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Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture

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Summary

Nutrient-efficient crops are a solution to the two grand challenges of modern agriculture: improving food security while reducing environmental impacts. The primary challenges are (1) nitrogen (N) and phosphorus (P) efficiency; (2) potassium (K), calcium (Ca), and magnesium (Mg) efficiency for acid soils; and (3) iron (Fe) and zinc (Zn) efficiency for alkaline soils. Root phenotypes are promising breeding targets for each of these. The *Topsoil Foraging* ideotype is beneficial for P capture and should also be useful for capture of K, Ca, and Mg in acid soils. The *Steep, Cheap, and Deep* ideotype for subsoil foraging is beneficial for N and water capture. Fe and Zn capture can be improved by targeting mechanisms of metal mobilization in the rhizosphere. Root hairs and phenes that reduce the metabolic cost of soil exploration should be prioritized in breeding programs. Nutrient-efficient crops should provide benefits at all input levels. Although our current understanding is sufficient to deploy root phenotypes for improved nutrient capture in crop breeding, this complex topic does not receive the resources it merits in either applied or basic plant biology. Renewed emphasis on these topics is needed in order to develop the nutrient-efficient crops urgently needed in global agriculture.

I. Nutrient-efficient crops are urgently needed in global agriculture

Global agriculture urgently needs crops with greater nutrient efficiency, meaning greater yield under suboptimal nutrient

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availability, and reduced fertilizer requirement to reach optimal yield (Lynch, 1998). In the low-input agroecologies characteristic of developing nations, nutrient deficiency is a primary limitation to crop productivity, and therefore to food security and economic development. In high-input agroecologies, intensive fertilization is

costly, causes massive environmental pollution, and is unsustainable. The prospect of using crops for biofuels and environmental remediation is only economically and energetically feasible if they do not require intensive fertilization. Ongoing soil degradation is decreasing soil fertility and the ability of soils to respond to fertilization in rich and poor nations alike. The accelerating effects of global climate change are likely to exacerbate soil degradation and limit crop yields (Lynch & St Clair, 2004), especially in developing nations (St Clair & Lynch, 2010). All of this is occurring against a backdrop of rapid expansion of the human population, the large majority of which is occurring in foodinsecure regions with inadequate soil fertility and fertilizer use, as well as increasing food demand per capita. Sustaining 10 billion people in a degraded environment is a paramount challenge of the 21st century. An inextricable component of that effort will be the development of crops with greater stress tolerance, reduced reliance on irrigation, and greater nutrient efficiency.

In this article I consider opportunities to breed more nutrientefficient crops by improving root phenotypes. Although crop breeding for nutrient efficiency has never received the priority it merits, efforts to breed nutrient-efficient crops started in the late 19th century, began in earnest in the 1960s, and have gained momentum over the past 20 yr. I will not attempt to review this effort. Instead, I provide a brief overview of salient issues, focusing on those studies most relevant to breeding, that employ contrasting crop phenotypes in realistic environments, rather than model organisms in very artificial environments. I will not focus on the genetic control of root phenotypes, which in general is poorly understood, highly quantitative, with important genotype \times environment ($G \times E$) interactions, and may be species specific. Rather, I focus on root phenotypes themselves, since it is our limited understanding of the root phenome, rather than genetic tools, that limits their deployment in crop breeding programs.

II. This is a hard problem

Nutrient efficiency has been subject to natural selection throughout plant evolution. In the aquatic ecosystems in which plants evolved, nitrogen (N), phosphorus (P), and iron (Fe) commonly limit plant growth (Elser et al., 2007). These challenges were compounded when plants colonized land nearly 500 Ma, since rather than acquire nutrients directly from water bathing the plant, plants had to acquire nutrients from the soil, in which the bioavailability of nutrients is typically suboptimal, varies greatly in time and space, and contrasts greatly among nutrients. Soil exploration became a primary function of terrestrial plants, a function that incurs substantial metabolic costs (Lambers et al., 2002), since roots and their microbial symbionts are heterotrophic. The contrasting availability of nutrients in time and space, and their dependence on soil chemistry and microbiology, entails trade-offs for root foraging strategies. For example, strategies to improve the capture of nitrate, which is highly mobile, often incur trade-offs for the capture of P, which is highly immobile. Soils are vastly more diverse than aquatic environments, which also creates challenges. For example, the utility of strategies to improve nutrient availability via rhizosphere modification depends on whether the bulk soil is acid or alkaline

(Hinsinger, 2001). In soil, unlike water, localized depletion of mineral nutrients by root uptake limits continued resource capture (Barber, 1984), necessitating continued exploration of new soil domains, and intensifying interplant competition. Root phenotypes are the result of long and intensive selection for efficient and effective capture of soil resources, and efficient utilization of acquired nutrients has been subject to natural selection since the origin of life.

These facts have several important implications for crop breeding. It is reasonable to assume that simple mechanisms that improve nutrient efficiency in many environments without incurring significant fitness trade-offs are already present in crop germplasm. Opportunities to manipulate single genes in order to substantially improve nutrient efficiency are probably limited, as they are likely to have already evolved via natural selection. It is more likely that traits improving nutrient efficiency are genetically and/or ecologically complex, involving quantitative variation for traits that crops already possess, and entailing fitness trade-offs that may restrict their utility to specific production environments. The complexity of traits improving nutrient efficiency calls for focused efforts to understand the biology of these traits, their fitness landscape in contrasting agroecologies, and their genetic control. This is a complex challenge that merits greater research effort than it presently receives.

III. Nutrient targets

1. Indirect selection for nutrient efficiency

A number of selection criteria can indirectly improve nutrient efficiency. For nutrient capture, these include resistance to root pathogens and herbivores, aluminum (Al) tolerance, which is critically important in acid soils (Ryan et al., 2011), the ability of roots to penetrate hard soil, which is especially important for subsoil foraging (Lynch & Wojciechowski, 2015), resistance to hypoxia (Striker, 2012), and, in temperate climates, the ability of roots to grow in cold soil (Kaspar & Bland, 1992). Traits that improve shoot function, including resistance to biotic and abiotic stress, optimal shoot architecture, harvest index, and so on, improve nutrient utilization. Vigor, an elusive but important target in most crop breeding programs, is related to both nutrient capture and utilization. Phenology regulates the duration and extent of soil exploration, as well as the duration of nutrient utilization in plant tissue, and is therefore closely linked to nutrient efficiency (Nord & Lynch, 2009; Voss-Fels et al., 2018). Many of these are common selection criteria in crop breeding. Indeed, the majority of crop breeding for nutrient efficiency consists of indirect selection, primarily resistance to biotic stress and selection for growth and yield in the target environment. Indirect selection for nutrient efficiency is important, but is not likely to be as effective or rapid as would be selection for traits more directly related to nutrient efficiency, as discussed later.

2. Top priority: N and P

Globally, N and P efficiency are the most important breeding targets. N and P limitations are ubiquitous in natural soils; and in

those rare soils with abundant N and P, intense belowground competition limits their availability to a given plant. As a result, N and P deficiencies are primary constraints to food production in low-input systems, and intensive N and P fertilization in highinput systems causes massive environmental pollution (Robertson & Vitousek, 2009; Vitousek, 2009). High-grade P ore deposits are nonrenewable and have limited geographic distribution, and some studies indicate that they may be substantially depleted in this century, forcing reliance on more costly feedstocks (Vance et al., 2003; Lynch, 2011; Richardson et al., 2011; Simpson et al., 2011). Conversion of atmospheric N2 gas to N fertilizer via the Haber-Bosch process is energy intensive and generates greenhouse gases, as does the use of N fertilizer. Many developing nations do not have the energy, financial resources and access to P deposits needed to generate their own N and P fertilizer, and fertilizer use in many developing countries, especially in sub-Saharan Africa, is negligible (World Bank, 2017). Our current use of N and P fertilizers is unsustainable and inequitable. Crops with reduced requirements for N and P fertilizer, and improved growth without N and P fertilizer, are urgently needed in global agriculture.

3. Second priority: acid soil complex (calcium, magnesium, potassium)

The second priority for nutrient-efficiency breeding is the acid soil complex, which consists of Al toxicity, possibly manganese (Mn) toxicity, and low availability of P, calcium (Ca), magnesium (Mg), and potassium (K) (Sanchez, 2018). Acid soils are common in humid environments, and sustain most of the forested biomass of the Earth, as well as important agroecosystems sustaining large and growing human populations in the developing world (von Uexkull & Mutert, 1995). Large areas of acid savannas in Latin America and sub-Saharan Africa have sufficient rainfall for expansion of arable lands. The development of P-efficient crops is a critical need for these areas and is an active area of research. Al tolerance is another essential need for these areas. Al tolerance has been intensively researched, is a relatively simple trait in some crop species, and is being deployed in crop breeding (Kochian et al., 2015). A neglected component of acid soil adaptation is efficient capture of K, Ca, and Mg. The relative paucity of research on these topics may be related to the fact that, in contrast to N and P, K, Ca, and Mg are not environmental pollutants, are not as scarce or costly, and are not limitations to the agroecologies of rich nations, where the bulk of research is conducted. Biofuel crops would also benefit from acid soil adaptation, since in the interests of food security these crops should not occupy prime cropland, and the majority of marginal lands with sufficient rainfall to sustain biofuel crops are acidic. Crop breeding for adaptation to acid soils, in addition to the efforts already underway for Al tolerance and P efficiency, is a neglected but important goal for global agriculture.

4. Third priority: iron and zinc

The third priority for nutrient efficiency breeding is the development of crops with greater iron (Fe) and zinc (Zn) content. Such crops would have two main benefits. The first is that, in alkaline soils, which are common in arid and semi-arid ecosystems, these nutrients (as well as Mn and copper) have limited plant bioavailability (Barber, 1984). Direct application of Fe and Zn salts is marginally effective because they are only sparingly soluble in alkaline soil. Soil application of chelated Fe and Zn is more effective but is costly. Foliar application of chelated metals is effective but costly, and is rare in the production of staple crops. In alkaline soils, more efficient capture of Fe and Zn is an effective strategy to improve yield (of grain as well as of micronutrients; White *et al.*, 2009). A second benefit is for the large number of people subsisting on grain-based diets who suffer from Fe and Zn deficiency (White *et al.*, 2009; Bouis & Welch, 2010). Indeed, the most well-funded effort to improve the nutrient efficiency of crops is the Harvest Plus program, to enhance Fe and Zn bioavailability in staple crops of developing nations (Bouis & Welch, 2010).

5. Low priority: remaining nutrients

Genotypic variation exists for the capture and utilization of all plant nutrients, including beneficial elements like silicon, and the development of crops with these abilities would be beneficial for specific agroecosystems. I rank them as low-priority targets in a global context because they are not as generally limiting for crop growth and human health, fertilization options are generally not as expensive or polluting, and selection for plant traits that improve the capture of N and P through better soil exploration is likely to also improve the capture of other nutrients.

IV. Nitrogen

1. Steep, cheap, and deep

The predominant form of N acquired by most crops is nitrate, which as a soluble anion is highly mobile. Nitrate mobility contributes to water pollution via leaching and to the low proportion of N fertilizer captured by roots, which scarcely exceeds 50% (Cassman et al., 2002; Ribaudo et al., 2011). The greatest, most accessible opportunity to improve N efficiency through breeding is simply to improve nitrate capture. The steep, cheap, and deep root ideotype for improved N capture in maize consists of architectural, anatomical, and physiological traits that promote rapid exploration of deep soil domains to capture nitrate as it leaches through the rootzone (Fig. 1; Table 1; Lynch, 2013). Architectural traits include steep root growth angles, few nodal roots and sparse lateral branching, and low architectural plasticity in response to environmental cues. Reduced root production is beneficial for N capture by reducing competition among root axes for internal (e.g. carbohydrate) and external (i.e. nitrate) resources (Postma et al., 2014). Recent evidence supports several elements of this ideotype: root depth, N capture, and plant growth and yield under N stress are substantially better in maize (Zea mays) lines with steeper root growth angles (Trachsel et al., 2013; Dathe et al., 2016), reduced production of crown roots (Saengwilai et al., 2014b), and reduced lateral root branching density (Postma et al., 2014; Zhan & Lynch, 2015). The value of architectural plasticity is unclear (Lynch, 2018). Mi et al. (2010) have proposed

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that plasticity is beneficial for N capture, without supporting evidence, and the same paper proposes root proliferation as beneficial for N capture, which is contrary to empirical evidence. Anatomical elements of the steep, cheap, and deep ideotype include greater root hair formation (Fig. 2), traits that reduce the metabolic cost of soil exploration, such as the formation of root cortical aerenchyma (RCA; Fig. 3), reduced cortical cell file number (Fig. 4), increased cortical cell size (Fig. 5), and root cortical senescence (Fig. 6); and traits that improve root penetration of hard subsoils. Genotypic variation for RCA formation is related to improved N capture in maize (Saengwilai et al., 2014a). Simulation modeling indicates that root cortical senescence improves N capture in barley (Schneider et al., 2017; Fig. 6), and that decreased cortical cell number and increased cortical cell size improve N capture in maize (Yang, 2017; Figs 4, 5). Root anatomy regulates penetration of hard soils and is related to rooting depth in maize (Chimungu et al., 2015a), which should improve N capture (Lynch & Wojciechowski, 2015). Modeling indicates that nitrate uptake kinetics could be altered to improve plant N capture in maize (Barber, 1984; York et al., 2016). Although much remains to be understood about root phenotypes capable of improving N capture, it is evident that existing phenotypic variation in crops such as maize is related to substantial variation in root depth and N capture that can be exploited in crop breeding.

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Fig. 1 Steep, Cheap, and Deep and Topsoil Foraging ideotypes in maize (upper panel) and common bean (lower panel) at 42 d after germination as simulated by OPENSIMROOT. The center image represents standard phenotypes in maize and common bean germplasm. In maize (representing a nontillering monocot root architecture), the Steep, Cheap, and Deep phenotype was generated by reducing the number of axial roots, decreasing lateral root branching density, and increasing the steepness of crown root growth angles, whereas the Topsoil Foraging phenotype was generated by doing the opposite. In common bean (representing an annual dicot root architecture). the Steep. Cheap, and Deep phenotype was generated by reducing the number of hypocotyl-borne roots, reducing the number of basal root whorls, decreasing lateral root branching density, and increasing the steepness of basal root growth angles, whereas the Topsoil Foraging phenotype was generated by doing the opposite. It has been proposed that the Steep, Cheap, and Deep phenotype is useful for the capture of subsoil resources, including water and leached nitrate, whereas the Topsoil Foraging phenotype is useful for the capture of topsoil resources including recently mineralized nitrate, ammonium, phosphorus, potassium, calcium, magnesium, and, in some cases, micronutrient metals. Model parameters are based on empirical observations (Table 1). Images courtesy of Ernst Schäfer.

2. Opportunities for associative N fixation

Efforts are underway to introduce symbiotic biological N fixation into nonlegumes via synthetic biology (Mus et al., 2016). The fact that few plant taxa have evolved this symbiosis suggests that this enterprise, even if successful, may generate plants with significant fitness trade-offs. A less risky path to exploit biological N fixation in nonlegumes is by selecting plants better able to exploit associative N fixation (ANF) with rhizosphere and endophytic diazotrophs, which can contribute substantial N to tropical grasses (James, 2000). Some of these microbes, such as Azospirillum, appear to have growth-promotive effects in addition to N fixation (Okon & Labandera-Gonzalez, 1994; Steenhoudt & Vandereyden, 2000). Large genotypic variation in the ability of host plants to exploit ANF (e.g. from 0 to 30% of plant N contributed by ANF in one study; Miranda et al., 1990) indicates that breeding for superior ANF, most feasibly in conjunction with specific seed inoculants, is promising.

V. Phosphorus

The large majority of soil P exists in pools of very low bioavailability. The predominant form acquired directly by roots is orthophosphate, which reacts with many soil constituents and is

Table 1	Parameters u	used to ge	nerate the	phenotype	s in Opens	SIMROOT sho	wn in Fig. 1.	

	Root phene	Steep, cheap, and deep	Normal	Topsoil foraging
Maize	Number of nodal roots	8 (4 brace roots, 6 crown roots)	33 (12 brace roots, 21 crown roots)	60 (24 brace roots, 36 crown roots)
	Nodal root growth angle (°), by node	Brace roots 1: 70 Brace roots 2: 60	Brace roots 1: 50 Brace roots 2: 40	Brace roots 1: 20 Brace roots 2: 10
		Crown roots 1: 90	Crown roots 1: 70	Crown roots 1: 40
		Crown roots 2: 80	Crown roots 2: 60	Crown roots 2: 30
		Crown roots 3: 70	Crown roots 3: 50	Crown roots 3: 20
		Crown roots 4: 60	Crown roots 4: 40	Crown roots 4: 10
	Lateral branching density of nodal roots (cm^{-1})	2.5	8.3	25
Bean	Basal root whorl number	1	3	4
	Basal root growth angle (°) by whorl position	Whorl 1: 60	Whorl 1: 65	Whorl 1: 55
			Whorl 2: 45	Whorl 2: 35
			Whorl 3: 25	whorl 3: 15
				whorl 4: -5
	Lateral branching density of basal roots ($\rm cm^{-1}$)	2	4	6
	Hypocotyl-borne roots	10	25	40

therefore highly immobile (Barber, 1984). Opportunities to increase P acquisition therefore center around (1) improving foraging in P-rich soil domains (i.e. the topsoil in most agricultural soils), and (2) improving exploitation of those domains through increased P solubilization.

1. Topsoil foraging

Phosphorus bioavailability is generally greatest in the topsoil because of P deposition from plant residues, limited P leaching to deeper soil strata, and greater biotic activity in the topsoil (Lynch & Brown, 2001). Topsoil foraging can be improved through greater production of axial roots, shallower axial root growth angles, greater lateral root density, reduced root metabolic cost, and greater root hair length and density (Figs 1, 2). Greater axial roots often emerge in the topsoil, and indirectly improves topsoil foraging by slowing the elongation of individual root axes into deeper soil domains. For example, maize (*Z. mays*) genotypes with greater production of crown roots (i.e. belowground nodal roots)

have greater topsoil foraging, P capture, growth, and yield in low-P soil than genotypes with fewer crown roots (Sun et al., 2018). Similarly, common bean (Phaseolus vulgaris) genotypes with more basal roots had greater P capture, growth, and yield under P stress than lines with fewer basal roots, in silico (Walk et al., 2006; Rangarajan et al., 2018), in controlled environments, and in the field (Miguel et al., 2013). The production of hypocotyl-borne roots improves P capture because these roots typically have very shallow growth angles and less metabolic cost than other axial root classes (Miller et al., 2003; Walk et al., 2006; Rangarajan et al., 2018). The growth angle of axial roots regulates topsoil foraging, and thereby P capture under P stress (Bonser et al., 1996; Liao et al., 2001; Lynch & Brown, 2001; Rubio et al., 2003; Zhu et al., 2005; Rangarajan et al., 2018). Greater density of lateral roots, as with greater production of axial roots, increases topsoil foraging both directly (when laterals are formed in the topsoil) and indirectly, by reducing root depth, as has been demonstrated in silico (Postma et al., 2014) and by comparison of maize genotypes with contrasting lateral root density (Zhu & Lynch, 2004; Jia et al., 2018).

Fig. 2 Long root hairs and shallow root growth synergistically improve phosphorus (P) capture. Shoot DW of common bean (*Phaseolus vulgaris*) with either short or long root hairs combined with either deep or shallow basal root growth angles grown under low and medium P availability in the field in Mozambique. Each mean is from four replicates of three genotypes. Error bars represent \pm SEM. Means followed by the same letter within each P level are not statistically different (P > 0.05). Data from Miguel *et al.* (2015). Image courtesy of Anica Massas.



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Fig. 3 Root cortical aerenchyma (RCA) improves nutrient capture. (a) Natural variation for RCA formation in closely related maize (*Zea mays*) genotypes. (b) Simulation of the utility of RCA formation for growth of maize plants under suboptimal availability of nitrogen (N), phosphorus (P), and potassium. On the x-axis, stress due to nutrient deficiency is expressed as the relative plant biomass at 40 d after germination compared with nonstressed plants. The benefit of RCA is expressed on the y-axis as growth increase due to RCA formation. From Postma & Lynch (2011). (c) Correlation between grain yield of maize and RCA under high (not significant) and low N (r = 0.40, $P \le 0.05$) conditions in the field. From Saengwilai *et al.* (2014a). (d) Grain yield of maize plants with low and intermediate living cortical area phenotypes, which is inversely related to RCA, under nonlimiting and suboptimal P availability in the field. Data are means (\pm SE) of four replicates of three high living cortical area (LCA), six intermediate-LCA, and two low-LCA genotypes. Means with the same letter are not significantly different (P > 0.05). From Galindo-Castañeda *et al.* (2018).

Reduced metabolic cost of soil exploration is important for P capture, because continued soil exploration is needed to grow beyond the depletion of available P in the rhizosphere (Barber, 1984). RCA decreases the respiration and P cost of maintaining root tissue, and therefore improves P capture by maize and bean *in silico* (Postma & Lynch, 2010, 2011). These results have recently been supported by empirical results with maize, which show that genotypes with greater RCA formation have greater topsoil foraging, P capture, growth, and yield in low-P soil than genotypes with less RCA, notwithstanding the reduction in mycorrhizal habitat by RCA formation (Galindo-Castañeda *et al.*, 2018). In dicots, P stress inhibits the secondary growth of roots, and common bean genotypes with greater inhibition of secondary growth under P stress have reduced root costs, greater P capture, and greater growth in low-P soil (Strock *et al.*, 2018; Fig. 7).

Root hairs are critical for P capture by extending the P depletion zone surrounding the root surface, and genotypic variation for root

hair length and density is closely associated with P capture from low-P soils (Gahoonia & Nielsen, 2003, 2004a; Zhu *et al.*, 2010b; Miguel *et al.*, 2015; Fig. 2).

2. Arbuscular mycorrhizas

Arbuscular mycorrhizal symbiosis (AMS) is important for P capture in most annual crops (Smith & Read, 2010). Genotypic variation in AMS opens the prospect of breeding for improved P capture (Kaeppler *et al.*, 2000; Fester & Sawers, 2011; Sawers *et al.*, 2017). However, it has not yet been demonstrated that this approach is feasible (Ryan & Graham, 2018). The fungal symbionts are ubiquitous in aerobic soils, both plant and fungal symbionts are promiscuous, AMS appears to already be highly effective in crop germplasm, appears to be under complex genetic control with strong G × E and G(plant) × G(fungus) × E interactions. These are all challenges to breeding crops for improved

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Fig. 4 (a) Genotypic variation in cortical cell file number (CCFN) in crown roots of maize. (b) Visualization of maize root phenotypes with large CCFN (17 files, left image) vs small CCFN (eight files, right image) after 40 d of growth at moderate nitrogen (N) stress (80 kg ha⁻¹; optimal N rate is 210 kg ha⁻¹). (c) Simulated total plant DW of root phenotypes with large CCFN (17 files) vs few CCFN (eight files) under N, phosphorus (P), and potassium (K) stress at 40 d after germination. N, P, and K availability was such that DW reduction in plants with many CCFNs was *c*. 90%. Error bars represent \pm SD in four repeated runs. Within a nutrient, bars with different letters are statistically different at $P \le 0.05$. Variation was caused by stochasticity in root growth rate, root branching frequency, and root growth angle. Image (a) courtesy of Stephanie Klein; image (b) courtesy of Xiyu Yang.



Fig. 5 (a) Genotypic variation in cortical cell size (CCS) in crown roots of maize. (b) Visualization of maize root phenotypes with small CCS (101 μ m², left image) vs large CCS (533 μ m², right image) after 40 d of growth at moderate nitrogen (N) stress (80 kg ha⁻¹; optimal N rate is 210 kg ha⁻¹). (c) Simulated total plant DW of root phenotypes with large CCS (533 μ m²) vs small CCS (101 μ m²) under N, phosphorus (P), and potassium (K) stress at 40 d after germination. N, P, and K availability was such that DW reduction in plants with small CCS was *c*. 90%. Error bars represent ± SD in four repeated runs. Within a nutrient, bars with different letters are statistically different at *P* ≤ 0.05. Variation was caused by stochasticity in root growth rate, root branching frequency, and root growth angle. Image (a) courtesy of Stephanie Klein; image (b) courtesy of Xiyu Yang.

AMS. Crop breeding for root architectural and anatomical phenotypes with better P capture could have important indirect consequences for AMS, however. For example, RCA formation, root cortical senescence, and reduced secondary growth all improve P capture, and all have important consequences for AMS by regulating the volume of AMS habitat in the root cortex (Galindo-

Castañeda *et al.*, 2018; Schneider & Lynch, 2018; Strock *et al.*, 2018). Architectural phenes that localize root foraging in shallow or deep soil domains may also affect AMS, since the propagules of fungal symbionts, as well as the foraging environments of extraradical hyphae, are more favorable in the topsoil (Lynch & Wojciechowski, 2015).



Fig. 6 Root cortical senescence (RCS) improves nutrient capture. The root cross-section image shows a barley (*Hordeum vulgare*) root with intact root cortex (left side of image) or lacking a cortex because of RCS (right side of image). RCS reduces the nutrient and respiratory costs of maintaining root tissue, permitting greater root growth, soil exploration, and nutrient capture from soils with suboptimal nutrient availability, as shown by the top images of barley root phenotypes as simulated in SIMROOT (Schneider *et al.*, 2017). Reduction of radial water and nutrient transport in axial root tissue with RCS has small effects on total plant nutrient acquisition, since lateral roots, which acquire the majority of nutrients and water, do not form RCS. From Schneider & Lynch (2018).

3. P solubilization in the rhizosphere

A substantial portion of soil P exists in pools of low bioavailability in both organic and inorganic forms that have the potential to be mobilized by root exudates, especially carboxylates, protons, and phosphatases (Hinsinger, 2001; Richardson et al., 2011). Significant research has assessed the possibility of harnessing genetic variation in P-solubilizing exudates to develop P-efficient crop lines (Richardson et al., 2009). Natural and induced genetic variation for the production of these compounds is associated with P mobilization in vitro, but rigorous analyses have failed to show a benefit of such variation for P acquisition in a range of soils in the field, whether it be due to carboxylates (Pearse et al., 2007; Ryan et al., 2014) or phosphatases (George et al., 2008). This lack of response may be due to various factors, including limited spatiotemporal distribution of exudate production in root systems, and their limited lifespan and mobility in the rhizosphere due to microbial metabolism and chemical fixation. Despite the genetic simplicity of root exudates in many cases, their bewilderingly complex interactions with the soil environment make them unattractive as breeding

targets. Root phenes that expand the volume of the rhizosphere, such as root hair formation, and that position roots in P-rich domains, are more appealing as selection criteria for root exudates than are the exudates themselves, by positioning exudates in the most productive soil domains (Lynch, 2011). Microorganisms capable of mobilizing P, especially through solubilization, are being used commercially as bioinoculants, with mixed and often limited success, which may again be due to the chemical and microbial complexity and diversity of agricultural soils (Barea & Richardson, 2015).

VI. Potassium, calcium, magnesium

1. Potassium

Of the three commonly limiting macronutrients in acid soils (K, Ca, and Mg), only K has received significant research attention in the context of acquisition efficiency, and even for K our understanding of the underlying mechanisms is poor. Like P, K is bound to soil constituents; so, like P, it moves primarily by diffusion, has greatest bioavailability in the topsoil, and K acquisition by roots centers on soil exploration and K solubilization from K pools of low bioavailability (Römheld & Kirkby, 2010). As with P, the dominance of diffusion in K transport to the root make transporter properties at the root surface, as reflected in K uptake kinetics, relatively unimportant for K acquisition as opposed to root growth and K mobilization in the rhizosphere (Barber, 1984). Although K leaching to the subsoil can occur in sandy soils with high leaching (Rengel & Damon, 2008), these soils are rare in agroecosystems, and most commonly K and P are relatively colocalized. Root phenotypes optimizing topsoil foraging for P capture (Fig. 1) should also, therefore, optimize K capture (Römheld & Kirkby, 2010), with the exception of arbuscular mycorrhizas, which benefit the acquisition of P more than K (Smith & Read, 2010). For example, RCA benefits both K and P capture (Postma & Lynch, 2011; Fig. 3), as do long, dense root hairs (Hogh-Jensen & Pedersen, 2003) and root cortical senescence (Schneider et al., 2017). Solubilization of K pools in the rhizosphere by root exudates and microbes can be important (Rengel & Damon, 2008), but our understanding of these processes is poor. As with P efficiency, both exudate production and associations with rhizosphere microbes are challenging breeding targets because of strong environmental interactions.

2. Calcium

Ca is critically important in acid soil because of its role in ameliorating Al and Mn toxicity, its importance for the growth of root tips, and its importance for legume N fixation, given the greater Ca requirement of dicots vs grasses (Lynch & Wojciechowski, 2015). Ca is primarily brought to the root by transpiration-driven mass flow of soil water, and is not actively taken up across the plasma membrane, so opportunities to increase Ca acquisition include greater transpiration, and greater topsoil foraging, where Ca availability is greatest in acid soils. In acid soils, selection for *Topsoil Foraging* to optimize P capture should be



Fig. 7 Reduced root secondary growth improves phosphorus (P) capture. Left panel shows cross-sections of basal roots of two common bean (*Phaseolus vulgaris*) genotypes with contrasting secondary growth under suboptimal P availability. All cross-sections are at the same scale (bars, 500 μ m). Right panel shows shoot P accumulation in bean phenotypes with advanced or reduced secondary growth under suboptimal P availability in the field. Error bars represent the \pm SE of the mean; means with different letters are significantly different at $P \le 0.05$. Redrawn from Strock *et al.* (2018).

beneficial for Ca capture as well. The best opportunities to directly improve Ca efficiency probably lie with shoot traits for reduced tissue Ca requirement through, for example, altered cell wall composition (Lynch & Wojciechowski, 2015).

3. Magnesium

Despite longstanding reports of crop genotypic variation in response to suboptimal Mg availability (Canizella *et al.*, 2015), mechanisms underlying this variation are virtually unknown. As with Ca, the majority of Mg acquired by roots is transported via transpiration-driven mass flow (Barber, 1984). Unlike Ca, Mg is actively transported at the root surface, so variation in Mg transport kinetics may be beneficial (Kelly & Barber, 2008). In acid soils, Mg availability is greatest in the topsoil, meaning that *Topsoil Foraging* root phenotypes optimized for P capture (Fig. 1) may also be useful for Mg capture.

VII. Iron, zinc

Diverse mechanisms are potential section targets to genetically improve the availability of Fe and Zn in staple foods, including mobilization in the rhizosphere, uptake from the soil, transport to seeds or harvested plant tissue, and greater bioavailability through increased promotor compounds (e.g. ascorbate, cysteine-rich polypeptides) and reduced antinutritive compounds (e.g. phytate) (White *et al.*, 2009). Plant bioavailability of Fe and Zn is greatly reduced in alkaline soil, and is subject to interactions with an array of soil chemical and biological agents (Hansen *et al.*, 2004). Plant strategies to acquire Fe include 'strategy I' in dicots, consisting of rhizosphere acidification, the formation of rhizodermal transfer cells specialized for transport, transmembrane Fe(III) reductases, and the production of phenolic compounds, and 'strategy II' in grasses, consisting of the production of phytosiderophores capable of chelating Fe even in soils of alkaline pH (Kobayashi & Nishizawa, 2012). Mycorrhizas can improve Zn capture, although they are not attractive breeding targets (see 'Arbuscular mycorrhizas' in Section V).

Genotypic variation in Fe and Zn bioavailability is substantial in key staple crops, which has been the basis of the success of the Harvest Plus program in breeding staple crops with better bioavailability of Fe and Zn (Bouis & Saltzman, 2017). The mechanisms by which these gains have been achieved may have combined increased uptake with better transport to harvested tissue as well as reduced antinutritive compounds. Substantial genotypic variation for Fe mobilization in the rhizosphere has been reported in multiple species, in some cases under simple genetic control (Rodriguez de Cianzio, 1991). Rapid screens of Fe deficiency chlorosis in seedlings are available. Transgenic upregulation of phytosiderophore production in rice improves Fe capture from alkaline soil (Takahashi *et al.*, 2001). This transgene combined with upregulation of the Fe storage protein ferritin appears to be a promising avenue to improve seed Fe bioavailability in rice (Trijatmiko *et al.*, 2016) that may also have utility in other cereals, such as wheat. Cakmak (2008) makes a strong case for the deployment of agronomic interventions such as fertilizer supplementation with Zn to complement breeding approaches for better Zn nutrition, which has had substantial benefit in alleviating Zn deficiency in the human population of Anatolia, for example (Cakmak, 2008).

VIII. Cross-cutting issues

1. The importance of water

Water deficit stress is a primary, pervasive constraint to crop production, so interactions between water availability and nutrient capture must be considered in crop breeding programs. Water is a mobile resource that tends to concentrate in deeper soil domains over time under most drought scenarios. In this regard it is similar to nitrate, which leaches to deeper soil domains over time, and it has been proposed that root phenotypes that increase subsoil foraging, and therefore N capture, may also improve water capture (Lynch, 2018). Several root phenotypes improve capture of both water and N, including reduced lateral root branching (Zhan & Lynch, 2015; Zhan et al., 2015), reduced production of crown roots (Saengwilai et al., 2014b; Gao & Lynch, 2016), steeper growth angle of axial roots (Manschadi et al., 2010; Comas et al., 2013; Trachsel et al., 2013; Dathe et al., 2016), and RCA formation (Postma & Lynch, 2010, 2011; Zhu et al., 2010a; Chimungu et al., 2015b; Galindo-Castañeda et al., 2018). Because of the solubility of nitrate in soil water, root phenotypes that increase water capture are also likely to increase the capture of nitrate through transpiration-driven mass flow. This effect also applies to Ca, Mg, sulfur, and to a lesser extent K (Barber, 1984). The potentiating effect of water capture on nutrient capture illustrates one of the many benefits of Al tolerance. Al toxicity generally increases with soil depth, so Al tolerance improves subsoil foraging, and thereby the capture of water and soluble nutrients, including nitrate (Lynch & Wojciechowski, 2015).

Root phenotypes have important trade-offs for the capture of water from deep soil domains and the capture of immobile nutrients from the topsoil, primarily P. In addition to the trade-off between deep and shallow soil foraging, the immobility of P requires intensive foraging strategies, whereas the mobility of water requires extensive foraging strategies. A third trade-off is that root uptake creates P depletion zones in the rhizosphere, whereas rhizosphere soil water is rapidly replenished, creating fitness trade-offs for continued root growth and exploration of undepleted soil (Lynch, 2018). For example, in maize, several root phenotypes that improve water capture (i.e. steep root growth angle, sparse lateral branching, few crown roots) are opposite of those phenotypes that improve P capture (i.e. shallow root growth angles, dense lateral branching, many crown roots) (Ho *et al.*, 2005; Gao & Lynch,

2016; Jia *et al.*, 2018; Sun *et al.*, 2018; Lynch, 2018; Table 2). Trade-offs for the acquisition of water and P, and more generally for mobile and immobile soil resources, may account for the large diversity of root phenotypes evident in crop germplasm, which could represent selection for diverse soil environments as well as contrasting co-optimizing solutions to complex selection regimes. Such trade-offs are also an implicit challenge to single-trait breeding solutions, although it has been proposed that selection of deep root phenotypes for water capture may be a good solution in high-input agroecologies (Lynch, 2018).

2. Dimorphic root phenotypes

Dimorphic root phenotypes, capable of effectively acquiring both deep and shallow resources, would be useful in co-optimizing the capture of water, N, and P, especially in low-input systems, in which the availability of all three resources is often suboptimal (Lynch, 2018). An example of a dimorphic root phenotype is increased basal root whorl number (BRWN) in common bean (P. vulgaris). Greater BRWN results in more basal roots with a greater range of growth angles, and therefore a greater vertical range of soil exploration, which improves water, N, and P capture (Miguel et al., 2013; Rangarajan et al., 2018). Production of hypocotyl-borne roots, which are generally shallow, could complement an otherwise deep architectural phenotype (Rangarajan et al., 2018). In maize, the production of crown roots with progressively steeper growth angles results in an architectural phenotype that is initially shallow, coinciding with the shallow availability of water, N, and P during seedling establishment, with progressively deeper soil exploration over time, coinciding with the increasing importance of nitrate and water in deeper soil strata as the season progresses. For water capture in fertile soil, a deep architectural phenotype may be the best option (Lynch, 2018), but in most agroecosystems dimorphic phenotypes capable of acquiring both deep and shallow resources would be preferable. Numerous combinations of root phenes could generate such integrated phenotypes (Rangarajan et al., 2018), and such combinations are likely to differ between monocots and dicots, and among taxa within these groups.

3. Exploiting the potential of cheap roots

The trade-offs evident with architectural strategies for the capture of deep or shallow soil resources do not appear to be as important for anatomical strategies to reduce the metabolic cost of soil exploration, which is quite significant under edaphic (i.e. soil-related) stress (Lynch & Ho, 2005; Lynch, 2014). Phenes that reduce the metabolic cost of soil exploration permit plants to acquire soil resources more efficiently and effectively (Lynch, 2014). As already noted, anatomical phenotypes that reduce the metabolic cost of soil exploration improve the capture of P and N. They also improve the capture of water: increased RCA (Zhu *et al.*, 2010a; Chimungu *et al.*, 2015b), reduced cortical cell file number (Chimungu *et al.*, 2014a), increased cortical cell size (Chimungu *et al.*, 2014b), and possibly cortical senescence (Schneider & Lynch, 2018) improve water capture under drought. The reduction

Nutrient	Selection targets	Evidence	Natural variation	Comments
z	Steep root growth angles	Strong benefits but few studies	substantial	Tradeoffs exist for topsoil foraging/P capture, and the optimal growth
	Fewer axial roots	Strong benefits but few studies	substantial	Tradeoffs exist for topsoil foraging/P capture
	Reduced lateral branching density	Strong benefits but few studies	substantial	Tradeoffs exist for topsoil foraging/P capture
	More RCA	Strong benefits but few studies	substantial	Benefits greater in monocots than dicots; RCA improves capture of P and
	Longer/denser root hairs	Strong benefits but few studies	substantial	Benefits for capture of multiple nutrients and possibly water, longer/
		: : : : : : : : : : : : : : : : : : :		denser root hairs expand rhizosphere and microbial associations therein
	Fewer cortical cell files	Strong benefits in limited <i>in silico</i> studies	intermediate	Benefits for capture of multiple nutrients and water, tradeoffs poorly understood
	Greater cortical cell size	Strong benefits in limited in silico studies	substantial	Benefits for capture of multiple nutrients and water, tradeoffs poorly
	Nitrate transport kinetics	Intermediate benefits but few studies	intermediate	unucratuou Genetically simple
	Improved Associative N Fixation	Strong benefits in multiple studies	substantial	Mechanisms of improved ANF poorly understood
	Greater root cortical senescence	Strong benefits in Triticeae but few studies	intermediate	Possible benefits for multiple nutrients and water
4	Longer/denser root hairs	Strong benefits in multiple studies	substantial	Benefits for capture of multiple nutrients and possibly water, longer/
	Shallow root growth angles	Strong benefits in multiple studies	substantial	denser root hairs expand rhizosphere and microbial associations therein Tradeoffs exist for subsoil exploration, water capture, N capture in
	Greater lateral branching density	Strong benefits in multiple studies	substantial	leaching environments Tradeoffs exist for subsoil exploration, water capture, N capture in
			1-11-14-4-4-1	leaching environments
	iviore axial roous	strong benefits but rew studies	substantial	i radeorrs exist for subsoil exploration, water capture, N capture in leaching environments
	More RCA	Strong benefits but few studies	substantial	Benefits greater in monocots than dicots; RCA
	More hypocotyl-borne roots	Strong benefits but few studies	substantial	Important recovery mechanism for root loss
	Greater cortical cell size	Strong benefits but few studies	substantial	Benefits for capture of multiple nutrients and water, tradeoffs poorly understood
	Fewer cortical cell files	Strong benefits but few studies	substantial	Benefits for capture of multiple nutrients and water, tradeoffs poorly
	Greater root cortical senescence	Strong benefits in Triticeae but few studies	intermediate	Possible benefits for multiple nutrients and water
×	Longer/denser root hairs	Intermediate benefits but few studies	substantial	Benefits for capture of multiple nutrients and possibly water, longer/ denser root hairs expand rhizosphere and microbial associations therein
	More RCA	Strong benefits in limited in silico studies	substantial	Benefits greater in monocots than dicots; RCA improves capture of N, P and water also
	Greater root cortical senescence Topsoil foraging ideotype	Strong benefits in Triticeae but few studies hypothetical	intermediate substantial	Possible benefits for multiple nutrients and water Poorly understood
Ca	Topsoil foraging ideotype	hypothetical	substantial	Poorly understood
Mg	Topsoil foraging ideotype	hypothetical	substantial	Poorly understood
Fe, Zn	Rhizosphere mobilization	Strong benefits in multiple studies	intermediate	Phytosiderophores very promising in grasses, dicot mechanisms more subject to complexities of rhizosphere chemistry

Table 2 Promising selection targets for breeding crops with improved nutrient acquisition, based on 1) the strength of published evidence mechanistically linking phenotypic variation for the indicated

of mycorrhizal habitat in anatomical phenotypes that reduce cortical volume does not appear to counteract the major benefit that these phenotypes confer for soil exploration and P capture (Galindo-Castañeda *et al.*, 2018; Strock *et al.*, 2018). RCA has the added benefit of improving root function under hypoxia, which is important for subsoil foraging (Lynch & Wojciechowski, 2015). Traits that reduce the metabolic cost of soil exploration merit attention as potential breeding targets (Lynch, 2014).

4. Root hairs: the low-hanging fruit for improved nutrient capture

Root hairs are subcellular protrusions of the root epidermis that extend into the soil, expanding the volume of the rhizosphere that is directly subject to nutrient capture, modification through root exudates, and microbial symbioses. Substantial phenotypic variation for root hair length and density are present in crop germplasm, and genotypes with longer, denser hairs have much greater P capture from low-P soil (Gahoonia & Nielsen, 2004b; Lynch, 2011; Fig. 2), a benefit that is evident regardless of mycorrhizal status (Miguel, 2004). Root hairs also improve the capture of other immobile resources, such as K, and improve nutrient capture in general even for mobile nutrients (Jungk, 2001) and water (Carminati et al., 2017), by increasing root surface area and expanding the volume of rhizosphere that can be ameliorated by root exudates (Yan et al., 2004) and microbial associations. Although the benefits of root hairs are not evident in high-fertility soils (Wen & Schnable, 1994), they do not appear to generate fitness trade-offs, possibly because they have little impact on root metabolic costs (Bates & Lynch, 2000). Root hair phenotypes can be rapidly screened in seedlings in growth pouches (Vieira et al., 2007), opening the possibility of direct phenotypic selection in poorly resourced breeding programs in developing countries. The substantial variation for root hair length and density in crop germplasm, the substantial benefit this variation affords for nutrient capture, and the ease of screening for these phenotypes call for aggressive deployment of this trait in crop breeding programs (Table 2).

5. Integrated phenotypes

Root systems consist of multiple phenes under distinct genetic control, interacting with each other and the environment to determine fitness. For example, significant fitness trade-offs exist between topsoil and subsoil foraging strategies, as already discussed. Significant interactions, both synergistic and negative, also exist among phenes. For example, large BRWN and long, dense root hairs both improve P capture in bean, but in combination their benefit is twice their additive effects (Miguel *et al.*, 2015). Multiple synergies and antagonisms exist among axial root phenotypes of bean for capture of P and N, resulting in multiple integrated phenotypes that co-optimize capture of these two resources (Rangarajan *et al.*, 2018). Fitness landscapes will also be influenced by management scenarios (Thorup-Kristensen & Kirkegaard, 2016). The substantial interactions of root phenes with each other and the environment means that the fitness landscape of integrated

root phenotypes against the multidimensional array of environmental and internal factors is highly complex. Additional complexity is created by the fact that the fitness landscape for root phenotypes is likely to vary among taxa. Annual and perennial species are subject to highly contrasting constraints and opportunities. Within annual crops, monocots and dicots have distinct root strategies, at architectural, anatomical, and physiological scales. Within annual dicots, some species have strong basal roots (e.g. P. vulgaris), whereas in others taproot laterals are dominant (e.g. Glycine max); in annual monocots a fundamental division exists between tillering and nontillering taxa. Anatomical phenes also vary among taxa; for example, root secondary growth is important for P capture in dicots (Strock et al., 2018) but does not occur in monocots, and root cortical senescence has only been observed in the Triticeae tribe of monocots (Schneider & Lynch, 2018). The fact that root phenotypes vary so much among crop taxa suggests that model organisms, which have been so useful for genetic studies, may have limited utility in understanding the root phenome. Given the rapid pace of advancement in our ability to understand and manipulate crop genomes, as well as recent advances in root phenotyping of mature plants in the field (e.g. York & Lynch, 2015), it may be more efficient to conduct research on the root phenome directly in crop species rather than rely on model species. The fitness landscape of integrated root phenotypes is highly complex yet poorly understood, and merits greater research attention if we are to understand how to deploy root phenes in breeding specific crops for specific production environments. In silico approaches capable of evaluating many phenotype-environment combinations, including those that do not yet exist in nature, will be an important element of this effort (Dunbabin et al., 2013).

6. Ecosystem impacts

In high-input agroecosystems, crops with improved nutrient acquisition should be entirely beneficial. Such crops would reduce the amount of fertilizer required to meet yield goals, and thereby the environmental, energy, and economic costs of fertilizer production and application. This is especially true for N and P. Improved capture of N and P should directly reduce environmental impacts through reduced fertilizer application as well as by reducing the pools of nutrients in the soil susceptible to runoff, leaching, and volatilization.

Two important classes of low-input agroecosystems are (1) pasture, agroforestry, biofuel, and other extensive production systems in which intensive input use is possible but is not economically or environmentally desirable, and (2) subsistence and smallholder agriculture characteristic of developing countries, where input use is desired but is not possible because of poverty and poor input availability. In the first case, crops with greater nutrient acquisition would reduce fertilizer requirements, thereby reducing the economic and environmental cost of production. Efficient N capture will be especially important for biofuel crops, given the very significant energy and environmental cost of N fertilizers (Scharlemann & Laurance, 2008). In the case of smallholder agriculture, there is a concern that crops with greater nutrient acquisition would 'mine the soil', accelerating the depletion of soil

fertility through crop offtake. However, loss of nutrients through crop offtake must be balanced against the positive effects of nutrient-efficient crops on nutrient cycling, including maintenance of soil fertility through greater biomass production, greater root and soil microbial activity with benefits, for example, for P bioavailability, for legumes' greater N inputs to the system through BNF, and reduced erosion, which is often a dominant source of nutrient loss in these systems. For example, compared with existing common bean lines, new lines with shallower roots, and hence greater P capture, substantially reduced P lost to runoff in smallholder systems of Costa Rica (Henry et al., 2010). Nutrient-efficient crops should also have very substantial benefits for smallholder farmers, since the improved yield of such crops in nutrient-poor soil will improve food security and household income (Lynch, 2007). Additional food and income create opportunities for improved health, education, and input intensification, so that eventually these farmers may escape the poverty trap of low inputs/low yield. At forest margins, nutrient-efficient crops could reduce deforestation by reducing the need to colonize new land once the brief fertility pulse from logging and burning is exhausted.

IX. Breeding strategies

1. The value of ideotype breeding

The complexity of the fitness landscape for root phenotypes calls for informed selection of specific phenotypes for specific agroecologies; that is, *ideotype breeding*. The large number of integrated phenotypes resulting from the interplay of dozens of subtending phenes and their interactions with the environment create an exceedingly large number of scenarios of interest. For example, six root phenes each existing in only three states (e.g. small, medium, large) generate 3⁶ (i.e. 729) phenotypes, each of which is likely to have significant interactions with water and nutrient availability. In reality, root phenes exist in more than three states, and multiple soil environments may be targeted. The likelihood of obtaining optimal root phenotypes in genotypes that also have local adaptation, vigor, disease resistance, and so on in a given screening location is therefore infinitesimal. Indeed, brute-force yield selection for edaphic stress has generally been inefficient and ineffective. This problem is compounded by the fact that root phenotypes for efficient nutrient capture may be present in landraces but lacking in elite germplasm selected under high-input conditions. Although we have much to learn about the fitness landscape of integrated root phenotypes, we know enough to deploy robust ideotypes as breeding targets, as has been achieved, for example, with the Topsoil Foraging ideotype for P capture in legumes.

2. Phenes are more useful than traits

A phene is an elemental unit of the phenotype at a given level of organization (York *et al.*, 2013). Phene selection is more genetically tractable than is selection for traits that aggregate multiple phenes (in the extreme case, yield itself), simply because phenes are axiomatically under simpler genetic control than any combination of phenes. Phene selection also permits more informed and more

flexible assembly of an optimal phenotype. For example, root depth is an important trait for the capture of subsoil N in maize, but root depth aggregates multiple distinct phenes, including axial root growth angle, reduced production of crown roots, reduced lateral branching density, RCA formation, reduced cortical cell file number, and increased cortical cell size. These six component phenes are under distinct genetic control and have important interactions with each other. Selection for root depth will, therefore, be less precise and more complex, both genetically and physiologically, than would selection for specific combinations of specific phenes.

3. Breed for specific stresses

Another corollary to the complexity of the fitness landscape for root phenotypes is that selection efficiency will benefit from a clear definition of the target environment. Selection for efficient N capture in high-input agroecosystems is an example of a fairly simple selection regime, since one resource is targeted. Breeding for low-input agroecosystems is more complex, because multiple stresses are often important in such systems (Lynch, 2018). For example, acid soils have multiple edaphic challenges, in addition to Al and possibly Mn toxicity (and in many cases drought). Al tolerance dramatically improves growth in acid soil by alleviating a primary constraint to root growth, but Al tolerance is distinct from phenes that confer efficient acquisition of Ca, Mg, K, and P, and tolerance to excess Mn (Fernando & Lynch, 2015). It is highly improbable that mass screening of germplasm in acid soil will identify phenotypes that have optimal combinations of Al tolerance, efficient acquisition of all these resources, as well as Mn tolerance, in addition to local adaptation, disease resistance, yield potential, and so on, simply because of the low probability that one genotype may possess all of these traits. Informed combination of key phenes into an ideotype suited to the target environment would be more efficient than would screening under combined stress. This is especially true when trade-offs exist between root strategies for resource capture, as noted with N and P, for example. In this case, an ideotype should be developed based on breeding objectives in the target agroecosystem. In some cases, one phene confers adaptation to multiple constraints, as is the case for RCA and also for root hairs. These multifunctional phenes should be priority targets for crop breeding.

4. Phenotypic vs genomic selection

The genetic control of most root phenes is poorly understood, complex, quantitative, and may be subject to significant (G \times E) interaction. Genomic selection is an option for well-resourced breeding programs, with the caveat that selection should include phene states and their markers (Spindel & McCouch, 2016), and integrated phenotypes, in addition to yield itself, for the reasons noted earlier. Consideration should also be given to the development of appropriate training sets, since elite germplasm, often developed through decades of selection in high-input environments, often lacks the phenotypic diversity and edaphic adaptations present in wild germplasm and landraces. For programs with more

modest resources, such as those in developing nations, direct phenotypic selection is an option that is increasingly viable given the development of simple, robust methods to phenotype root systems of mature crops in the field (Trachsel *et al.*, 2011; Colombi *et al.*, 2015). In some cases, phenotyping is effective in seedlings grown in controlled environments, as is the case with root hairs and BRWN in common bean (Miguel *et al.*, 2013), or nodal root growth angle in sorghum (Joshi *et al.*, 2017).

5. Multidisciplinary teams are needed – relevant training is scarce

Breeding programs commonly include expertise in genetics, plant pathology and agronomy, but only rarely include the expertise in soil science, plant nutrition, and ecophysiology needed to guide the development of crop ideotypes for improved nutrient capture. The training of plant biologists increasingly focuses on molecular disciplines rather than organismal and environmental science, and the training of crop breeders increasingly focuses on modern methods of genomic manipulation and selection rather than organismal biology. A concerted effort to rationalize funding and training priorities is needed if we are to develop the cadre of young people capable of working across disciplinary boundaries to develop more nutrient-efficient crops.

X. Perspectives

Nutrient-efficient crops hold substantial promise to address pressing global challenges. Understanding plant adaptation to nutrient constraints is also fundamental to our understanding of plant evolution and biology. Given the importance and relevance of this issue, it is somewhat perplexing that this topic receives relatively little attention in basic and applied plant biology. Several interrelated factors contribute to this imbalance of need, opportunity, and effort. Paradoxically, one factor is the dramatic expansion of our ability to understand and manipulate the plant genome, and the understandable desire of both the research and sponsor communities to deploy these magnificent capabilities. In a few cases, such as Al tolerance, these tools have been useful in understanding and deploying single-gene traits for edaphic stress adaptation in crop breeding, but in many, if not most, cases, such traits are genetically and physiologically complex, and do not readily align with the gene-centric paradigm that dominates elite plant biology. A related factor is the inherent transdisciplinarity of this research domain, encompassing expertise in fields such as soil science, ecophysiology, and *in silico* biology that are increasingly scarce in plant biology research and training programs. A third related factor is the sheer complexity of the underlying processes, as evident, for example, in the interactions of root exudates with rhizosphere microbial communities and soil chemistry to determine nutrient mobilization. A fourth factor is the long-term nature of such research, involving crops in fields rather than rapid cycling model organisms, since many funding schemes are of a 3-5 yr duration. A fifth factor is the inertial and autocatalytic nature of science, in which active fields garner additional fame, funding, training, and hiring, at the expense of fields that are viewed as less

tractable or riskier, regardless of their importance and relevance. These factors are creating a challenging career landscape for young scientists that is retarding progress at a moment when breakthroughs are urgently needed to address a growing global crisis for food security. Considering the decadal timelines required to train young scientists, conduct research, and deploy resulting tools in crop breeding, our collective failure to address this imbalance of need, opportunity, and effort will result in significant opportunity costs for the environment and for our species. On a positive note, renewed emphasis on plant phenomics in the field, in silico biology, and the plant/soil microbiome are all very promising developments. To those young people considering careers in this field, I note that opportunities to make substantive contributions are more abundant in research domains that are neglected, important, yet increasingly tractable. Crop nutrient efficiency is just such a domain.

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