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Review

Toward an Integrated Root Ideotype for Irrigated Systems

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Breeding towards root-centric ideotypes can be a relatively quick trait-based strategy to improve crop resource use efficiency. Irrigated agriculture represents a crucial and expanding sector, but its unique parameters require traits distinct from previously proposed rainfed ideotypes. We propose a novel irrigated ideotype that integrates traits across multiple scales to enhance resource use efficiency in irrigated agroecosystems, where resources are concentrated in a relatively shallow 'critical zone'. Unique components of this ideotype include rapid transplant recovery and establishment, enhanced exploitation of localized resource hotspots, adaptive physiological regulation, maintenance of hydraulic conductivity, beneficial rhizosphere interactions, and salinity/waterlogging avoidance. If augmented by future research, this target could help to enhance agricultural sustainability in irrigated agroecosystems by guiding the creation of resource-efficient cultivars.

Trends

Ideotypes combining advantageous root traits have been proposed as breeding targets for rainfed systems, but the unique environment of irrigated agriculture has been neglected.

Recent advances in belowground phenotyping, genomics, and our understanding of rhizosphere processes have helped to improve adaptive root responses to heterogeneous nutrient and water availability, but the results have rarely been applied to irrigated systems.

Plasticity and intensive exploitation of concentrated resources appear to be more important than the previous emphasis on rooting depth and low metabolic cost.

Increasing Resource Use Efficiency Requires a Novel Root Ideotype Tailored to Irrigated Systems

If current **water use efficiency** (WUE, see Glossary) does not increase, irrigated land area is projected to increase by 40 million ha by 2030, and water needs by 20% by 2050, to sustain food production required for a growing population [1–6]. Many economically and nutritionally important fruit and vegetable crops are produced in irrigated agroecosystems located in arid and semi-arid climates with scarce and unreliable water resources. Given tight linkages between irrigation water management, nutrient cycling, and yields in irrigated systems [7], improving **water productivity** is crucial to sustain healthy and productive food systems while decreasing pressure on the environment and limited water supplies in a changing climate [8].

Breeding resource-efficient cultivars could complement improvements in irrigation technology, such as **micro-irrigation** [9], to maintain the sustainability of irrigated agriculture in an uncertain future. Root-based approaches present untapped potential to create cultivars adapted to the unique resource environment of irrigated crops because most research has been directed toward exploiting root traits to enhance nitrogen (N), water, and phosphorus (P) use efficiency in rainfed systems [10]. We argue that rainfed root ideotypes likely do not translate to the unique irrigated context, and that addressing architectural and morphological traits without sufficient attention to rhizosphere functions [11,12] fosters incomplete understanding of beneficial root traits for specific soil and management practices, as well as of genotype-specific responses to environmental cues. A novel root ideotype for irrigated annual crops, which integrates a large suite of architectural, morphological, physiological, and biotic traits, is crucially needed to enhance agricultural productivity and decouple the necessary intensification from environmental degradation. This ideotype can guide the development of resource-efficient cultivars adapted to irrigated agroecosystems which better capture costly water inputs, reduce the environmental footprint of irrigated agricultural landscapes, and dynamically cope with limiting nutrient resources or acute shortages of irrigation water.

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The Unique Irrigated Environment

Previous discussions of beneficial root traits [11,13,14] and ideotypes for rainfed systems [15] have greatly contributed to our understanding of the root functions and mechanisms that are essential to efficiently capture resources. A frequently cited rainfed-environment ideotype to enhance cereal foraging and the acquisition of water and mobile nutrients combines steep root angle, deep taproot development, unresponsive lateral branching, and low metabolic investment (Figure 1, Key Figure) [10,15]. Although this ideotype offers useful insights into the importance of individual phenes and their interactions, rainfed ideotypes do not necessarily translate to irrigated systems where temporal and spatial resource dynamics differ at the system, field, and rhizosphere scales.

First, root ideotype models developed to perform under resource-limited rainfed conditions [15,16] may not suit intensive irrigated environments, where nutrients rarely limit productivity

Box 1. Environment-Specific Tradeoffs of Component Traits

A key aspect of the irrigated ideotype is that it must be tailored to its environment to minimize undesirable tradeoffs (Table I) in terms of metabolic cost, foraging ability, responsiveness, and nutrient uptake. Soil characteristics such as resource availability and compaction establish the framework for cost–benefit analyses specific to each root trait. For instance, in a compacted and intensively managed system with high inorganic P availability, C investment in shallow lateral root proliferation could be more advantageous than root hair development and the recruitment of microbes that solubilize organic P. Long-lived and highly vesseled roots could increase nutrient transport but might compromise rapid foraging responses to capture nutrient pulses; the former strategy is most attractive when resources are homogeneous and abundant. While determining the relative benefit of traits for each specific soil environment represents an increase in complexity over a universal ideotype, this approach could help to maximize resource use efficiency.

Table I. Potential Tradeoffs Associated with Ideotype Traits

Category	Trait	Tradeoffs
Morphology	Few axial roots with varied angles	Reduced patch exploitation in any single direction and/or capture of mobile nutrients below the wetting zone
	Plastic, localized, and prolific lateral root proliferation	Maladaptive when resources are very heterogeneous because of construction and maintenance costs [79,94]
		Restricted foraging outside the wetting zone could limit immobile resource availability
Anatomy	Long, dense root hairs	Construction and maintenance costs; less beneficial in compacted soil because of the already high root–soil contact [95]
	Aerenchyma formation	Aerenchyma may decrease lodging resistance [17] and radial water and nutrient transport [18]
	Endodermal barrier development	Potential impacts on nutrient transport
Physiology	Inducible transporters and aquaporins	Manipulation of transporters might not result in improved N acquisition [43]; feedback regulation mechanisms
	High V_{max} for nitrate and ammonium transporters; low K_m for immobile nutrients	Potential tradeoffs with plasticity versus optimal V_{max} or K_m
	Low root turnover near wetting boundary	May decrease responsiveness to localized resource availability
	Mucilage exudation	Cost of production; becomes hydrophobic if dehydrated [62]
Biology	Production and exudation of microbial substrates	Substantial C investment may not be worth the cost in intensive systems

Glossary

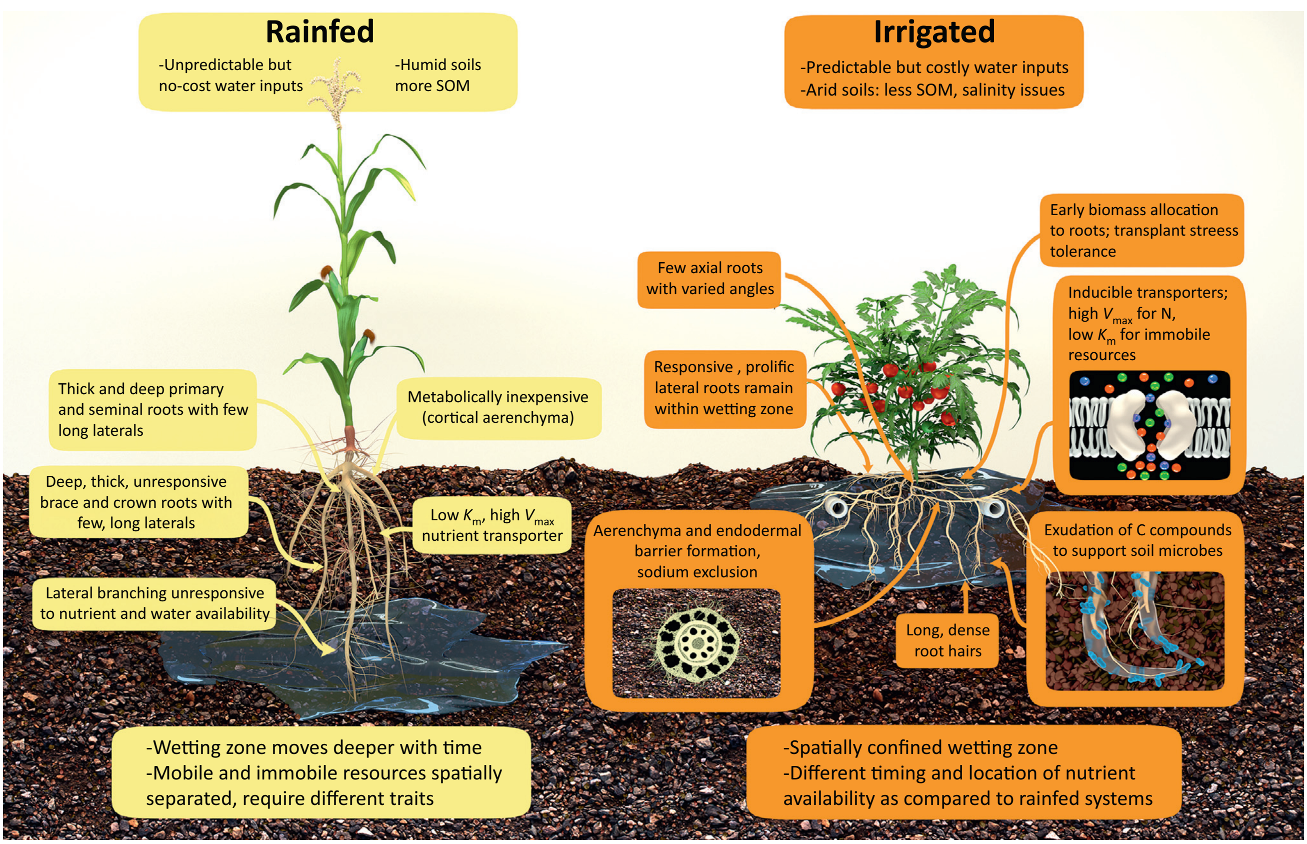
Deficit irrigation (DI): application of a reduced volume of water, typically 60–100% of crop evapotranspiration [82].
Fertigation: simultaneous delivery of irrigation water and dissolved fertilizer.
Furrow irrigation: delivery of water between crop rows.
K_m: transporter affinity for its substrate (Michaelis constant).
Micro-irrigation: surface or subsurface technologies that deliver water to the root zone, often increasing yield and irrigation water productivity [83].
Nitrogen use efficiency (NUE): 'The proportion of all N inputs that are removed in harvested crop biomass, contained in recycled crop residues, and incorporated into soil organic matter and inorganic N pools' [84].
Partial root-zone drying (PRD): application of water to alternate sides of the root system when soil water content reaches a specified level [85].
Root length density (RLD): cm root length/cm^3 soil.
Root proliferation: the initiation of new lateral roots rather than the elongation of existing roots; species- and context-dependent [44].
Specific root length (SRL): cm root length/g root mass.
V_{max}: maximum uptake rate of a transporter (maximum velocity).
Water productivity: yield, economic, social, and ecosystem benefits produced per unit of water used [8].
Water use efficiency (WUE): 'The yield of harvested product achieved from the water made available to the crop through precipitation and/or irrigation' [34].

[17] and where costly inputs are precisely delivered to surface or shallow subsurface soil to minimize losses below the root zone. The intensive nature of irrigated agriculture therefore likely incentivizes uptake efficiency over foraging, and alleviates the need for metabolically inexpensive roots, which may present tradeoffs for transport (Box 1) [18].

Drastic differences in the location and dynamics of resource availability between irrigated and rainfed systems [19] also call for ideotypes emphasizing localized responses to resource distribution rather than foraging strategies based on nutrient mobility. More targeted, predictable, and frequent water inputs than precipitation during the growing season result in less-intense wet–dry cycles which affect nutrient cycling and mineralization [20,21] and may favor constant over pulsed resource availability. Even so, attempts at a conclusive summary of differences in the duration and intensity of wet–dry cycles between rainfed and irrigated

Key Figure

A Comparison of Irrigated and Rainfed Ideotypes.



Trends in Plant Science

Figure 1. For a Figure360 author presentation of Figure 1, see the figure online at http://dx.doi.org/10.1016/j.tplants.2017.02.001#mmc1.
Differences in resource distribution between rainfed and irrigated environments pose the need for an alternative set of root phenes. The irrigated ideotype emphasizes investment in the water- and nutrient-rich zone around the water source, with shallower axial roots of varied angles and lateral foraging being restricted to the wetting zone. Transplant vigor and salinity tolerance represent traits unique to the irrigated environment. The inclusion of rhizosphere interactions is a novel addition to ideotype breeding. Integration of the traits proposed here could guide the creation of resource-efficient cultivars for irrigated systems. Abbreviation: SOM, soil organic matter.

systems are confounded by the irrigation technology implemented and scale- and site-dependent characteristics (Box 2). **Fertigation** or multiple targeted fertilizer applications throughout the growing season are also common practices to improve **nitrogen use efficiency** (NUE) ([84,22]; J.R. Olson, PhD Thesis, Kansas State University, 2011), and nutrients, especially immobile P, remain concentrated where applied in micro-irrigated and fertigated systems ([23,24]; J.R. Olson, PhD Thesis, Kansas State University, 2011). Best management strategies that reduce runoff and leaching thus create resource-rich hotspots near the root zone where plasticity, root physiological activity, and rhizosphere interactions become crucial for resource use efficiency. Local **root proliferation** coupled with high uptake rates to mine this critical zone may therefore be more favorable than the foraging strategies suggested by earlier models [25]. Although simulations of root system development are now complex, dynamic, and optimized for capture of both mobile and immobile nutrients [26], they remain focused on large-scale soil exploration to capture the more ephemeral and dispersed resources of rainfed systems. In addition, repeated wetting and evaporation of saline irrigation water creates localized waterlogging and salt accumulation,

Box 2. The Complexity of Irrigated Environments

Labeling agricultural systems as merely 'rainfed' or 'irrigated' admittedly oversimplifies the substantial diversity within contemporary irrigated agriculture as well as within rainfed systems experiencing different precipitation patterns. While a full discussion of the intricacies of irrigation technologies is beyond the scope of this review, it is crucial to acknowledge that differences in frequency, location, and amount of water application generate distinct wetting patterns across time and space, and these may subsequently affect nutrient distribution, microbe-mediated biogeochemical cycling, and beneficial root traits for resource capture.

Frequency

Irrigation frequency is typically higher in micro-irrigated than in furrow-irrigated systems, allowing more-precise adjustment of irrigation volume to match crop demand, increased yields, and decreased percolation and leaching losses [83]. When irrigation occurs often enough to prevent crop stress, C mineralization may not be affected by slight variations in frequency [86].

Location

Partial root-zone drying (PRD) shows how concentrated wetting zones may increase WUE but can incur negative tradeoffs compared to even moisture. The more extreme wet–dry cycles in PRD increase C and N mineralization [85,87,88], accelerating losses of nutrients and organic matter. Depth of irrigation also affects yield and soil parameters, with subsurface micro-irrigation improving yields but potentially contributing to higher salinity in the root zone compared to surface micro-irrigation [83].

Volume

Deficit irrigation (DI) can increase water productivity and N use efficiency [82], but may increase microbial C/N ratios [89]. By favoring fungi over bacteria, DI could potentially decrease bacteria-mediated C and N cycling, but long-term studies of soil health indicators such as organic matter content and microbial activity are needed for a more comprehensive cost–benefit analysis of DI.

High-resolution description of the effects of variation in frequency, location, and volume at the scale encountered by roots throughout a growing season will be necessary to improve understanding of how ideal root traits may vary between irrigated systems (see Outstanding Questions). Modeling studies can complement field-level studies by predicting variation in water, nutrient, and salinity dynamics for system-specific plant, soil [90], and microclimatic [91] characteristics at scales relevant to roots and crop growth cycles. For instance, models such as HYDRUS-2D can more accurately and cost-effectively predict variations in salinity and water distribution between pulsed versus continuous [92] and deficit versus full [93] drip-irrigated almond compared to field studies. Applying similar approaches to annual crops could help in understanding how root exploitation of the wetting zone varies with growth stages, a topic that has not received sufficient attention because of the difficulty of high-frequency and non-destructive field monitoring. Modeling approaches incorporating variations in soil and microclimatic characteristics at a rhizosphere-relevant scale should be used to compare wetting zones and wet–dry cycles between irrigated and rainfed systems or between irrigation technologies at a given location.

and inclusion of root traits conferring salinity and waterlogging tolerance in the irrigated ideotype is crucial to avoid yield reductions.

Rhizosphere biological processes and the outcomes of microbe-mediated carbon (C) and N cycling [27] are also affected by agroecosystem properties and management practices that differ between rainfed and irrigated systems, and must be better integrated with other root phenes to develop comprehensive ideotypes (Box 3). Irrigated soils in arid climates typically have lower organic C contents [28], and low precipitation de-incentivizes organic matter additions to improve water retention and infiltration. Reduction in available substrates [29] combined with intensive management could diminish populations of disturbance-sensitive microbes in bulk and rhizosphere soils [30] and their contribution to crop nutrition and productivity.

These altered agroecosystem properties highlight the need for a unique and more integrated root ideotype for irrigated systems. We reconcile here sparse knowledge of root system response to irrigated environments with fundamental differences in soil water and nutrient resource dynamics between rainfed and irrigated systems to conceptualize key components of this novel ideotype and identify knowledge gaps and future research needs.

Toward an Integrated Ideotype for Irrigated Agriculture

Integrating morphological traits with root eco-physiological properties to achieve resource use efficiency is a novel approach to develop functionality-oriented root ideotypes tailored to specific agroecosystems (Box 1). We propose that, in irrigated systems, desirable root functions confer rapid transplant recovery, and include efficient proliferation and plasticity in resource-rich patches, high physiological plasticity and hydraulic conductivity, promotion of rhizosphere interactions, and tolerance to salinity and waterlogging (Figure 1).

Rapid Transplant Recovery and Vigorous Establishment

Vigorous germination, rapid root elongation, and cold tolerance, which help rainfed crops to establish in low-temperature spring soils, are likely less relevant in irrigated systems where

Box 3. The Potential of Integrating Rhizosphere Functions into Ideotypes

Although microbial associations are rarely included in ideotypes, root traits supporting active microbial communities could contribute to efficient water and nutrient acquisition and improvements in soil structure. Potential for microbial associations is determined in part by root system characteristics such as the presence of fine roots [96], while root hairs are involved in colonization by N-fixing bacteria [97] and arbuscular mycorrhizal fungi (AMF) [98]. The extent of colonization may therefore be affected by interactions with host genotype, resource availability, soil compaction, and other factors that drive morphological development. Root turnover and mucilage could represent an important source of labile C in low-C environments [99]. Likewise, exudation of organic compounds feed microbial communities that fix and cycle various forms of N [100], solubilize P [100], improve macro- and micronutrient uptake [100], and translocate P and N to crops through hyphal networks [101]. However, exudates that promote microbial associations represent a significant investment of photosynthate, and their contribution to plant nutrient status is likely greatest in lower-input or deficient systems [102] or for the acquisition of immobile nutrients in the resource-depleted wetting zone. Rhizodeposition of organic C that stimulates organic matter decomposition (i.e., priming effects) could release additional nutrients but may incur hidden tradeoffs for soil organic matter formation and C sequestration which remain unclear. In intensively managed systems with high nutrient availability, microbial enhancement of soil structure through exopolysaccharide production and hyphal binding of aggregates may represent a greater contribution to crop resource acquisition by promoting water availability and uptake.

Rhizosphere processes may be even more important in irrigated than in rainfed systems because localized water inputs overlap with C sources supplied by roots, providing the conditions necessary for microbial ‘hotspots’of intense activity and resource cycling [99]. Recruitment of beneficial bacteria may be facilitated by more-constant soil moisture that increases the range of microbial mobility. Additional research on specific spatial and temporal patterns of microbial activity in irrigated systems is required, particularly in the rhizosphere. A better understanding of genetic variation for exudate quantity and quality; the heritability of microbial community composition, activity, and function; and crucial cost–benefit analysis of rhizosphere investment in intensively managed systems would aid the integration of these traits in breeding programs.

seedlings are transplanted into warm soils and yield is mostly affected by transplanting depth [31]. Therefore, the irrigated ideotype requires transplant recovery through early C allocation to basal roots [32], extensive micronutrient uptake to meet increased needs early in development [33], and abiotic stress tolerance. Although rapid axial root elongation may remain beneficial to capture resources delivered deeper in the soil profile, early lateral proliferation to exploit the wetting zone may be more advantageous for low-cost resource acquisition. Although not experimentally confirmed, these traits may allow faster transplant recovery and earlier canopy development, and ultimately enhance WUE and yields by maximizing C capture throughout the crop growth period [34].

Efficient Exploration of Resource-Rich Patches

The irrigated ideotype ideally combines few axial roots at varied angles from the main stem, and highly plastic root proliferation in the shallow wetting zone via extensive, responsive lateral branching to help crops to efficiently acquire concentrated resources and minimize leaching losses [35,36].

At the macro scale (m to cm), few axial roots at more obtuse angles rather than being uniformly steep could help to maximize resource acquisition at minimal metabolic cost. Irrigated field studies have shown preferential investment in shallow rooting, and **root length density** (RLD) tends to decrease rapidly with soil depth and lateral distance from the water source [37,38]. Early-developing shallow axial roots with extensive lateral branching could maximize uptake of banded pre-plant N and help to capture multiple N surface applications throughout the season, while few steeper-angled axial roots could increase capture of mobile resources leaching past the wetting zone [39] and increase anchorage [17].

At the meso scale (cm to mm), lateral root plasticity in response to resource heterogeneity would allow plants to rapidly exploit shallow irrigation system-specific wetting zones and nutrient-rich patches [40]. Irrigation timing and frequency constantly shape the wetting zone, in turn affecting the location of maximum RLD and triggering roots to elongate towards the moving moisture boundary [37,38,41]. This lateral root phenotype could play a leading role in adaptive plasticity by allowing small spatial scale proliferation at low metabolic cost and support the majority of root hairs [42]. While they primarily facilitate the acquisition of immobile nutrients in rainfed topsoils [43], shallow foraging accesses both mobile and immobile resources in irrigated systems. Responsive lateral root proliferation and higher **specific root length** [44] in the wetting zone would likely be beneficial. Nonetheless, metabolically cheap and localized lateral root plasticity can incur multiple tradeoffs, and the advantages must be thoroughly assessed (Box 1).

Micro-scale (mm to μm) strategies such as root hair development could help to address some of these tradeoffs by compensating for reduced proliferation by increasing the uptake and use efficiency of immobile nutrients per unit root length [45–47]. Long, dense root hairs can also enhance root ability to penetrate non-compacted soils [48] and increase surface area for uptake and microbial interactions. Because root hair length is a plastic trait [49], responsiveness rather than constitutive expression might be advantageous to lower specific root respiration and increase biomass accumulation [49].

Adaptive Physiological Regulation

Long-lived roots and rapidly inducible water and nutrient transporters to enhance plasticity of nutrient uptake per unit root length and better match wet–dry cycles [50] may be important traits to consider for a resource-efficient ideotype adapted to resource dynamics in irrigated systems. Induction of nutrient transporters allows quicker exploitation of heterogeneous resources with fewer tradeoffs for growth and proliferation responses [44]. For rainfed maize, maximum nitrate uptake rates ($\boldsymbol{V_{max}}$) and transporter affinities ($\boldsymbol{K_m}$) vary by root type, and V_{max} has a greater effect on uptake and shoot growth [51]. In irrigated systems, lateral root development combined with high V_{max} could improve N acquisition. However, manipulating nitrate and ammonium transporter expression has been investigated in model species and extensive feedback regulation mechanisms exist [43,52]. Because NUE depends on soil N concentrations, benefits may vary with the K_m of the transporter apparatus. A flexibility-based strategy incorporating inducible and cell-specific transporter activation along the roots might be more beneficial. Emphasizing low K_m would likely aid immobile nutrient acquisition more than high V_{max} because depletion in the root-dense wetting zone and restricted lateral foraging. Likewise, plastic aquaporin regulation could aid rapid physiological adaptation to changing soil water conditions [10].

Root turnover is an important but often overlooked physiological trait in annual crops, and rapid turnover can accompany high proliferation in nutrient-rich patches [53]. However, studies have found increases in the longevity of newly initiated roots in fertile patches [54], and frequent turnover may be disadvantageous due to construction costs under resource-scarce conditions such as the edge of the wetting zone [55] (Box 1). Integrating measurements of nutrient uptake and maintenance costs for each root type with turnover rates could show whether increased mortality in combination with the proliferation response is more adaptive than proliferation alone. In fertilized, irrigated agroecosystems with predictable nutrient availability, long-lived and highly vesseled roots might be beneficial for hydraulic conductance [56] and efficient nutrient uptake because transport costs are minimal relative to root construction and maintenance [57].

Maintaining Hydraulic Conductivity in a Heterogeneous Environment

High rhizosphere hydraulic conductivity through morphological and physiological strategies including long, dense root hairs and mucilage production could help irrigated crops to maintain water and dissolved nutrient uptake during expansions and contractions of the wetting zone. While rhizosphere hydraulic conductivity could also improve yields in rainfed systems with irregular precipitation events; small-scale rapid and regular shifts in the extent and morphology of the wetting zone may accentuate the importance of these traits in irrigated systems. Genotypes with greater root hair length could potentially increase hydraulic conductivity by decreasing resistance at the soil–root interface that restricts maximal water utilization [58], and enhance irrigation water capture because root hairs create larger depletion zones in drying soils [59], and also increase soil–water contact and surface area for uptake. Studies suggest that root hair length is more important for the acquisition of water and other resources and is less sensitive to soil moisture conditions than the density of root hairs along the main root [60,61]. Increased hydraulic contact generated by mucilage could also be a relatively low-cost strategy to maintain root–water contact and thus maximize WUE because mucilage increases rhizosphere water content and root–soil contact during drying [62–64], with significant impacts on plant performance under dry conditions [65].

Fostering Rhizosphere Interactions

Under intensive irrigation conditions, microbial effects on soil structure may be more important than for nutrient cycling and acquisition (Box 3). Enhanced rhizosphere soil aggregation and porosity through organic matter metabolism and exopolysaccharide production [66] can help roots to maintain rhizosphere hydraulic conductivity and maximize water uptake. Ideotypes which foster mycorrhizal symbioses may also yield benefits because arbuscular mycorrhizal fungi (AMF) improve soil structure and access, transport water through hyphal networks, and modify root hydraulic conductance, aquaporin expression, abscisic acid (ABA) production, root growth-promoting phytohormones, and plant nutritional status [67–70]. This might be especially relevant under **deficit irrigation** (DI) or suboptimal irrigation scenarios in which mycorrhizal plants can access a greater proportion of applied water, improving uptake, drought resistance, and ultimately yield resilience [71]. Bacteria that produce ACC (1-aminocyclopropane-1-carboxylate) deaminase can also prevent drought-induced yield reductions through local and systemic pathways [72], and affect plant phenotypic plasticity by direct abiotic stress alleviation or modulation of developmental pathways [73]. However, the utility of microbial associations for breeding programs and ideotype development is currently compromised by a lack of knowledge about the genetic variation and heritability of microbe-related host root traits, and further research is required (Box 3).

Coping with Salinity and Waterlogging

Because roots are concentrated in shallow soils where water-filled pore space and salinity are highest, an irrigated root ideotype must possess physiological and morphological traits to minimize structural and physiological damage from hypoxia, salinity, and their interactions.

Inducible development of adventitious roots with cortical aerenchyma, endodermal barriers, and heightened sodium exclusion mechanisms [74,75] could be beneficial in irrigated saline soils. Extensive development of short adventitious roots and subsequent aerenchyma formation can provide alternative airflow pathways that prevent hypoxic root conditions, as shown in natural systems with waterlogging cycles such as mangrove swamps [75], while providing axial support for lateral branching once optimal conditions resume. Development of a barrier to restrict radial oxygen and water loss [75,76], and to promote sodium exclusion through selective uptake and loading into root xylem vessels, or via removal from the xylem at the root–shoot boundary [77], could avoid yield reductions due to salinity–waterlogging interactions. Salinity tolerance may be most important later in the season and in shallow soils where salts accumulate.

Concluding Remarks and Future Perspectives

There is an urgent need to investigate crop root development and beneficial traits that enhance water use efficiency of irrigated systems to increase yields under constant or reduced water inputs [78]. The novel ideotype proposed here (Figure 1) integrates traits contributing to resource use efficiency across scales, emphasizes adaptive acquisition in the resource-concentrated critical zone unique to the irrigated environment, and lay the foundation for research on specific phenes. Future research exploring crop- and irrigation system-specific traits and the poorly understood interactions with soil ecology and functions could significantly contribute to the development of an irrigated ideotype and guide breeding efforts (see Outstanding Questions). Ideotype breeding can provide more rapid gains than yield-based selection in limiting environments [10], and breeding toward a novel irrigated ideotype could provide a faster, targeted strategy to enhance the sustainability of irrigated agriculture. This will be conditioned by our ability to move away from snapshot measurements of coarse variables such as RLD and biomass which have limited ability to predict resource acquisition, plasticity, and yield [39,79]. Imaging technologies [80,81], which have recently exposed artifacts of previous methodology [41], coupled with genotyping, now provide unprecedented prospects to study morphological and temporal variability in root response to efficient irrigation technologies. This will help to identify beneficial root and rhizosphere traits, their interactions, and the underlying genetic basis and variability available for breeding. Although these techniques remain to be adapted to irrigated systems [65], they could vastly improve our ability to harness belowground structures while creating positive feedback loops to agroecosystem functions essential for the sustainability and resilience of irrigated systems. Roots acquire resources, but also sequester C, and therefore mediate crucial ecosystem functions essential to agricultural sustainability and climate change adaptation and mitigation.

Outstanding Questions

Could the generalized irrigated ideotype be improved by tailoring it to specific crops? Crop-specific versions of this irrigated ideotype likely must be developed by integrating information about unique adaptive traits and root structure. A large number of annuals with distinct root structures are grown in irrigated systems, while orchard ideotypes might require additional deep roots for physical stability. Rootstock ideotypes could also factor in characteristics such as disease resistance which might be of greater relative importance in long-lived perennials.

Are irrigation system-specific traits necessary? While this irrigated ideotype seeks to combine traits that are generally applicable across different irrigation systems, zones of resource distribution, microbial activity, and salt accumulation may differ depending on subsurface drip, sprinkler, **furrow irrigation**, and flood irrigation, the timing of irrigation, and interaction with other management practices. As a result, system-specific traits are likely required.

Can **partial root-zone drying** (PRD) enhance resource use efficiency, and, if so, how could it be integrated into an ideotype? Applying water to one side of the root zone while the other is allowed to dry is hypothesized to increase resource use efficiency, but PRD is not currently widely applied. The potential benefits warrant further analysis of the effect of PRD on root architecture and uptake rates as well as on the soil microbial community.

How can breeding programs enhance plant–microbe interactions in an irrigated context? Plant–microbe interactions can contribute substantially to resource acquisition, but knowledge of how they are affected by irrigation is limited, and the extent of genetic variation and heritability for microbial associations remains to be characterized. Modeling studies of irrigation systems and crop roots have not included soil microorganisms as a parameter.

What are the implications of integrating ecosystem functions into an agricultural ideotype? Roots are important drivers of C sequestration, N cycling, and other ecosystem processes, but it is unclear how these roles could be integrated into an ideotype, or what the potential tradeoffs would be.

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