. Functional diversity of various constituents of a single root system. In *Plant Roots: The Hidden Half*, 3rd ed.; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, 2002; pp. 157–174.
36. Rewald, B.; Ephrath, J.E.; Rachmilevitch, S. A root is a root is a root? Water uptake rates of Citrus root orders. *Plant Cell Environ.* **2011**, *34*, 33–42. [CrossRef] [PubMed]
37. Furbank, R.T.; Tester, M. Phenomics—Technologies relieve the phenotyping bottleneck. *Trends Plant Sci.* **2011**, *16*, 635–644. [CrossRef] [PubMed]
38. Fiorani, F.; Schurr, U. Future scenarios for plant phenotyping. *Annu. Rev. Plant Biol.* **2013**, *64*, 267–291. [CrossRef] [PubMed]
39. Guo, Q.; Zhu, Z. Phenotyping of plants. *Encycl. Anal. Chem.* **2014**, *34*, 1–15.
40. Mohamed, M.F.; Keutgen, N.; Tawfik, A.A.; Noga, G. Dehydration-avoidance responses of tepary bean lines differing in drought resistance. *J. Plant Physiol.* **2002**, *159*, 31–38. [CrossRef]
41. Manschadi, A.M.; Hammer, G.L.; Christopher, J.T.; de Voil, P. Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). *Plant Soil* **2008**, *303*, 115–129. [CrossRef]

42. Gupta, P.K.; Balyan, H.S.; Gahlaut, V.; Kulwal, P.L. Phenotyping, genetic dissection, and breeding for drought and heat tolerance in common wheat: Status and prospects. In *Plant Breeding Reviews*; Janick, J., Ed.; John Wiley and Sons: Hoboken, NJ, USA, 2012; pp. 85–168.
43. Lynch, J. Root architecture and plant productivity. *Plant Physiol.* **1995**, *109*, 7–13. [CrossRef] [PubMed]
44. Zhu, J.; Ingram, P.A.; Benfey, P.N.; Elich, T. From lab to field, new approaches to phenotyping root system architecture. *Curr. Opin. Plant Biol.* **2011**, *14*, 310–317. [CrossRef] [PubMed]
45. Esau, K. *Plant Anatomy*, 2nd ed.; John Wiley and Sons: New York, NY, USA, 1965.
46. Weinhold, L. Histogenetische Studien zum Grenzwurzelproblem. *Beitr. Biol. Pfl.* **1967**, *43*, 367–454.
47. Henry, A.; Gowda, V.R.P.; Torres, R.O.; McNally, K.L.; Serraj, R. Variation in root system architecture and drought response in rice (*Oryza sativa* L.): Phenotyping of the Oryza SNP panel in rainfed low land fields. *Field Crops Res.* **2011**, *120*, 205–214. [CrossRef]
48. Pierret, A.; Moran, C.J.; Doussan, C. Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. *New Phytol.* **2005**, *166*, 967–980. [CrossRef] [PubMed]
49. Manske, G.G.B.; Vlek, P.L.G. Root architecture—Wheat as a model plant. In *Plant Roots: The Hidden Half*, 3rd ed.; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, 2002; pp. 249–259.
50. Bengough, A.G.; Gordon, D.C.; Al-Menaie, H.; Ellis, R.P.; Allan, D.; Keith, R.; Thomas, W.T.B.; Forster, B.P. Gel observation chamber for rapid screening of root traits in cereal seedlings. *Plant Soil* **2004**, *262*, 63–70. [CrossRef]
51. Rostamza, M.; Richards, R.A.; Watt, M. Response of millet and sorghum to a varying water supply around the primary and nodal roots. *Ann. Bot.* **2013**, *112*, 439–446. [CrossRef] [PubMed]
52. Comas, L.H.; Mueller, K.E.; Taylor, L.L.; Midford, P.E.; Callahan, H.S.; Beerling, D.J. Evolutionary patterns and biogeochemical significance of angiosperm root traits. *Int. J. Plant Sci.* **2012**, *173*, 584–595. [CrossRef]
53. Suzuki, N.; Taketa, S.; Ichii, M. Morphological and physiological characteristics of a root-hairless mutant in rice (*Oryza sativa* L.). *Plant Soil* **2003**, *255*, 9–17. [CrossRef]
54. Fitter, A. Characteristics and functions of root systems. In *Plant Roots: The Hidden Half*, 3rd ed.; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, 2002; pp. 15–32.
55. 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. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *J. Exp. Bot.* **2012**, *63*, 3485–3498. [CrossRef] [PubMed]
56. Uga, Y.; Kitomi, Y.; Ishikawa, S.; Yano, M. Genetic improvement for root growth angle to enhance crop production. *Breed. Sci.* **2015**, *65*, 111–119. [CrossRef] [PubMed]
57. Zhu, J.; Brown, K.M.; Lynch, J.P. Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant Cell Environ.* **2010**, *33*, 740–749. [PubMed]
58. Lilley, J.M.; Kirkegaard, J.A. Benefits of increased soil exploration by wheat roots. *Field Crops Res.* **2011**, *122*, 118–130. [CrossRef]
59. Clark, R.T.; MacCurdy, R.B.; Jung, J.K.; Shaff, J.E.; McCouch, S.R.; Aneshansley, D.J.; Kochian, L.V. Three-dimensional root phenotypingwith a novel imaging and software platform. *Plant Physiol.* **2011**, *156*, 455–465. [CrossRef] [PubMed]
60. Pfeifer, J.; Kirchgessner, N.; Colombi, T.; Walter, A. Rapid phenotyping of crop root systems in undisturbed field soils using X-ray computed tomography. *Plant Methods* **2015**, *11*, 41. [CrossRef] [PubMed]
61. Richards, R.A.; Condon, A.G.; Rebetzke, G.J. Traits to improve yield in dry environments. In *Application of Physiology in Wheat Breeding*; Reynolds, M.P., Ortiz-Monasterio, J.I., McNab, A., Eds.; CIMMYT: El Batan, Mexico, 2001; pp. 88–100.
62. Nardini, A.; Salleo, S.; Tyree, M.T. Ecological aspects of water permeability of roots. In *Plant Roots: The Hidden Half*, 3rd ed.; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, 2002; pp. 683–698.
63. Sinclair, T.R. Limits to crop yield? In *Physiology and Determination of Crop Yield*; Boote, K.J., Bennett, J.M., Sinclair, T.R., Paulsen, G.M., Eds.; American Society of Agronomy: Madison, WI, USA, 1994; pp. 509–532.
64. Turner, N.C.; Wright, G.C.; Siddique, K.H.H. Adaptation of grain legumes (pulses) to water-limited environments. *Adv. Agron.* **2001**, *71*, 193–231.
65. Vadez, V.; Rao, J.S.; Bhatnagar-Mathur, P.; Sharma, K.K. *DREB1A* promotes root development in deep soil layers and increases water extraction under water stress in groundnut. *Plant Biol.* **2013**, *15*, 45–52. [CrossRef] [PubMed]

66. Steele, K.A.; Price, A.H.; Witcombe, J.R.; Shrestha, R.; Singh, B.N.; Gibbons, J.M.; Virk, D.S. QTLs associated with root traits increase yield in upland rice when transferred through marker-assisted selection. *Theor. Appl. Genet.* **2013**, *126*, 101–108. [CrossRef] [PubMed]
67. Hammer, G.L.; Dong, Z.S.; McLean, G.; Doherty, A.; Messina, C.; Schusler, J.; Zinselmeier, C.; Paszkiewicz, S.; Cooper, M. Can changes in canopy and/or root system architecture explain historical maize yield trends in the US corn belt? *Crop Sci.* **2009**, *49*, 299–312. [CrossRef]
68. Reynolds, M.; Dreccer, F.; Trethowan, R. Drought-adaptive traits derived from wheat wild relatives and landraces. *J. Exp. Bot.* **2007**, *58*, 177–186. [CrossRef] [PubMed]
69. Manschadi, A.M.; Christopher, J.T.; Hammer, G.L.; de Voil, P. Experimental and modeling studies of drought adaptive root architectural traits in wheat (*Triticum aestivum* L.). *Plant Biosyst.* **2010**, *144*, 458–462. [CrossRef]
70. Krishnamurthy, L.; Johansen, C.; Sethi, S.C. Investigation of factors determining genotypic differences in seed yield of non-irrigated and irrigated chickpeas using a physiological model of yield determination. *J. Agron. Crop Sci.* **1999**, *183*, 9–17. [CrossRef]
71. Kashiwagi, J.; Krishnamurthy, L.; Crouch, J.H.; Serraj, R. Variability of root length density and its contributions to seed yield in chickpea (*Cicer arietinum* L.) under terminal drought stress. *Field Crops Res.* **2006**, *95*, 171–181. [CrossRef]
72. Eissenstat, D.M. Costs and benefits of constructing roots of small diameter. *J. Plant Nutr.* **1992**, *15*, 763–782. [CrossRef]
73. Sadok, W.; Sinclair, T.R. Crops yield increase under water–limited conditions: Review of recent physiological advances for soybean genetic improvement. *Adv. Agron.* **2011**, *113*, 313–337.
74. Varshney, R.K.; Pazhamala, L.; Kashiwagi, J.; Gaur, P.M.; Krishnamurthy, L.; Hoisington, D. Genomics and physiological approaches for root trait breeding to improve drought tolerance in chickpea (*Cicer arietinum* L.). In *Root Genomics*; Springer: Berlin, Heidelberg, 2011; pp. 233–250.
75. Forster, B.P.; Thomas, W.T.B.; Chloupek, O. Genetic controls of barley root systems and their associations with plant performance. *Asp. Appl. Biol.* **2005**, *73*, 199–204.
76. Passioura, J.B. The role of root system characteristics in the drought resistance of crop plants. In *Drought Resistance in Crops with Emphasis on Rice*; International Rice Research Institute: Los Banos, Philippines, 1982; pp. 71–82.
77. Landi, P.; Giuliani, S.; Salvi, S.; Ferri, M.; Tuberosa, R.; Sanguineti, M.C. Characterization of root–yield–1.06, a major constitutive QTL for root and agronomic traits in maize across water regimes. *J. Exp. Bot.* **2010**, *61*, 3553–3562. [CrossRef] [PubMed]
78. Hund, A.; Reimer, R.; Messmer, R. A consensus map of QTLs controlling the root length of maize. *Plant Soil* **2011**, *344*, 143–158. [CrossRef]
79. Henry, A.; Cal, A.J.; Batoto, T.C.; Torres, R.O.; Serraj, R. Root attributes affecting water uptake of rice (*Oryza sativa* L.) under drought. *J. Exp. Bot.* **2012**, *63*, 4751–4763. [CrossRef] [PubMed]
80. Ho, M.D.; Rosas, J.C.; Brown, K.M.; Lynch, J.P. Root architectural tradeoffs for water and phosphorus acquisition. *Funct. Plant Biol.* **2005**, *32*, 737–748. [CrossRef]
81. Osmont, K.S.; Sibout, R.; Hardtke, C.S. Hidden branches: Developments in root system architecture. *Annu. Rev. Plant Biol.* **2007**, *58*, 93–113. [CrossRef] [PubMed]
82. Agbicodo, E.M.; Fatokun, C.A.; Muranaka, S.; Visser, R.G.F.; van der Linden, C.G. Breeding drought tolerant cowpea: Constraints, accomplishments, and future prospects. *Euphytica* **2009**, *167*, 353–370. [CrossRef]
83. Lopes, M.S.; Araus, J.L.; van Heerden, P.D.R.; Foyer, C.H. Enhancing drought tolerance in C4 crops. *J. Exp. Bot.* **2011**, *62*, 3135–3153. [CrossRef] [PubMed]
84. Garay, A.F.; Wilhelm, W.W. Root system characteristics of two soybean isolines undergoing water stress conditions. *Agron. J.* **1982**, *75*, 973–977. [CrossRef]
85. Zhao, J.; Fu, J.; Liao, H.; He, Y.; Nian, H.; Hu, Y.; Qiu, L.; Dong, Y.; Yan, X. Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. *Chin. Sci. Bull.* **2004**, *49*, 1611–1620. [CrossRef]
86. Manschadi, A.M.; Christopher, J.T.; DeVoil, P.; Hammer, G.L. The role of root architectural traits in adaptation of wheat to water-limited environments. *Funct. Plant Biol.* **2006**, *33*, 823–837. [CrossRef]
87. Tucker, S.S.; Craine, J.M.; Nippert, J.B. Physiological drought tolerance and the structuring of tall grass prairie assemblages. *Ecosphere* **2011**, *2*, 1–19. [CrossRef]

88. Clark, L.J.; Price, A.H.; Steele, K.A.; Whalley, R.R. Evidence from near-isogenic lines that root penetration increases with root diameter and bending stiffness in rice. *Funct. Plant Biol.* **2008**, *35*, 1163–1171. [CrossRef]
89. Zhao, S.H.; Wang, F.Z.; Lu, L.; Zhang, H.Y.; Zhang, X.Y. Breeding and selection of drought resistant and salt tolerant wheat variety Cang 6001. *Acta Agric. Boreal Sin.* **2000**, *15*, 113–117.
90. Armengaud, P.; Zambaux, K.; Sulpice, R.; Pattiso, R.; Blatt, M.; Amtmann, A. EZ-Rhizo: Integrated software for the fast and accurate measurement of root system architecture. *Plant J.* **2009**, *57*, 945–956. [CrossRef] [PubMed]
91. Lobet, G.; Pages, L.; Draye, X. A novel image-analysis toolbox enabling quantitative analysis of root system architecture. *Plant Physiol.* **2011**, *157*, 29–39. [CrossRef] [PubMed]
92. Arsenault, J.L.; Pouleur, S.; Messier, C.; Guay, R. WinRhizo, a root measuring system with a unique overlap correction method. *Hort. Sci.* **1995**, *30*, 906.
93. Abramoff, M.D.; Magelhaes, P.J.; Ram, S.J. Image processing with Image. *J. Biophotonics Int.* **2004**, *11*, 36–42.
94. Pound, M.P.; French, A.P.; Atkinson, J.; Wells, D.M.; Bennett, M.J.; Pridmore, T.P. Rootnav: Navigating images of complex root architectures. *Plant Physiol.* **2013**, *162*, 1802–1814. [CrossRef] [PubMed]
95. Pierret, A.; Gonkhamdee, S.; Jourdan, C.; Maeght, J.L. IJ_RHIZO: An open-source software to measure scanned images of root samples. *Plant Soil* **2013**, *373*, 531–539. [CrossRef]
96. Leitner, D.; Felderer, B.; Vontobel, P.; Schnepf, A. Recovering root system traits using image analysisexemplified by two-dimensional neutron radiography images of lupine. *Plant Physiol.* **2014**, *164*, 24–35. [CrossRef] [PubMed]
97. Clark, R.T.; Famoso, A.N.; Zhao, K.; Shaff, J.E.; Craft, E.J.; Bustamante, C.D.; Mccouch, S.R.; Aneshansley, D.J.; Kochian, L.V. High-throughput two-dimensional root system phenotyping platform facilitates genetic analysis of root growth and development. *Plant Cell Environ.* **2013**, *36*, 454–466. [CrossRef] [PubMed]
98. Watt, M.; Moosavi, S.; Cunningham, S.C.; Kirkegaard, J.A.; Rebetzke, G.J.; Richards, R.A. A rapid, controlled-environment seedling root screen for wheat correlates well with rooting depths at vegetative, but not reproductive, stages at two field sites. *Ann. Bot.* **2013**, *112*, 447–455. [CrossRef] [PubMed]
99. Lopes, M.S.; Reynolds, M.P. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Funct. Plant Biol.* **2010**, *37*, 147–156. [CrossRef]
100. Le Mari, C.; Norbert, K.; Daniela, M.; Achim, W.; Andreas, H. Rhizoslides: Paper-based growth system for non-destructive, high throughput phenotyping of root development by means of image analysis. *Plant Methods* **2014**, *10*, 13. [CrossRef] [PubMed]
101. Nagel, K.A.; Kastenholz, B.; Jahnke, S.; Van Dusschoten, D.; Aach, T.; Mühlich, M.; Truhn, D.; Scharr, H.; Terjung, S.; Walter, A.; et al. Temperature responses of roots: Impact on growth, root system architecture and implications for phenotyping. *Funct. Plant Biol.* **2009**, *36*, 947–959. [CrossRef]
102. Downie, H.; Holden, N.; Otten, W.; Spiers, A.J.; Valentine, T.A.; Dupuy, L.X. Transparent soil for imaging the rhizosphere. *PLoS ONE* **2012**, *7*, e44276. [CrossRef] [PubMed]
103. De Dorlodot, S.; Bertin, P.; Baret, P.; Draye, X. Scaling up quantitative phenotyping of root system architecture using a combination of aeroponics and image analysis. *Asp. Appl. Biol.* **2005**, *73*, 41–54.
104. Tuberosa, R.; Sanguineti, M.C.; Landi, P.; Giuliani, M.M.; Salvi, S.; Conti, S. Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Plant Mol. Biol.* **2002**, *48*, 697–712. [CrossRef] [PubMed]
105. Courtois, B.; Audebert, A.; Dardou, A.; Roques, S.; Ghneim-Herrera, T.; Droc, G.; Frouin, J.; Rouan, L.; Gozé, E.; Kilian, A.; et al. Genome-wide association mapping of root traits in a japonica rice panel. *PLoS ONE* **2013**, *8*, e78037. [CrossRef] [PubMed]
106. Zhu, J.M.; Kaeppler, S.M.; Lynch, J.P. Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theor. Appl. Genet.* **2005**, *111*, 688–695. [CrossRef] [PubMed]
107. Trachsel, S.; Messmer, R.; Stamp, P.; Hund, A. Mapping of QTLs for lateral and axile root growth of tropical maize. *Theor. Appl. Genet.* **2009**, *119*, 1413–1424. [CrossRef] [PubMed]
108. Pfeifer, J.; Faget, M.; Walter, A.; Blossfeld, S.; Fiorani, F.; Schurr, U.; Nagel, K.A. Spring barley shows dynamic compensatory root and shoot growth responses when exposed to localised soil compaction and fertilisation. *Funct. Plant Biol.* **2014**, *41*, 581–597. [CrossRef]

109. Landi, P.; Sanguineti, M.C.; Darrah, L.L.; Giuliani, M.M.; Salvi, S.; Conti, S.; Tuberosa, R. Detection of QTLs for vertical root pulling resistance in maize and overlap with QTLs for root traits in hydroponics and for grain yield under different water regimes. *Maydica* **2002**, *47*, 233–243.
110. Bohn, M.; Novais, J.; Fonseca, R.; Tuberosa, R.; Grift, T.E. Genetic evaluation of root complexity in maize. *Acta Agron. Hung.* **2006**, *54*, 291–303. [CrossRef]
111. Grift, T.E.; Novais, J.; Bohn, M. High-throughput phenotyping technology for maize roots. *Biosyst. Eng.* **2011**, *110*, 40–48. [CrossRef]
112. Perkons, U.; Kautz, T.; Uteau, D.; Peth, S.; Geier, V.; Thomas, K.; Holz, K.L.; Athmann, M.; Pude, R.; Köpke, U. Root-length densities of various annual crops following crops with contrasting root systems. *Soil Tillage Res.* **2014**, *137*, 50–57. [CrossRef]
113. Nielsen, K.L.; Lynch, J.P.; Weiss, H.N. Fractal geometry of bean root systems: Correlations between spatial and fractal dimension. *Am. J. Bot.* **1997**, *84*, 26–33. [CrossRef] [PubMed]
114. Benjamin, J.G.; Nielsen, D.C. A method to separate plant roots from soil and analyze root surface area. *Plant Soil* **2004**, *267*, 225–234. [CrossRef]
115. Böhm, W. *Methods of Studying Root Systems*; Springer Science and Business Media: Heidelberg, Germany, 2012.
116. Bucksch, A.; Burridge, J.; York, L.M.; Das, A.; Nord, E.; Weitz, J.S.; Lynch, J.P. Image-based high-throughput field phenotyping of crop roots. *Plant Physiol.* **2014**, *166*, 470–486. [CrossRef] [PubMed]
117. Herrera, J.M.; Stamp, P.; Liedgens, M. Dynamics of root development of spring wheat genotypes varying in nitrogen use efficiency. In *Wheat Production in Stressed Environments*; Springer: Dordrecht, The Netherlands, 2007; pp. 197–201.
118. Chloupek, O. Evaluation of size of a plants-root system using its electrical capacitance. *Plant Soil.* **1977**, *48*, 525–532. [CrossRef]
119. Messmer, R.; Fracheboud, Y.; Baenziger, M.; Stamp, P.; Ribaut, J.M. Drought stress and tropical maize: QTLs for leaf greenness, plant senescence, and root capacitance. *Field Crop Res.* **2011**, *124*, 93–103. [CrossRef]
120. Harris, K.; Subudhi, P.K.; Borrell, A.; Jordan, D.; Rosenow, D.; Nguyen, H.; Klein, P.; Klein, R.; Mullet, J. Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. *J. Exp. Bot.* **2007**, *58*, 327–338. [CrossRef] [PubMed]
121. Dietrich, R.C.; Bengough, A.G.; Jones, H.G.; White, P.J. Can root electrical capacitance be used to predict root mass in soil? *Ann. Bot.* **2013**, *112*, 457–464. [CrossRef] [PubMed]
122. Dietrich, R.C.; Bengough, A.G.; Jones, H.G.; White, P.J. A new physical interpretation of plant root capacitance. *J. Exp. Bot.* **2012**, *63*, 6149–6159. [CrossRef] [PubMed]
123. Heeraman, D.A.; Hopmans, J.W.; Clausnitzer, V. Three dimensional imaging of plant roots in situ with X-ray computed tomography. *Plant Soil.* **1997**, *189*, 167–179. [CrossRef]
124. Rashid, A.; Stark, J.C.; Tanveer, A.; Mustafa, T. Use of canopy temperature measurements as a screening tool for drought tolerance in spring wheat. *J. Agron. Crop Sci.* **1999**, *182*, 231–237. [CrossRef]
125. Royo, C.; Villegas, D.; Del Moral, L.G.; Elhani, S.; Aparicio, N.; Rharrabti, Y.; Araus, J.L. Comparative performance of carbon isotope discrimination and canopy temperature depression as predictors of genotype differences in durum wheat yield in Spain. *Crop Pasture Sci.* **2002**, *53*, 561–569. [CrossRef]
126. Zhu, Z.; Momeu, C.; Zakhartsev, M.; Schwaneberg, U. Making glucose oxidase fit for biofuel cell applications by directed protein evolution. *Biosens. Bioelectron.* **2006**, *21*, 2046–2051. [CrossRef] [PubMed]
127. Zheng, B.S.; Yang, L.; Zhang, W.P.; Mao, C.Z.; Wu, Y.R.; Yi, K.K.; Liu, F.Y.; Wu, P. Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. *Theor. Appl. Genet.* **2003**, *107*, 1505–1515. [CrossRef] [PubMed]
128. Fita, A.; Pico, B.; Roig, C.; Nuez, F. Performance of Cucumis melo ssp. agrestis as a root stock for melon. *J. Hortic. Sci. Biotechnol.* **2007**, *82*, 184–190. [CrossRef]
129. Hargreaves, C.; Gregory, P.; Bengough, A. Measuring root traits in barley (Hordeum vulgare ssp. vulgare and ssp. spontaneum) seedlings using gel chambers, soil sacs and X-raymicro-tomography. *Plant Soil* **2009**, *316*, 285–297. [CrossRef]
130. Wu, J.; Guo, Y. An integrated method for quantifying root architecture of field-grown maize. *Ann. Bot.* **2014**, *114*, 841–851. [CrossRef] [PubMed]
131. Armengaud, P. EZ-Rhizo software the gateway to root architecture analysis. *Plant Signal. Behav.* **2009**, *4*, 139–141. [CrossRef] [PubMed]

132. Mulayim, A.Y.; Yılmaz, U.; Atalay, V. Silhouette-based 3d model reconstruction from multipleimages. *IEEE Trans. Syst. Man Cy-Bern. Part B* **2003**, *33*, 1–10.
133. Das, A.; Schneider, H.; Burridge, J.; Ascanio, A.K.M.; Wojciechowski, T.; Topp, C.N.; Lynch, J.P.; Weitz, J.S.; Bucksch, A. Digital imaging of root traits (DIRT): A high-throughput computing and collaboration platform for field-based root phenomics. *Plant Methods* **2015**, *11*, 51. [CrossRef] [PubMed]
134. Paez-Garcia, A.; Motes, C.M.; Scheible, W.R.; Chen, R.; Blancaflor, E.B.; Monteros, M.J. Root traits and phenotyping strategies for plant improvement. *Plants* **2015**, *4*, 334–355. [CrossRef] [PubMed]
135. Mahan, J.R.; Young, A.W.; Payton, P. Deficit irrigation in a production setting: Canopy temperature as an adjunct to ET estimates. *Irrig. Sci.* **2011**, *30*, 127–137. [CrossRef]
136. Rebetzke, G.J.; Rattey, A.R.; Farquhar, G.D.; Richards, R.A.; Condon, A.G. Genomic regions for canopy temperature and their genetic association with stomatal conductance and grain yield in wheat. *Funct. Plant Biol.* **2013**, *40*, 14–33. [CrossRef]
137. Cohen, Y.; Alchanatis, V.; Meron, M.; Saranga, Y.; Tsipris, J. Estimation of leaf water potential by thermal imagery and spatial analysis. *J. Exp. Bot.* **2005**, *56*, 1843–1852. [CrossRef] [PubMed]
138. Ayeneh, A.; van Ginkel, M.; Reynolds, M.P.; Ammar, K. Comparison of leafspike, peduncle and canopy temperature depression in wheat under heatstress. *Field Crop Res.* **2002**, *79*, 173–184. [CrossRef]
139. Balota, M.; Payne, W.A.; Evett, S.R.; Lazar, M.D. Canopy temperature depression sampling to assess grain yield and genotypic differentiation in winter wheat. *Crop Sci.* **2007**, *47*, 1518–1529. [CrossRef]
140. Karmizadeh, R.; Mohammadi, M. Association of canopy temperature depression with yield of durum wheat genotypes under supplementary irrigated and rainfed conditions. *Aust. J. Crop Sci.* **2011**, *5*, 138–146.
141. Reynolds, M.P.; Balota, M.; Delgado, M.I.B.; Amani, I.; Fischer, R.A. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Funct. Plant Biol.* **1994**, *21*, 717–730. [CrossRef]
142. Purushothaman, R.; Thudi, M.; Krishnamurthy, L.; Upadhyaya, H.D.; Kashiwagi, J.; Gowda, C.L.L.; Varshney, R.K. Association of mid-reproductive stage canopy temperature depression with the molecular markers and grain yields of chickpea (Cicer arietinum L.) germplasm under terminal drought. *Field Crops Res.* **2015**, *174*, 1–11. [CrossRef]
143. Chaerle, L.; Leinonen, I.; Jones, H.G.; Van Der Straeten, D. Monitoring and screening plant populations with combined thermal and chlorophyll fluorescence imaging. *J. Exp. Bot.* **2007**, *58*, 773–784. [CrossRef] [PubMed]
144. Hashimoto, H.; Fujii, R.; Yanagi, K.; Kusumoto, T.; Gardiner, A.T.; Cogdell, R.J.; Frank, H.A. Structures and functions of carotenoids bound to reaction centers from purple photosynthetic bacteria. *Pure Appl. Chem.* **2006**, *78*, 1505–1518. [CrossRef]
145. Horie, T.; Horie, R.; Chan, W.Y.; Leung, H.Y.; Schroeder, J.I. Calcium regulation of sodium hypersensitivities of sos3 and athkt1 mutants. *Plant Cell Physiol.* **2006**, *47*, 622–633. [CrossRef] [PubMed]
146. Amani, A.; Lebel, T.; Rousselle, J.; Taupin, J.D. Typology of rainfall fields to improve rainfall estimation in the Sahel by the area threshold method. *Water Resour. Res.* **1996**, *32*. [CrossRef]
147. Batts, G.R.; Ellis, R.H.; Morison, J.I.L.; Nkemka, P.N.; Gregory, P.J.; Hadley, P. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO_2 and temperature in field studies using temperature gradient tunnels. *J. Agric. Sci.* **1998**, *130*, 17–27. [CrossRef]
148. Deery, D.M.; Rebetzke, G.J.; Jimenez-Berni, J.A.; James, R.A.; Condon, A.G.; Bovill, W.D.; Hutchinson, P.; Scarrow, J.; Davy, R.; Furbank, R.T. Methodology for high-throughput field phenotyping of canopy temperature using airborne thermography. *Front. Plant Sci.* **2016**, *7*, 1808. [CrossRef] [PubMed]
149. Fischer, R.A.; Rees, D.; Sayre, K.D.; Lu, Z.M.; Condon, A.G.; Saavedra, A.L. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Sci.* **1998**, *38*, 1467–1475. [CrossRef]
150. Smith, S.; De Smet, I. Root system architecture: Insights from Arabidopsis and cereal crops. philosophical transactions of the royal society of London. *Biol. Sci.* **2012**, *367*, 1441–1452. [CrossRef] [PubMed]
151. Pinter, P.J.; Zipoli, G., Jr.; Reginato, R.J.; Jackson, R.D.; Idso, S.B.; Hohman, J.P. Canopy temperature as an indicator of differential water use and yield performance among wheat cultivars. *Agric. Water Manag.* **1990**, *18*, 35–48. [CrossRef]
152. Pinto, R.S.; Reynolds, M.P. Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. *Theor. Appl. Genet.* **2015**, *128*, 575–585. [CrossRef] [PubMed]

153. Guo, D.L.; Xia, M.X.; Wei, X.; Chang, W.J.; Liu, Y.; Wang, Z.Q. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytol.* **2008**, *180*, 673–683. [CrossRef] [PubMed]
154. Xia, M.X.; Guo, D.L.; Pregitzer, K.S. Ephemeral root modules in Fraxinus mandshurica. *New Phytol.* **2010**, *188*, 1065–1074. [CrossRef] [PubMed]
155. Jones, H.G.; Serraj, R.; Loveys, B.R.; Xiong, L.; Wheaton, A.; Price, A.H. Thermal infrared imaging of crop canopies for the remote diagnosis and quantification of plant responses to water stress in the field. *Funct. Plant Biol.* **2009**, *36*, 978–989. [CrossRef]
156. Costa, J.M.; Grant, O.M.; Chaves, M.M. Thermography to explore plant—Environment interactions. *J. Exp. Bot.* **2013**, *64*, 3937–3949. [CrossRef] [PubMed]
157. White, J.W.; Andrade-Sanchez, P.; Gore, M.A.; Bronson, K.F.; Coffelt, T.A.; Conley, M.M. Field-based phenomics for plant genetics research. *Field Crop Res.* **2012**, *133*, 101–112. [CrossRef]
158. Zhang, X.; Zhou, S.; Fu, Y.; Su, Z.; Wang, X.; Sun, C. Identification of a drought tolerant introgression line derived from Dongxiang common wild rice (*O. rufipogon* Grif.). *Plant Mol. Biol.* **2006**, *62*, 247–259. [CrossRef] [PubMed]
159. Hoisington, D.; Jiang, C.; Khairallah, M.; Ribaut, J.M.; Bohn, M.; Melchinger, A.; Willcox, M.; Gonzalez-de Leon, D. QTL for insect resis-tance and drought tolerance in tropical maize: Prospects for marker assisted selection. *Symp. Soc. Exp. Biol.* **1996**, *50*, 39–44. [PubMed]
160. Yoshida, S.; Hasegawa, S. The rice root system: It development and function. In *Drought Resistance in Crops with Emphasis on Rice*; International Rice Research Institute: Los Banos, Philippines, 1982; pp. 97–114.
161. Philippe, R.; Philippe, R.; Courtois, B.; McNally, K.L.; Mournet, P.; El-Malki, R.; Le Paslier, M.C.; Fabre, D.; Billot, C.; Brunel, D.; et al. Structure, allelic diversity and selection of Asr genes, candidate for drought tolerance, in Oryza sativa L. and wild relatives. *Theor. Appl. Genet.* **2010**, *121*, 769–787. [CrossRef] [PubMed]
162. Pathan, M.S.; Lee, J.D.; Shannon, J.G.; Nguyen, H.T. Recent advances in breeding for drought and salt stress tolerance in soybean. In *Advances in Molecular Breeding toward Drought and Salt Tolerant Crops*; Jenks, M.A., Hasegawa, P.M., Jain, S.M., Eds.; Springer: New York, NY, USA, 2007; pp. 739–773.
163. Hamada, A.; Nitta, M.; Nasuda, S.; Kato, K.; Fujita, M.; Matsunaka, H.; Okumoto, Y. Novel QTLs for growth angle of seminal roots in wheat (*Triticum aestivum* L.). *Plant Soil* **2012**, *354*, 395–405. [CrossRef]
164. Ren, Y.; He, X.; Liu, D.; Li, J.; Zhao, X.; Li, B.; Tong, Y.; Zhang, A.; Li, Z. Major quantitative trait loci for seminal root morphology of wheat seedlings. *Mol. Breed.* **2012**, *30*, 139–148. [CrossRef]
165. Coudert, Y.; Périn, C.; Courtois, B.; Khong, N.G.; Gantet, P. Genetic control of root development in rice, the model cereal. *Trends Plant Sci.* **2010**, *15*, 219–226. [CrossRef] [PubMed]
166. Tanksley, S.D. Mapping polygenes. *Annu. Rev. Genet.* **1993**, *27*, 205–233. [CrossRef] [PubMed]
167. Feng, Z.; Mao, Y.; Xu, N.; Zhang, B.; Wei, P.; Yang, D.L.; Wang, Z.; Zhang, Z.; Zheng, R.; Yang, L.; et al. Multi-generation analysis reveals the inheritance, specificity and patterns of CRISPR/Cas induced gene modification in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 4632–4637. [CrossRef] [PubMed]
168. Feuillet, C.; Leach, J.E.; Rogers, J.; Schnable, P.S.; Eversole, K. Crop genome sequencing: Lessons and rationales. *Trends in Plant Sci.* **2011**, *16*, 77–88. [CrossRef] [PubMed]
169. Tanksley, S.D.; McCouch, S.R. Seed banks and molecular maps: Unlocking genetic potential from the wild. *Science* **1997**, *277*, 1063–1066. [CrossRef] [PubMed]
170. Tanksley, S.D.; Grandillo, S.; Fulton, T.M.; Zamir, D.; Eshed, Y.; Petiard, V.; Lopez, J.; Beck-Bunn, T. Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. Pimpinellifolium*. *Theor. Appl. Genet.* **1996**, *92*, 213–224. [CrossRef] [PubMed]
171. Bauer, S.; Hymowitz, T.; Noel, G.R. Soybean cyst nematode resistance derived from Glycine tomentella in amphiploid (Glysine max × Glysine tomentella) hybrid lines. *Nematropica* **2007**, *37*, 277–285.
172. Lenis, J.M.; Ellersieck, M.; Blevins, D.G.; Sleper, D.A.; Nguyen, H.T.; Dunn, D.; Lee, J.D.; Shannon, J.G. Differences in ion accumulation and salt tolerance among Glycine accessions. *J. Agron. Crop Sci.* **2011**, *197*, 302–310. [CrossRef]
173. Xiao, J.; Li, J.; Grandillo, S.; Ahn, S.N.; Yuan, L.; Tanksley, S.D.; McCouch, S.R. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon*. *Genetics* **1998**, *150*, 899–909. [PubMed]
174. MacMillan, K.; Emrich, K.; Piepho, H.P.; Mullins, C.E.; Price, A.H. Assessing the importance of genotype × environment interaction for root traits in rice using a mapping population. I: A soil-filled box screen. *Theor. Appl. Genet.* **2006**, *113*, 977–986. [CrossRef] [PubMed]

175. Lakshmi, P.; Manavalan, S.K.; Guttikonda, L.P.T.; Henry, T.N. Physiological and Molecular Approaches to Improve Drought Resistance in Soybean. *Plant Cell Physiol.* **2009**, *50*, 1260–1276.
176. Landi, P.; Sanguineti, M.C.; Liu, C.; Li, Y.; Wang, T.Y.; Giuliani, S.; Bellotti, M.; Salvi, S.; Tuberosa, R. Root-ABA1 QTL affects root lodging, grain yield, and other agronomic traits in maize grown under well-watered and water-stressed conditions. *J. Exp. Bot.* **2007**, *58*, 319–326. [CrossRef] [PubMed]
177. Courtois, B.; McLaren, G.; Sinha, P.K.; Prasad, K.; Yadav, R.; Shen, L. Mapping QTLs associated with drought avoidance in upland rice. *Mol. Breed.* **2000**, *6*, 55–66. [CrossRef]
178. Steele, K.A.; Price, A.H.; Shashidhar, H.E.; Witcombe, J.R. Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian upland rice variety. *Theor. Appl. Genet.* **2006**, *112*, 208–221. [CrossRef] [PubMed]
179. Steele, K.A.; Virk, D.S.; Kumar, R.; Prasad, S.C.; Witcombe, J.R. Field evaluation of upland rice lines selected for QTLs controlling root traits. *Field Crops Res.* **2007**, *101*, 180–186. [CrossRef]
180. Tuberosa, R.; Sanguineti, M.C.; Landi, P.; Salvi, S.; Casarini, E.; Conti, S. RFLP mapping of quantitative trait loci controlling abscisic acid concentration in leaves of drought-stressed maize (*Zea mays* L.). *Theor. Appl. Genet.* **1998**, *97*, 744–755. [CrossRef]
181. Giuliani, S.; Sanguineti, M.C.; Tuberosa, R.; Bellotti, M.; Salvi, S.; Landi, P. Root-ABA1, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes. *J. Exp. Bot.* **2005**, *56*, 3061–3070. [CrossRef] [PubMed]
182. Walter, A.; Liebisch, F.; Hund, A. Plant phenotyping: From bean weighing to image Analysis. *Plant Methods* **2015**, *11*, 1–11. [CrossRef] [PubMed]