Rightsizing root phenotypes for drought resistance

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Highlight: Parsimonious root phenotypes may benefit water capture under drought.

Abstract

I propose that reduced root development would be advantageous for drought resistance in high-input agroecosystems. Selection regimes for crop ancestors and landraces include multiple stresses, intense competition, and variable resource distribution, which favored prolific root production, developmental plasticity in response to resource availability, and maintenance of unspecialized root tissues. High-input agroecosystems have removed many of these constraints to root function. Therefore, root phenotypes that focus on water capture at the expense of ancestral adaptations would be better suited to high-input agroecosystems. Parsimonious architectural phenotypes include fewer axial roots, reduced density of lateral roots, reduced growth responsiveness to local resource availability, and greater loss of roots that do not contribute to water capture. Parsimonious anatomical phenotypes include reduced number of cortical cell files, greater loss of cortical parenchyma to aerenchyma and senescence, and larger cortical cell size. Parsimonious root phenotypes may be less useful in low-input agroecosystems, which are characterized by multiple challenges and tradeoffs for root function in addition to water capture. Analysis of the fitness landscape of root phenotypes is a complex challenge that will be aided by the development of robust functional-structural models capable of simulating the dynamics of root-soil interactions.

Keywords: root development; drought; root architecture; root depth; root anatomy, phosphorus, nitrogen, water

Introduction

Here I consider the hypothesis that root phenotypes for optimal crop yield under drought differ from those resulting from natural selection, domestication, and traditional crop breeding. Specifically, I consider the hypothesis that reduced root development has benefits for crop yield under water stress. I focus on annual crops grown for seed yield, but many elements of this consideration pertain to annual crops grown for biomass yield and perennial crops. Some elements of my discussion are supported by the research literature, others are more speculative. I will not attempt a comprehensive review of all relevant literature but where appropriate cite recent reviews.

In the large majority of agroecosystems, seeds are planted in moist soil, so that soil moisture is adequate for germination and emergence. As soil moisture is depleted the crop becomes increasingly reliant on precipitation to meet its water requirement. A common scenario is progressively increasing water deficit over time as soil moisture is exhausted, crop growth increases water demand, and evapotranspiration increases as the season progresses. Sporadic rainfall may be inadequate to meet evapotranspiration, causing progressively increasing water stress over time, the extreme scenario being terminal drought. In other cases, temporary water deficit develops earlier in the season, which can have severe effects on reproduction by affecting seed formation or fertilization. I focus here on progressive water stress as the archetypal drought scenario, in which water is more available in deep soil strata than at the soil surface over time. Some elements of my discussion also pertain to sporadic drought scenarios in which water is available in surface strata. I also focus on growth itself rather than specific effects of water stress on reproduction, which are important (Saini and Westgate, 2000), and I focus on phene states (‘phene’ is to ‘phenotype’ as ‘gene’ is to ‘genotype’, (York *et al.*, 2013)) that do not incur inherent yield penalties (Blum, 2005), as is the case, for example, with shorter phenology (Nord and Lynch, 2009).

1. Do crop plants make too many roots?

Terrestrial plants evolved in environments that favor phenotypes with aggressive root proliferation. The soil is a hostile environment for roots. Soils can be too dry or too wet (hypoxic) to sustain root tissue, can be too hard to permit root penetration, can present toxins or deficiencies that directly limit root growth (*e.g.* Ca deficiency, Al toxcity), and are inhabited by many herbivores and pathogens, resulting in substantial root turnover (Fisher *et al.*, 2002). In natural ecosystems, intense belowground competition means that failure to produce sufficient roots to capture soil resources will cede a competitive advantage to neighbors. Furthermore, the availability of soil resources in time and space is nonuniform and in many cases unpredictable. The three primary soil resources that limit plant growth in the vast majority of terrestrial ecosystems are N, P, and water. In those rare soil environments that have abundant N, P, and water, dense plant growth results in intense belowground competition, which reduces the availability of these resources for individual plants. Phosphorus is generally more available in surface horizons because of continual deposition on the soil surface in plant residues, and its low mobility in soil (Lynch, 2011). However shallow soil strata may become hostile to root foraging because of temperature extremes (both hot and cold) as well as drying from root uptake and direct evaporation. Nitrogen in natural systems is released from mineralization of soil organic matter through microbial activity, forming ammonium, which is slowly mobile, which is in turn readily converted to nitrate, which is highly soluble in water and therefore can move to deeper soil strata through leaching. Since soil organic matter is concentrated in shallow soil strata, its mineralization is subject to variation in temperature and water availability. The leaching of nitrate to deeper soil strata is also subject to water availability and soil physical conditions. Therefore, the spatiotemporal availability of N, like P, is subject to water availability (Thorup-Kristensen and Kirkegaard 2016; Dathe *et al.*, 2016). Since water availability (generally in the form of precipitation) is itself highly stochastic in time and space, N and P availability in time and space are also to some extent unpredictable. Because of the unpredictability of resource availability, belowground competition, and the inevitability of root loss, plants have been selected for aggressive root proliferation and architectural plasticity, resulting in focused proliferation in response to patches of the primary resources of N, P, and water.

The strategy of aggressive root production may be counterproductive in high-input agroecosystems. In such systems, intensive fertilization has removed P and N as growth limitations. Indeed, overuse of fertilizers in such systems has created substantial environmental pollution with global repercussions. Intensive application of pesticides, modern crop management, and ongoing crop breeding for pest resistance have significantly reduced the risk of root loss from pathogens, herbivores, and some abiotic stresses that are important in natural systems such as soil acidity. Herbicides and reduced tillage, coupled with herbicide-resistant GM crops have substantially reduced root competition with weeds. Many of the technological elements of modern crop production can be viewed as means to eliminate constraints to root function. High-input agriculture has therefore mitigated many of the constraints to root function that are important in the ecosystems in which crop ancestors evolved, and in which crops were domesticated. As a result, we cannot assume that the ancestral strategy of producing many roots and aggressively exploiting resource patches is adaptive in high-input agroecosystems.

The one stress factor that has remained important throughout plant evolution and crop domestication, and that remains important in modern agroecosystems, is drought. It is probable that drought stress will increase in the future as a result of global climate change, which will increase atmospheric temperature and thereby soil water loss and crop water demand, and is projected to alter precipitation patterns in time and space, which can have large effects on crop water demand and water availability even if total annual precipitation is unchanged (Nord and Lynch, 2009). The increasing probability of drought is coinciding with both substantially increasing demand for agricultural production from a growing human population as well as increasing degradation of fresh water resources. ‘High input’ therefore does not include irrigation in most regions. There are insufficient fresh water resources to meet global demand for agricultural production, and the gap between fresh water resources and crop water demand is projected to grow. The importance of drought for high-input agroecosystems is therefore a paramount challenge of the 21st century. Drought stress has always been a primary factor in the evolution of terrestrial plants, but in high-input agriculture it has become the single greatest production risk.

The ancestral root phenotype of aggressive root proliferation results from selection regimes characterized by multiple biotic and abiotic constraints. It has been proposed that this phenotype is actually maladaptive for drought resistance (Lynch, 2013). Specifically, it has been proposed that root phenotypes for superior drought resistance should have fewer axial roots, fewer lateral roots, and less architectural plasticity in response to resource patches ((Lynch, 2013), Fig. 1). Recent evidence supports elements of this hypothesis, as summarized below. The idea that parsimonious root phenotypes in general are useful for drought resistance is supported by van Oosterom et al (2016), who showed that drought resistance in maize is associated with 'root system efficiency' (RSE), defined as transpiration per unit leaf area per unit of root mass, meaning that genotypes capable of maintaining transpiration at low root mass are advantageous. Another study with maize showed that lines resulting from 8 cycles of selection for grain yield under drought had 33% less root biomass in the topmost 50 cm of soil (Bolaños *et al*., 1993). These studies support the concept that more parsimonious root phenotypes are useful under drought, but are not mechanistic, since root biomass is a coarse metric aggregating many distinct root phenes and phene states. Evidence for the utility of parsimonious root phenes for drought resistance is summarized below.

1a. Evidence that reducing the number of axial roots improves drought resistance

A recent study supports the hypothesis that reduced production of axial roots is advantageous under drought (Gao and Lynch, 2016). Maize recombinant inbred lines with shared genetic backgrounds but with contrasting production of crown roots (*i.e.* belowground nodal roots, which are the dominant class of axial roots in this species) were grown under water deficit stress in field rainout shelters and soil mesocosms. Water stress reduced the production of crown roots, and lines with fewer crown roots under stress had substantially deeper rooting and greater capture of subsoil water, and consequently improved plant water status, stomatal conductance, leaf and canopy photosynthesis, biomass, and yield (Fig. 2).

The Gao and Lynch (2016) study observed that water stress reduced the production of axial roots in maize. While growth reduction under stress could simply be a symptom of stress injury, it could also reveal an adaption mechanism, especially if it is regulated by stress response pathways in a coordinated manner. In this context, it is noteworthy that water stress indeed downregulates the production of crown roots in grasses through coordinated developmental pathways (Sebastian *et al.*, 2016). Sebastian *et al.* found that water deficit inhibits the production of crown roots in several grass species including *Setaria viridis*, *Setaria italica*, and both wild (teosinte) and cultivated *Zea mays,* by local sensing of soil water availability. Water deficit inhibited crown root production more strongly in wild taxa than in cultivated taxa, and genetic variation was observed in crown root arrest among maize lines. Under water deficit a maize mutant that lacks the ability to form nodal roots (*rtcs*) maintained better soil and plant water status (but did not have different shoot biomass) than a wildtype line. The authors propose that "*… severe reductions in shoot-borne root growth are crucial to prevent overdrawing of water from the soil and water loss through crown root growth*." (Sebastian *et al.*, 2016). This is an important study that generally supports the hypothesis that phenotypes with fewer nodal roots are useful under water stress. However, the ecophysiological interpretation of these results is debatable. It is unclear why conserving soil moisture under water deficit would be advantageous to wild plants subject to competition. Water left in the soil by reduced root growth would be subject to loss to competitors. We might assume that when competition is limited to monogenetic stands as occurs in high-input agriculture, a 'water banking' strategy may be useful for stand-level reproductive output. The observation that cultivated taxa have less rather than more root inhibition by water stress argues against this however. The proposal that roots directly consume significant amounts of water is unsubstantiated, since the amount of water stored in root tissue is only a very small fraction of the amount of water transpired. A gram of dry root tissue might require 1.5 g of water for hydration (Guo *et al.*, 2013) yet a gram of dry plant tissue requires 250-350 g of transpired water in C4 plants and 650-800 g of transpired water in C3 plants (Ehleringer and Monson, 1993). An alternate ecophysiological interpretation is that reduced production of nodal roots reduces competition among root axes of the same plant for both internal resources (photosynthates) and external resources (in this case, water), meaning that a phenotype with fewer axial roots may actually have greater root depth and greater water acquisition from deep soil strata (Fig. 3, Saengwilai *et al.*, 2014*b*; Gao and Lynch, 2016). This is an important conceptual difference since root phenotypes that reduce whole-plant water acquisition are likely to also reduce yield, because of the close association of shoot water use with shoot C gain (Blum, 2009). While root phenotypes that conserve soil water are useful in systems that rely on stored soil water, their yield penalty reduces their utility in rainfed systems with variable water stress. The ecophysiological interpretation of Sebastian *et al.* is based on comparison of one wildtype phenotype with one mutant with a severely reduced root phenotype grown as young seedlings in small containers of synthetic media in growth chambers at unspecified light intensity. No growth benefit associated with root phenotypes was observed. Greater root depth improves soil water capture in the field and in large mesocosms but may not do so in small containers with limited water supply. A more rigorous ecophysiological analysis would compare stands of mature plants with a range of varying crown root production in actual soil with normal transpiration regimes. This was the approach employed by Gao and Lynch, who observed that under water stress, phenotypes with reduced crown root production had greater acquisition of subsoil water rather than less, which contradicts the 'water banking' hypothesis (Gao and Lynch, 2016).

Indirect evidence for reduced intraplant competition as the physiological benefit of reduced nodal root production under drought comes from a study of the effect of genotypic variation in crown root production in maize under suboptimal N availability (Saengwilai *et al.*, 2014*b*). Under N limitation, N can be localized in deeper soil strata over time because of leaching, which is comparable to the deep localization of water under progressive drought. In this study maize lines with fewer crown roots had deeper rooting, better capture of subsoil N, and consequently better growth and yield under N stress than genetically related lines with more crown roots (Saengwilai *et al.*, 2014*b*). The fact that reduced production of nodal roots increases N acquisition from deep soil strata, which is similar to the enhanced capture of deep soil water by maize lines with fewer crown roots (Gao and Lynch, 2016), argues against the 'resource banking' hypothesis. It is noteworthy that N stress, like water stress, reduced crown root production in some maize lines, which may suggest that these stresses share signaling pathways in regulating the production of nodal roots.

An additional indirect line of evidence for the utility of reduced crown root production is the observation that the past 100 years of maize breeding has resulted in root phenotypes with fewer nodal roots (Fig. 4, York *et al.*, 2015). During this period maize planting density has more than doubled and yield has increased by a factor of 8, resulting in greater belowground competition and resource efficiency. Inadvertent selection for reduced production of nodal roots would be expected if this phenotype was useful for more efficient capture of soil resources. Indeed, disaggregation of maize root phenes using the functional-structural model *SimRoot* showed that the observed reduction in nodal root production makes the root phenotypes of lines from a century ago as productive and fit as modern root phenotypes in modern production environments (Fig. 5, York *et al.*, 2015).

The production of axial roots in tillering species, an important group of grain crops that includes wheat, rice, barley, oat, rye, and millet is complicated by the fact that the majority of nodal roots in these species are produced by tillers. Reduced tillering can be a useful water banking strategy in semi-arid and Mediterranean environments with predictable water limitation (Blum, 2005), but reduced tillering also reduces yield potential, which limits its utility in normal rainfed systems. In rice, reduced nodal root number is associated with improved drought resistance (Catolos et al 2017). The utility of reduced nodal root production per tiller merits attention.

1b. Evidence that reducing the density of lateral roots improves drought resistance

Reduced production of lateral roots and the associated phenotype of longer lateral roots has been proposed to be beneficial under drought (Lynch, 2013, Fig. 3). The rationale for this proposal is the same as that described in section (1a) for reduced production of axial roots, *i.e.* that for a mobile soil resource like water, the production of too many lateral roots is counterproductive by increasing intraplant competition for internal resources (primarily carbohydrates) needed for root growth, as well as competition for the capture of mobile soil resources, in this case water.

Direct evidence in support of this hypothesis was provided by analysis of maize recombinant inbred lines sharing genetic backgrounds but with contrasting production of lateral roots grown under water stress in field rainout shelters, in natural drought conditions in the field, and in soil mesocosms (Zhan *et al.*, 2015). Water stress reduced lateral branching of crown roots, and lines with fewer lateral roots under stress had substantially deeper rooting, greater capture of subsoil water, and consequently improved plant water status, stomatal conductance, leaf photosynthesis, biomass, and yield (Fig. 6).

Indirect evidence supporting the utility of this phenotype is provided by the ‘era’ study of root phenotypes from 100 years of maize breeding (York *et al.*, 2015). This study found that modern maize root phenotypes have greater distance from the point of crown root emergence form the shoot to the first lateral root, a phene state that effectively reduces lateral root production at the organismic level, as well as longer lateral roots.

1c. Is architectural plasticity useful under drought?

It has been proposed that unresponsiveness of lateral branching to localized resource availability would be advantageous under drought (Lynch, 2013). Localized root proliferation in response to local water availability may be counterproductive because water is an ephemeral resource subject to movement and depletion, whereas root growth is relatively slow, and building and maintaining roots incur significant long-term costs, especially considering that roots are not actively senesced (Fisher et al, 2002). In addition, construction of roots in moist soil domains may incur opportunity costs of failing to build roots in domains that may have greater water availability over time. For example, intermittent rain under drought may cause shallow wetting of surface soil that is rapidly depleted. Root production in shallow soil in response to this ephemeral resource would divert resources from exploitation of deeper strata with greater water availability (Lynch, 2013). In natural ecosystems and low-input agroecosystems, exploitation of localized water patches through root plasticity can confer a competitive advantage, but in high-input monoculture this is less important. Indirect evidence for this is the observation by that axial root development in cultivated taxa is less sensitive to local water status than in wild taxa (Sebastian *et al.*, 2016). The utility of root plasticity under drought is unclear and merits research.

1d. Can root lifespan be optimized under drought?

Substantial root loss occurs because of both abiotic and biotic stress. Root loss due to biotic stress (pathogens, root-feeding insects, nematodes, etc.) is mitigated by pesticides in high-input systems, but drought stress increases root loss (Huck *et al.*, 1987). The functional impacts of root loss have been analyzed via microeconomic analysis, in which costs and benefits are compared (Eissenstat and Yanai, 1997). The cost of root loss for plant function includes 1) the loss of the nonrecoverable resources in the lost tissue (*e.g.* energy and material invested in cell wall construction); 2) the opportunity cost of reduced soil resource capture, anchorage, lateral root formation, protective barriers, etc. from the lost segment; and 3) loss of these resources and functions from roots subtending the lost segment. Benefits resulting from root loss include termination of the metabolic costs of maintaining the lost segment, primarily carbohydrate lost to respiration, and allocation of primary resources such as N and P invested in root tissue, and the opportunity to allocate future resources to more productive soil domains. The C costs of maintaining root tissue exceed the C costs of constructing root tissue after a short initial period (Lambers *et al.*, 1996), and are a significant component of daily C budgets, especially under edaphic stress (*e.g.*, Nielsen *et al.*, 1998). It is therefore possible that root loss may be beneficial, if the benefit of reduced maintenance costs exceeds the cost of the lost root functions (Eissenstat and Yanai, 1997; Steingrobe *et al.*, 2001). Under drought stress, the soil typically dries from the top down because of greater root activity in the topsoil as well as direct evaporation of soil water. The death of roots in dry topsoil may be beneficial by reducing the cost of maintaining roots that are not contributing to water capture. This is especially true for fine roots, since they are more metabolically active per unit root mass and can be replaced after soil rewetting by lateral branching of axial roots. The loss of shallow roots would permit greater resource allocation to deep roots, which would improve water capture. Compensatory regrowth following mechanical root loss has been observed in common bean (Rubio and Lynch, 2007). It has been proposed that root turnover can increase the capture of the immobile nutrients P and K by permitting greater exploration of new soil, although evidence for this comes from simulation models that do not simulate intraplant competition in a robust manner, and from empirical studies with ingrowth cores that restrict competition and soil resource depletion (Yanai *et al.*, 1995; Steingrobe *et al.*, 2001). The proposal that root loss may be beneficial under drought is speculative and is difficult to verify, since the rate, timing, and position of root loss are difficult to control in empirical studies. *In silico* approaches using modern functional-structural models that explicitly model the spatiotemporal dynamics of root growth and soil resource capture would be useful in this context.

2. Do crop roots make too much tissue?

Section 1 considered root phenotypes that optimize water capture under drought by reducing investment in organs with an unfavorable cost/benefit ratio. This section considers optimization of root phenotypes for water capture by reducing investment in cells and tissues with an unfavorable cost/benefit ratio.

2a. *Maize genotypes with fewer root cortical cell files have superior drought resistance*

A large portion of primary root structure is cortical parenchyma that is metabolically active but has no specialized function in water acquisition. Cortical parenchyma is important in radial transport of water from the epidermis to the stele however. In older root segments this function might be reduced without compromising drought resistance, because older root segments are generally located in soil domains in which water has already been depleted, and older root segments can serve axial transport, relying on subtending segments, including lateral branches, for resource capture. In monocotyledonous crop species that lack secondary growth, the cortex can remain viable for extended periods. It was proposed that maize lines with reduced cortical tissue would have reduced metabolic costs of soil exploration, which would enable greater rooting depth and water capture under drought (Lynch, 2013; Lynch *et al.*, 2014). In a study testing this hypothesis, maize lines with contrasting cortical tissue expressed as *Living Cortical Area* (LCA: total transversal root cortical area minus Root Cortical Aerenchyma (RCA) area and intercellular air space area) were exposed to drought stress in soil mesocosms (Jaramillo *et al.*, 2013). Lines with less LCA had less respiration, greater elongation of axial roots, and better growth under water stress than lines with more LCA. The primary components of LCA are the number of cortical cell files (CCFN, Fig. 7b) and cortical cell size (CCS, Fig. 7c), minus intercellular air space and the tissue lost to aerenchyma formation (RCA, Fig. 7a). It was therefore hypothesized that reduced CCFN, CCS, and RCA could all contribute to water capture under drought through their effects on the metabolic cost of soil exploration (Lynch, 2009).

The hypothesis that reduced CCFN improves water capture under drought was tested by comparison of maize lines with contrasting CCFN under water stress in soil mesocosms and field environments in the USA and Malawi. Lines with fewer cortical cell files had less respiration, greater root depth, greater exploitation of deep soil water, and therefore better water status, growth, and substantially greater yield than comparable lines with greater more cortical cell files (Fig. 7, Chimungu *et al.*, 2014*b*). Substantial genetic variation for CCFN is present in maize (Burton *et al.*, 2013; Chimungu *et al.*, 2014*b*), so this phene merits attention as a potential breeding target for improved drought resistance.

2b. Loss of root cortical tissue via aerenchyma formation improves drought resistance

Many crop species form aerenchyma in the root cortex through programmed cell death. The conversion of living cortical cells to air space allows reinvestment of nutrient resources to other plant tissues, including growing root tips, and reduces the metabolic cost of maintaining the root cortex. It was therefore hypothesized that RCA formation is advantageous for soil exploration and the capture of soil resources under edaphic stress (Lynch and Brown, 1998; Fan *et al.*, 2003). *In silico* analysis in *SimRoot* indicates that the effects of RCA formation on root metabolic costs can improve soil exploration and the capture of N, P, and K when those resources limit growth (Postma and Lynch, 2011). Empirical support for improved N capture with greater RCA formation was provided by comparison of maize lines with contrasting RCA formation under suboptimal N regimes in the field in Africa and North America as well as in soil mesocosms (Saengwilai *et al.*, 2014*a*). Under N stress, high RCA genotypes had less root respiration and N content, and greater rooting depth, N capture, growth and yield. The benefit of RCA for N capture suggests that it may also be useful for water capture, as both nitrate and water tend to be deep soil resources (Thorup-Kristensen and Kirkegaard 2016; Dathe *et al.*, 2016). It was therefore proposed that RCA formation would improve water capture under drought (Lynch, 2013). Under water stress in field rainout shelters and soil mesocosms, maize genotypes with greater RCA formation had reduced root respiration and greater rooting depth, water capture, growth, and yield than related lines with less RCA (Zhu *et al.*, 2010) These results were recently supported by an on-farm analysis of maize lines grown under natural drought conditions by smallholder farmers in Malawi, which showed that lines with greater RCA formation had better water status, growth, and yield than lines with less RCA (Fig. 8, Chimungu *et al.*, 2015*b*).

It has been proposed that RCA may be beneficial under drought by reducing radial water conductance, thereby slowing the depletion of soil water (Vadez, 2014). In addition to conserving soil water for later growth, limited water uptake under drought is also likely to incur benefits from reduced shoot growth hence reduced water demand, more efficient use of water in leaf transpiration, and maintenance of wetter, softer soil surrounding growing root tips (Lynch *et al.*, 2014). RCA formation does reduce the radial transport of water (Fan *et al.*, 2007) and nutrients (Hu *et al.*, 2014). While reduced radial water transport may be a benefit of RCA under drought, several lines of evidence suggest that the effects of RCA on the metabolic costs of soil exploration are important. One line of evidence is *SimRoot* modeling, which correctly predicts benefits of RCA for nutrient capture based on reduced metabolic costs without considering reduced water transport. Another line of evidence is that root phenes apart from RCA that reduce root metabolic costs also improve drought resistance despite the fact that their effects on radial water transport are unclear, including reduced production of axial roots (Gao and Lynch, 2016), reduced lateral root branching (Zhan *et al.*, 2015), reduced CCFN (Chimungu *et al.*, 2014*b*), and increased CCS (Chimungu *et al.*, 2014*a*). It is also noteworthy that lateral roots have less RCA than axial roots, and lateral roots are more important for soil exploration and water capture. It would be challenging to directly assess the relative importance of these two effects of RCA, *i.e.* effects on radial water transport *vs.* effects on the metabolic costs of soil exploration. These effects could be uncoupled *in silico*, as was accomplished for example to uncouple the effects of RCA formation on reduced C costs vs. nutrient remobilization in *SimRoot* (Postma and Lynch, 2011). For this to occur we need more robust models of dynamic interactions of root phenotypes with soil water availability.

Substantial variation for RCA among crop genotypes, and its apparent utility under drought, nutrient stress, and hypoxia suggest that it merits attention as a potential breeding target (Lynch *et al.*, 2014; Lynch and Wojciechowski, 2015).

2c. Does loss of root cortical tissue via cortical senescence improve drought resistance?

Root cortical senescence (RCS) occurs in several important species including wheat (*Triticum aestivum*), triticale (*Triticosecale*), barley (*Hordeum vulgare*, Yeates and Parker, 1985; Liljeroth, 1995), rye (*Secale cereale*) (Deacon and Mitchell, 1985; Jupp and Newman, 1987) and oat (*Avena sativa*) (Yeates and Parker, 1985). Unlike RCA formation, which typically leaves files of living cortical cells connecting the epidermis and endodermis, RCS results in complete loss of living cortical tissue. By analogy with RCA, RCS may be beneficial under drought by reducing the metabolic costs of soil exploration and hence water capture. In barley, RCS substantially reduces root respiration and nutrient content, as well as radial transport of water, nitrate, and phosphate (Schneider *et al.*, 2017*b*). RCS was increased by N and P limitation, and a landrace had greater RCS than a modern cultivar (Schneider *et al.*, 2017*b*), which is indirect evidence that it may be adaptive under edaphic stress. Functional-structural modeling in *SimRoot* showed that RCS could substantially improve the growth of barley under suboptimal availability of N, P, or K, with the main benefit due to nutrient remobilization from senesced tissue (Schneider *et al.*, 2017*a*). The ability of RCS to reduce root metabolic costs and thereby to increase rooting depth, and to reduce the radial hydraulic conductance of older root segments suggests that it may be useful for water capture from drying soils (Schneider and Lynch in press, Fig. 9).

2d. ***Maize genotypes with larger root cortical cells have superior drought resistance***

Greater cortical cell size (CCS) could reduce the metabolic cost of soil exploration, and thereby water capture under drought, since larger cells have proportionately more volume occupied by the vacuole, which has less N, P and respiratory cost than does cytoplasm. Direct evidence to support this proposal is provided by a comparison of maize lines with contrasting CCS grown under drought in soil mesocosms, field rainout shelters in the

USA, and natural drought in the field in Malawi (Chimungu *et al.*, 2014*a*). Maize lines with greater CCS had less root respiration, greater root depth, and therefore greater capture of subsoil water, better water status, photosynthesis, growth, and yield (Fig. 7).

These results are consistent with the hypothesis that reducing root metabolic costs increases water capture from drying soil. Reduced production of axial roots and lateral roots allow remaining roots to reach deep soil water. Reduced cortical burden, by increased aerenchyma formation, decreased number of cortical cell files, or increased cell size, increases water capture under drought by increasing internal resources available for deeper rooting. Root cortical senescence and some degree of root loss may have similar benefits.

2e. Overcoming soil impedance is an important feature of drought resistance

In most soils, soil impedance increases with soil depth and also with soil drying (Bengough *et al.*, 2006; Lynch and Wojciechowski, 2015). The ability of roots to penetrate hard soils is therefore an important aspect of water capture under drought, especially water capture from deep soil strata. Phenes like RCA and RCS that reduce cortical burden in mature root segments are not likely to affect soil penetration, which is a function of the root tip. Anatomical phene states like reduced CCFN could reduce root diameter, which would be expected to reduce penetration of hard soil (Bengough *et al.*, 2006). In this context, it is noteworthy that several anatomical phenes were related to the biomechanical properties of maize roots and their ability to penetrate hard wax layers independently of root diameter, including cell size in the distal cortex, cortical cell wall area, and stele diameter (Chimungu *et al.*, 2015*a*). The architectural phene states of reduced axial root and lateral root production may enable remaining roots to have larger diameter, which would improve their penetration of hard soil. Phene states that reduce radial water transport, like RCA and RCS, may permit growing root tips to remain hydrated and would allow them to penetrate soil with greater water content and therefore less impedance (Lynch *et al.*, 2014).

2f. Root phenotypes that optimize water capture may also optimize N capture

Suboptimal N availability is second only to water as a global limitation to crop productivity. In low-input systems, suboptimal N limits yield, while in high-input systems, intensive N fertilization is a primary economic, energy, and environmental cost of the production of non-leguminous crops (Hirel *et al.*, 2011; Cassman *et al.*, 2002; Ribaudo *et al.*, 2011). In most agroecosystems N accumulates in deeper soil strata over time as a result of leaching (Thorup-Kristensen and Kirkegaard 2016), which led to the proposal that deeper rooting will improve the capture of both N and water (Lynch 2013). For example, steeper root growth angles improve water capture in several crop species (*e.g.*, Manschadi *et al.*, 2006; Singh *et al.,* 2012), and in maize also improve N capture (Trachsel *et al.*, 2013; Dathe *et al.*, 2016). In maize, root phenes that regulate root depth and thereby the capture of both water and N when those resources are limiting include the number of nodal roots (Gao and Lynch 2016; Saengwilai *et al.*, 2014b), lateral root branching density (Zhan *et al.*, 2015; Zhan and Lynch 2015), and root cortical aerenchyma (Zhu *et al.,* 2010; Saengwilai *et al.*, 2014a; Chimungu *et al.,* 2015b). Optimization of root phenotypes for water capture may therefore also improve N capture, with benefits for both high-input and low-input agroecosystems.

3. The challenges of low-input systems

Many important agroecosystems do not receive intensive inputs. These include systems in which intensive management is possible yet is uneconomical, such as pastures, rangeland, or production of biofuel crops, and systems in which intensive use of inputs is not an option because of lack of capital, lack of expertise, or poor availability of inputs, as occurs in smallholder agriculture in developing nations. Such systems suffer from many of the constraints found in natural ecosystems, including multiple biotic and abiotic stresses, intense weed competition, and spatiotemporal variability in the availability of soil resources, especially water. As a result, optimal root phenotypes for drought resistance in high-input systems may be suboptimal in low-input systems.

Phosphorus availability is a key difference between high-input and low-input systems. Intensive P fertilization is characteristic of high-input agriculture, whereas low P availability is a primary constraint to crop productivity in the majority of low-input systems.

This is because of the inherently low P availability in the weathered soils characteristic of the tropics and subtropics, in addition to ongoing soil degradation. Root strategies to acquire P have several important tradeoffs for water acquisition. Phosphorus is an immobile soil resource that concentrates in the topsoil over time, whereas water is highly mobile and moves to deep soil strata over time. The low mobility of P in soil means that roots (and their symbionts) must be in close proximity to P in order to acquire it (Barber, 1995), while water can move to the root from much larger distances, thereby creating tradeoffs for intensive *vs.* extensive soil foraging strategies. A third tradeoff is that root uptake creates P depletion zones that only slowly replenish, whereas soil domains depleted of soil water may be rapidly replenished. This means that continued root growth and exploration of undepleted soil domains is more important for P capture than for water capture.

Clear tradeoffs for water and P capture are evident for several root architectural phenes. Shallow root growth angles promote topsoil foraging and P capture (Lynch, 2011), whereas steep root growth angles promote subsoil foraging and water capture (Ho *et al.*, 2005). In maize, dense lateral root branching promotes P capture (Postma *et al.*, 2014), whereas sparse lateral branching promotes water capture (Zhan *et al.*, 2015). Production of few axial roots is beneficial for water capture by allowing root axes to grow to greater soil depths (Gao and Lynch, 2016), whereas increased nodal root number improves P capture (Bayuelo-Jiménez et al., 2011). Anatomical phenes that reduce cortical parenchyma, like RCA, RCS, and reduced CCFN, are beneficial for water capture but may reduce symbiotic P capture by reducing mycorrhizal habitat. In contrast, anatomical phenes that reduce the metabolic cost of soil exploration should have benefits for the capture of both mobile and immobile resources. For example, RCA is beneficial for the capture of the mobile resources water (Zhu *et al.*, 2010; Chimungu *et al.*, 2015*b*) and N (Saengwilai *et al.*, 2014*a*), while also being beneficial for the capture of the immobile resources P and K (Postma and Lynch, 2010, 2011). Root hairs are useful for capture of P (Bates and Lynch, 2000*a*; Miguel *et al.*, 2015) as well as water (Carminati *et al.*, 2017), while incurring little direct metabolic cost (Bates and Lynch, 2000*b*).

In considering the optimal root phenotype for low-input systems it must be considered that many such systems employ polycultures composed of different crop species and/or different genotypes of the same species instead of the genetic monocultures characteristic of high-input systems. The fitness value of root phenotypes in polycultures may differ from monocultures due to resource competition and complementarity, and fitness impacts upon the polyculture as a whole rather than just to one species. For example, the ancient maize/bean/squash polyculture is more efficient in capturing mineral N than are the component single species because of niche complementarity (Postma and Lynch, 2012; Zhang *et al.*, 2014). It is likely that water capture by polycultures is also affected by interactions among the roots of each species. In addition to niche complementarity it is possible that members with deeper and shallower roots may benefit each other through root-mediated hydraulic redistribution (Brooker *et al.*, 2015).

The greater intensity of biotic and abiotic stress in low-input systems, and greater variability in the distribution of soil resources in time and space, may make the production of numerous axial roots and plasticity in response to local resource availability more important than they are in high-input systems. Better understanding of the fitness landscapes of root phenotypes in the progression of wild taxa in natural systems through landraces in low-input systems to elite monogenetic stands in high-input systems would be useful in resolving these issues, and in guiding the development of more drought resistant crops in developing nations.

4. Future Prospects

The need for drought resistant crops is critical, and will surely grow in years ahead because of a growing human population with increasing food demand per capita, ongoing degradation of soil and water resources, and the accelerating effects of global climate change. Crops with improved root phenotypes will be an important element of future agroecosystems. In recent years significant progress has been achieved in discovering specific root phenes, phene states, and integrated phenotypes for superior water capture. Ideotype breeding, grounded in an understanding of the fitness landscape of specific root phenes in specific phenotypic, environmental, and management contexts, would be an effective path to deploy root phenotypes in crop breeding (Cooper et al. 2014; Lynch, 2015). For this to succeed it is important that phenes, elemental units of the phenotype, are evaluated rather than phene aggregates, which are under more complex genetic control and have more complex environmental interactions. For example, although root depth is generally viewed as a 'secondary trait' that offers mechanistic insight into drought resistance, recent research shows that root depth is in fact regulated by multiple independent phenes and phenes states (Lynch and Wojcieshowski, 2015), whose interactions with each other and with the environment are quite complex (Thorup-Kristensen and Kirkegaard, 2016). Better definition of target phenes would greatly facilitate both genetic and functional analysis. An excellent example of this approach is the work at IRRI to understand how specific QTL affect resistance to specific types of drought in specific production environments by regulating specific root phene states such as root growth angle and nodal root number (e.g. Catolos et al 2017).

In this article, I propose that the optimal root phenotype for drought resistance in high-input agroecosystems is fundamentally different from ancestral root phenotypes that have been selected in natural ecosystems and traditional low-input agroecosystems. A possible exception is wild taxa adapted to arid environments. Many arid environments are characterized by severe water limitation but good availability of other soil resources and relatively low plant density, hence relatively slight belowground competition, and less soil biotic activity, hence reduced root loss. Therefore, they may possess the parsimonious root phenotype that I propose here. Several important crop species have wild relatives adapted to arid conditions. It would be useful to study the root phenotypes of such taxa, although their deployment in elite crop breeding could be complex. In some cases, cultivated taxa exist that are related to principal crops, that might serve as models or genetic resources for crop breeding. For example, the tepary bean, *Phaseolus acutifolius*, is a close relative of the common bean, *Phaseolus vulgaris*, but is native to semi-arid regions of North America, and has much greater resistance to heat and drought than does common bean (Pratt and Nabhan, 1988; Federici *et al.*, 1990; Rao *et al.*, 2013). Interspecific hybridization of tepary bean with common bean has led to the development of common bean lines with substantially improved resistance to drought and heat (Mejia-Jimenez *et al.*, 1994; Muñoz *et al.*, 2004; Rao *et al.*, 2013). Other cases exist in which principal global crops are genetically related to other crop taxa from semiarid regions, as is the case with maize (*Zea mays*) *vs.* sorghum (*Sorghum bicolor*). Comparative analysis of root phenotypes from such taxa would be useful in identifying phenes and potentially genes for improvement of the drought resistance of a target species. In addition to analysis of related taxa from semiarid environments, it would be useful to profile root phenotypes of a diverse set of elite lines and landraces within crops, to establish the range of variation present and identify patterns associated with drought resistance. This has not often been attempted, possibly because of the difficulty in phenotyping roots under realistic conditions. The advent of high-throughput methods to quantify root phene states under realistic conditions is a promising development in this context (*e.g.* Bucksch *et al.*, 2014).

The use of modern *in silico* approaches will be invaluable in testing the validity of the ideas proposed here, and more generally in understanding the fitness landscape of root phenotypes. This is because of the large number of interactions among specific root phenes and the environment, and the large number of environmental scenarios of interest, including different soil water regimes as well as future environments with drought coinciding with elevated atmospheric CO_2 and high heat, both of which could strongly interact with drought stress, as well as novel management scenarios. Modeling is particularly attractive for drought, because of the difficulty of imposing managed drought regimes in the field and in replicating realistic drought stress in controlled environments. To be useful in this context, models should faithfully capture the essential elements of the acquisition and transport of water by roots in drying soil, shoot responses to water stress, as well as interactions of roots with shoots. Presently no models exist with these capabilities at the level of detail that would enable evaluation of specific phenes and phene states, or that could faithfully model emergent properties resulting from soil-root-shoot interactions (Tardieu *et al.*, 2017). Parsimony is a valuable quality in heuristic models, because of the difficulty in understanding and interpreting results from models with many variables, as well as the problem of error propagation. To paraphrase Einstein's famous quote regarding theories, 'a model should be as simple as possible, but no simpler'. Rather than construct complex models attempting to simulate all relevant processes, a more feasible and robust option would be to integrate a family of models, each focusing on a distinct set of processes, within a larger framework capable of exchanging data among the submodels, checking for error propagation, and capturing emergent properties. Increasingly robust models exist for water movement in soil, canopy responses to water stress, and the capture of soil resources by roots. The rapid development of functional-structural plant models is a very promising development in this context (e.g. (Dunbabin *et al.*, 2013; Marshall-Colon *et al.*, 2017; Postma *et al.*, 2017).

I propose that a parsimonious root phenotype would be advantageous for drought resistance in high-input agroecosystems. These concepts may also apply to the shoot phenotype. Reduced shoot branching, reduced leaf production, greater turnover of older/shaded leaves, reduced investment in parenchyma tissue in the stem and in leaves, narrower leaves that permit better light penetration of the canopy while improving leaf energy budgets under drought, reduced stem production and elongation in species that are not already dwarfed, *etc.*, could result in greater drought resistance without compromising yield potential by focusing resource allocation to the most productive tissues. For example, reduced tillering and leaf size improves drought resistance in sorghum by reducing soil water depletion prior to anthesis (Borrell *et al.,* 2014). As with parsimonious root phenotypes, parsimonious shoot phenotypes may not be advantageous in low-input agroecosystems however.

5. Conclusion/summary

I propose that parsimonious root phenotypes would be advantageous for drought resistance in high-input agroecosystems. Selection regimes for crop ancestors and landraces include an array of biotic and abiotic stresses, intense belowground competition, and spatiotemporal variability in the distribution of soil resources. These factors favored phenotypes with prolific production of axial and lateral roots, developmental plasticity in response to local resource availability, and maintenance of unspecialized root tissues such as cortical parenchyma. Phosphorus in particular has important tradeoffs with water for root structure and function, since water is highly mobile, whereas phosphorus is highly immobile. High-input agroecosystems have removed many of these constraints to root function. Intensive fertilization removes P limitation and other abiotic limitations to root function like soil acidity. Pesticide application reduces root loss to herbivores and pathogens, and belowground competition from weeds. High-density monocultures insure that soil resources lost to neighboring plants still contribute to crop production. Management regimes create regular and predictable resource availability in time and space. However, drought stress remains a primary risk to crop production in rainfed agriculture, and this risk is likely to grow in the future. Therefore, root phenotypes that focus on water capture at the expense of ancestral adaptations would be better suited to high-input agroecosystems. Parsimonious architectural and anatomical phenotypes would permit greater resource allocation to deeper roots, which in most agroecosystems results in greater water capture. Specific phene states contributing to parsimonious architectural phenotypes include fewer axial roots, reduced density of lateral roots, reduced growth responsiveness to local resource availability, and greater loss of roots that do not contribute to water capture, for example in dry topsoil. Specific phene states contributing to parsimonious anatomical phenotypes include reduced production of cortical parenchyma through reduced production of cortical cell files, greater loss of cortical parenchyma through formation of root cortical aerenchyma and root cortical senescence, and larger cortical cell size. Parsimonious root phenotypes may be less useful in low-input agroecosystems, which are characterized by multiple challenges and tradeoffs for root function in addition to water capture. Although some of these ideas are supported by empirical evidence, they remain largely hypothetical. Analysis of the fitness landscape of specific root phenes, phene states and integrated phenotypes is a complex research challenge that will be aided by the development of robust functional-structural models capable of simulating the dynamics of root-soil interactions.

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Figure Legends

Figure 1. Visualization of maize root phenotypes 42 days after germination in *OpenSimRoot*. Phenotype (a) has 25 crown roots, 10 lateral roots per cm of axial root, and 1 cm distance from stem to first lateral emergence. Phenotype (b) has 10 crown roots, 5 lateral roots per cm of axial root, and 0.5 cm distance from stem to first lateral emergence. Images are the same scale. These phene values have been observed in plants in the field (see citations in text). Plants were simulated at 105 kg ha^{-1} soil N availability, which represents moderate N stress, to illustrate the effect of these phene states on root development when soil resources are limited. Image courtesy of Xiyu Yang.

Figure 2. Correlations between crown root number and shoot biomass of maize at 35 days after planting in greenhouse mesocosms (A), and shoot biomass (B) and relative yield (WS:WW, %) (C) at anthesis in the field under water-stressed conditions. Each point is means of four replicates of each genotype ± SE. From Gao and Lynch 2016.

Figure 3. Visualization of maize root phenotypes 42 days after germination in *SimRoot*, showing the effects of varying the number of crown roots from 46 (left) to 6 (right) on root depth and lateral root development. Roots are shown reflecting back to the center to represent roots from neighboring plants of the same phenotype. Hotter colors represent more N capture. Image courtesy of Larry York.

Figure 4. Nodal root number has declined over the past 100 years of maize breeding. Dotted lines represent planting density with gaps between dots being proportional to differences in densities, with 20K, 40K, and 80K being 20,000, 40,000, and 80,000 plants ha^{-1}. Triangles are in low nitrogen and circles in high nitrogen. Points represent the mean of the four varieties in that Era time period in the specific nitrogen and density combination, and vertical lines the standard error. Letters demonstrate a significant difference between the first and last Era periods based on a *t*-test ($p = 0.01541$) conducted after ANOVA demonstrated a significant effect of Era period. Presence or absence of an asterisk next to a treatment in the legend indicates whether a treatment effect is significant or not, respectively. From York *et al.* 2015.

Figure 5. Effects of specific root phenes on shoot mass of modern maize cultivars and cultivars from 100 years ago as simulated in *SimRoot*. Plants were simulated in a current environment of very high density (120,000 plants ha^{-1}) and high nitrogen (120K HN), and a historic environment of low density (40,000 plants ha^{-1}) and low nitrogen (40K LN). Solid bars represent the means with lines being the standard error. Abbreviations at the bottom of the bar give the phenotype, as follows. The *Old* (O) phenotype has a steeper angle and a few more nodal roots than the *Modern* (M) phenotype. *Old* and *Modern* have low aerenchyma. *Old* + Angle (OA) is the same as the *Old* phenotype but with the same shallow angle as the *Modern*, while *Old* + NRN (ON) is the same as the *Old* phenotype but with the same fewer nodal roots as the *Modern*. *Modern* + RCA (MR) is the *Modern* phenotype but with high aerenchyma. From York *et al*. 2015.

Figure 6. Correlation between lateral root branching density of maize crown roots and A: relative shoot dry weight (% relative to greatest shoot dry weight within each location) in greenhouse mesocosms (GH), in the field in Arizona (AZ) and Pennsylvania (PA), B: relative yield (% relative to greatest yield) in PA under water stress conditions. Each point is the mean of four replicates of each genotype. From Zhan, Schneider, Lynch 2015.

Figure 7. Phenotypic variation in maize for Root Cortical Aerenchyma (RCA, 7a), Cortical Cell File Number (CCFN, 7b) and Cortical Cell Size (CCS, 7c). 7d: Under water stress genotypes with greater RCA have less respiration (nmol CO_2 s^{-1} cm^{-1}), deeper rooting (7a: cm roots at 40-50 cm soil depth; 7b,c: D_{95}, which is the depth in cm attained by the 95th percentile of roots), and greater yield (g/plant), as did genotypes with reduced CCFN (7e) and greater CCS (7f). Data shown are means ± SE (n= 3 or 4). Means with different letters are significantly different ($p \leq 0.05$). Redrawn from Zhu, Brown, Lynch 2010 and Lynch 2015.

Figure 8. Correlation between maize yield and root cortical aerenchyma (% of cortical cross-sectional area) under water stress condition in two field environments in Malawi: **(A)** Bunda and **(B)** Chitala. From Chimungu et al. 2015b.

Figure 9. Root cortical senescence in barley reduces root respiration and the radial transport of water and nutrients, yet permits greater root depth and nutrient capture. From Schneider and Lynch, in press.