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Seedling root architecture and its relationship with seed yield across diverse environments in *Phaseolus vulgaris*

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Seedling root architecture and its relationship with seed yield across diverse environments in *Phaseolus vulgaris*



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ABSTRACT

Seedling root phenotypes may have important impacts on fitness and are more easily measured than mature root phenotypes. We phenotyped the roots of 577 genotypes of common bean (*Phaseolus vulgaris*), representing the bulk of the genetic diversity for recent cultivars and landraces in this species. Root architectural phenotypes of seedlings germinated for nine days were compared to root architectural phenotypes in the field as well as seed yield across 51 environments with an array of abiotic stresses including drought, nutrient deficiency, and heat, as well as non-stress conditions. We observed repeatability ranging from 0.52–0.57 for measures of root phenotypes in seedlings, significant variation in root phenotypes between gene pools and races, relationships between seedling and field phenotypes, and varying correlations between seedling root phenotypes and seed yield under a variety of environmental conditions. Seed yield was significantly related to seedling basal root number in 22% of environments, seedling adventitious root abundance in 35% of environments, and seedling taproot length in 12% of environments. Cluster analysis grouped genotypes by their aggregated seedling root phenotype, and variation in seed yield among these clusters under non-stress, drought, and low fertility conditions was observed. These results highlight the existence and influence of integrated root phenotypes for adaptation to edaphic stress, and suggest root phenotypes have value as breeding targets under real-world conditions.

1. Introduction

Malnutrition afflicts approximately 795 million people, particularly in sub-Saharan Africa where one in four people (23.2%) are malnourished (FAO, 2015). As the world's population is projected to gain 2.3 billion people by the year 2050, it is estimated that food production will need to increase by 25–70% to keep up with demand (Hunter et al., 2017). An important food security crop for some of the most vulnerable regions is common bean (*Phaseolus vulgaris* L.) (Porch et al., 2013). Common bean has greater volume for direct human consumption than

any other grain legume, and more than half of global production occurs in regions with food deficit (Beebe, 2012; Porch et al., 2013). Despite its significance, yield of *P. vulgaris* in developing countries is currently only one-third of what is achievable in developed nations where resources such as fertilizers, pesticides, and irrigation are available to reduce abiotic and biotic growth constraints (Lynch, 2007; Porch et al., 2013; Beebe et al., 2014; Vandemark et al., 2014). Climate change is projected to further reduce both the regions and seasons suitable for bean cultivation by two-thirds (IPCC, 2007; Rippke et al., 2016).

Drought and soil infertility are difficult constraints to sustainably

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mitigate in remote agroecosystems with limited access to irrigation and fertilizers. The development of cultivars with increased capacity for soil resource acquisition is an effective method for improving yields in marginal environments (Bishopp and Lynch, 2015; Lynch, 2018). While shoots have important impacts on the utilization of water and nutrients under stress, the root system is directly responsible for the acquisition of these resources. The importance of roots for adaptation to nutrient and water limitation is exemplified in the increase in allocation to root growth relative to shoot growth under edaphic stress (Fohse et al., 1988; Nielsen et al., 2001; Ho et al., 2005; Strock et al., 2018), and it has been demonstrated that the root genotype has a significant effect on bean yield under water stress (White and Castillo, 1989).

Root phenotypes are comprised of phenes, phenes are the fundamental units of the phenotype that are both unique and elementary to a given level of biological organization (York et al., 2013), many of which are under quantitative genetic control with environmental interactions. Root phenotypes can improve crop yield under edaphic stress by increasing the metabolic efficiency of soil exploration and by placing roots in soil domains where limiting resources are most available (Nielsen et al., 1994; Lynch, 2018). Phosphorus (P), nitrogen (N), and water are the three principal resources most often limiting plant growth (Lynch, 2018). Phosphorus is generally more available in the epipedon due to deposition of plant residues at the soil surface and low mobility in the soil (Lynch, 2011; Richardson and Simpson, 2011). Root phenes that increase the exploration of surface strata are beneficial for P capture (Lynch, 2011). Nitrogen can exist as either immobile ammonium, or water-soluble nitrate, which is leached through the soil profile with irrigation or rainfall events and localized in deeper horizons over time (Dathe et al., 2016; Thorup-Kristensen and Kirkegaard, 2016). Root phene states that encourage deeper soil exploration increase nitrate acquisition (Chimungu and Lynch, 2015). Similar to root systems optimized for nitrate capture, root phene states that promote deeper soil exploration benefit plant water uptake (Lynch, 2018). Water stress is commonplace in non-irrigated agricultural systems and as drought progresses, shallow soil horizons are the first to dry, leading to superior water uptake associated with root phenotypes with greater rooting depth (Lynch, 2013).

In *P. vulgaris*, root phenes that modify soil foraging depth include basal root growth angle (Bonser et al., 1996; Zhenyang et al., 2000; Liao et al., 2001; Rubio et al., 2003; Liao et al., 2004; Fenta et al., 2014; Miguel et al., 2015; Rangarajan et al., 2018), basal root whorl number (Basu et al., 2007; Miguel et al., 2013; Rangarajan et al., 2018), adventitious root abundance (Miller et al., 2003; Ochoa et al., 2006; Walk et al., 2006; Rangarajan et al., 2018), and lateral root branching density (Rangarajan et al., 2018). The divergence in spatiotemporal availability of multiple resources results in tradeoffs in the value of these phene states, as the benefit of shallower or deeper root growth for plant fitness is dependent upon the predominant edaphic stress. For example, phene states such as shallow basal root growth angle, and more numerous basal and adventitious roots that improve P acquisition would likewise reduce nitrate and water uptake, while deeper basal root growth angle and less allocation to root classes foraging the epipedon would improve the capture of water and nitrate but reduce P acquisition. Shallow root systems may also be detrimental to plant performance in environments with temperature extremes, but beneficial in locations with sparse intermittent rainfall (Lynch, 2018).

Quantifying the contribution of individual root architectural phene states to nutrient and water capture permits a more comprehensive understanding of root system function, and can also be deployed in ideotype breeding to improve resource acquisition efficiency and yield of the crop under stress (Donald, 1968; York et al., 2013). Ideotype breeding focuses on the development of an ideal phenotype composed of select phene states, or phene aggregates, that optimize growth and yield. Identification and aggregation of beneficial phene states from diverse sources into a single elite genotype can improve yields more efficiently than yield-based selection (Donald, 1968; Lynch, 2015).

While advances in QTL mapping and marker assisted selection have contributed greatly to the speed and efficiency of this ideotype breeding strategy, breeding efforts are still constrained by limited knowledge of specific phenes and phene states contributing to plant productivity under edaphic stress, as well as the ability to predict the agronomic value of integrated phenotypes (Blum, 1988; Passioura, 2002).

In addition to the direct contribution of a single root phene state for soil resource capture, phene states may interact synergistically to influence soil resource capture. This synergistic benefit has been observed in the effect of coalescing shallow rooting growth angle and long and dense root hairs, which in combination improve P capture twice as much as the additive effects of these solitary phenes (Miguel et al., 2015). *In silico* results from the structural-functional model *SimRoot* also highlight the concept of phene synergism, where the density, length, and geometry of root hairs in *Arabidopsis* had a synergistic effect on P acquisition 371% in excess of their additive effects (Ma et al., 2001). Another *in silico* study also showed that in maize (*Zea mays* L.), the utility of root cortical aerenchyma for P capture was 2.9 times greater in plants with greater lateral branching density than in plants with normal branching density (Postma and Lynch, 2011). The interaction of shallow basal root growth angle and greater basal root whorl number had a synergistic effect on P uptake in common bean *in silico* (Rangarajan et al., 2018). Despite the clear potential for exponential improvements in plant performance from synergistic effects between phenes, this concept of aggregating phenes into an integrated phenotype is not widely appreciated.

Phenotyping roots of seedlings has been shown to be an effective method for characterizing genetic diversity of root phene states across a variety of crop species including sorghum (*Sorghum bicolor* L.) (Joshi et al., 2017), common bean (Lynch and Vanbeem, 1993), pearl millet (*Pennisetum glaucum* L.) (Passot et al., 2016), wheat (*Triticum turgidum* L.) (Ruiz et al., 2018), maize (Sanchez et al., 2018), and rice (*Oryza sativa* L.) (Tomita et al., 2017). While these studies quantify genetic variation for root architectural parameters in seedlings, most do not explore the utility of root phenes by comparing seedling phenotypes to performance in the field. While Ruiz et al. (2018) did correlate individual seedling root architectural traits of wheat with agronomic parameters in the field, the scope of this work did not address the effects of phene aggregates on resource acquisition under multiple stresses. Additionally, many trait association studies of *P. vulgaris* grown under stress utilize only a limited number of genotypes with narrow diversity and do not explore the full range of natural genetic variation that is present for a given root phene (Asfaw et al., 2017). Characterization of the limited phenotypic variation present among only elite breeding material not only provides a truncated perspective of the true genetic variation available for a given trait, but also constrains the ability to detect the effects of this variation on plant performance. In the present study, research gaps in the phenotyping of diverse germplasm, exploration of integrated root phenotypes, and connecting seedling phenotypes to performance in real-world conditions are addressed by exploring the connection between integrated root phenotypes and seed yield across a broad diversity of germplasm and environments.

2. Materials and methods

2.1. Germplasm

Genotypes from the genetically differentiated Andean and Mesoamerican gene pools were used (Schmutz et al., 2014). In total, 577 genotypes comprised of cultivars, breeding lines, and landraces originating from Africa, the Caribbean, North America, Central America, and South America were obtained from The International Center for Tropical Agriculture (CIAT) as well as the United States Department of Agriculture, Agriculture Research Service (USDA-ARS) and screened for seedling root architecture (Table S1). Of all genotypes screened, 234 genotypes were from the Andean gene pool and 329

genotypes were from the Mesoamerican gene pool as part of the Andean (ADP) and Mesoamerican diversity panels (MDP) (Pérez et al., 2011; Cichy et al., 2015; Moghaddam et al., 2016). Genotypes from the Mesoamerican gene pool were further subdivided into 128 genotypes from the Mesoamerican race and 201 genotypes from the Durango-Jalisco race as part of the Durango diversity panel (DDP) (Blair et al., 2009; Kwak and Gepts, 2009). Fourteen interspecific genotypes resulting from crosses between *P. vulgaris* and *P. coccineus* (ALB lines), *P. dumosus* (MIB lines), or *P. acutifolius* (INB lines) were also included in this study. Because the Andean gene pool has narrower genetic diversity than the Mesoamerican gene pool, it was analyzed as one aggregate group (Bitocchi et al., 2013; Mamidi et al., 2013; Schmutz et al., 2014).

2.2. Seedling phenotyping

Seed was surface sterilized in a 25% NaOCl solution for 2 min, rinsed in deionized water, and five seeds of each genotype were rolled up 2.5 cm from the top edge of a sheet of 39 lb. germination paper (Anchor Paper Co., St. Paul, MN, USA). The rolls with seed were placed upright in a 2.0 L beaker containing 500 ml of 0.5 mM CaSO₄ solution and germinated in the dark at 28 °C for nine days. At nine days, the rolls were removed from the beaker and unrolled to expose the seedling root system. Seedling root systems were measured for the number of basal roots (BRN) (Fig. 1B), the number of tetrarch arrangements of basal roots known as basal root whorls (BRWN) (Fig. 1B), adventitious root abundance score (1 = none; 2 = 2–4 roots; 3 = more than 4 roots) (ARN) (Fig. 1C), and taproot length (Fig. 1A). Each genotype was germinated on four separate occasions and only representative seedlings were phenotyped at each occasion. A minimum of six seedlings were phenotyped for each genotype. Seedling root data were analyzed

as a completely randomized design (CRD) with the mean architectural phene for each genotype being calculated from all seedlings. This genotypic mean of each phene was used for all subsequent analyses.

To compare root phene states between gene pool and races, ANOVA and Tukey's honestly significant difference (HSD) test were performed using the genotypic means for each phene. Repeatability (R^2) was calculated for each root phene measured in seedlings according to Fehr (1987) where $\sigma^2(G)$ is the genotypic variance and $\sigma^2(E)$ is the error variance (Eq. 1). Genotypic and error variance were generated for each phene from linear mixed models fit by the restricted maximum likelihood (REML) method. In the determination of variance components, each occasion that a genotype was germinated in was considered a replicate.

$$R^2 = \frac{\sigma^2(G)}{(\sigma^2(E) + \sigma^2(G))}$$

Equation 1. Calculation of repeatability (R^2).

Seed mass for each genotype was determined from the weight of 50 seeds. To explore the relationships between seed mass and phene states, as well as the interactions between phene states in seedlings, Pearson's product-moment correlation analysis was performed. These correlation analyses were conducted using the genotype means for each phene.

2.3. Relating seedling root architecture to field root architecture

Comparisons of seedling root architecture and field root architecture were made in subsets of the genotypes ($N = 38$ –155) grown at five field sites (Table S2: PAL, DAR, CHO, AZ, OTH) under non-stress, drought, and low fertility conditions. Amalgamation of all locations and conditions provided a total of 17 environments for these comparisons

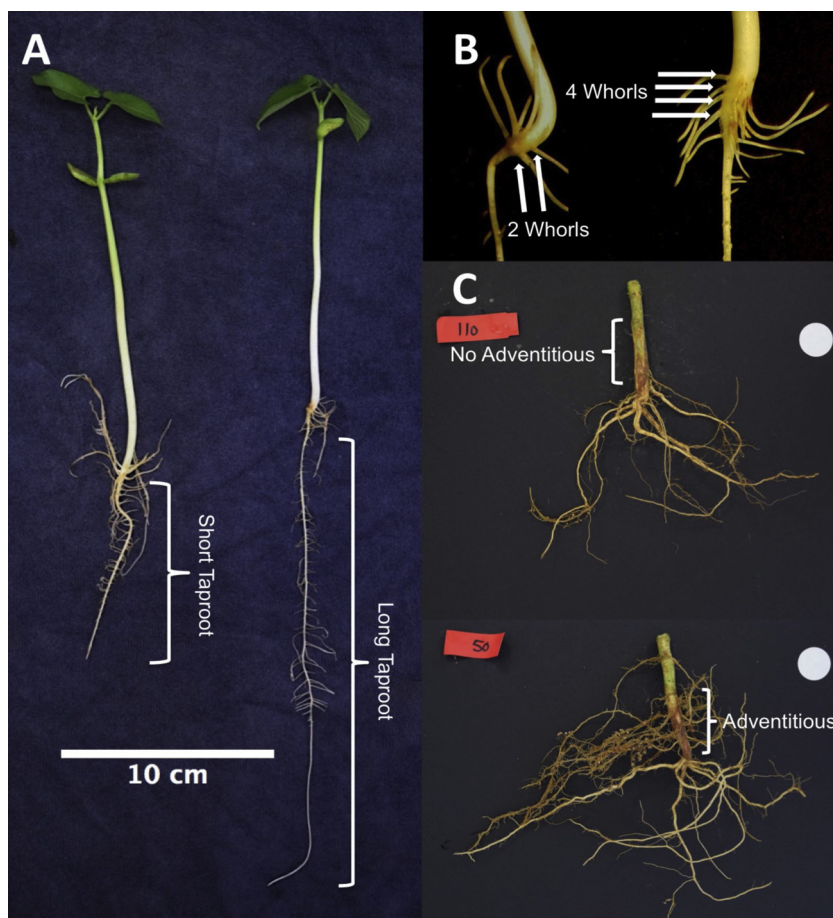


Fig. 1. Images highlighting contrast in seedling taproot length (A), basal root whorl number and basal root number (B), and adventitious root number (C).

Table 1
Repeatability (R^2) of basal root whorl number (BRWN), basal root number (BRN), adventitious root number (ARN), and taproot length (cm) as measured in seedlings.

Root Phene	R^2
BRWN	0.52
BRN	0.55
ARN	0.57
Taproot Length	0.52

between seedling and field root architecture. Roots from each of these 17 environments were phenotyped at flowering (~45 days after planting) by excavating and washing root crowns, and counting the number of basal roots, basal root whorls, and adventitious roots as described in [Burrige et al. \(2017\)](#). Pearson's product-moment correlation analysis was used for comparisons of phenes measured in seedlings with the same phenes measured in the field at each of the 17 environments. These correlation analyses were conducted using the genotype means for each phene in seedlings and in the field. The frequency of association between seedling and field root phenes was determined from the proportion of these 17 environments where statistically significant correlations were found. In addition to exploring these relationships within each environment, broader associations between seedling and field root phenotypes were also explored using the mean root phenotypes for each genotype measured from all environments.

2.4. Relating seedling root architecture to seed yield

Seed yield was collected from 51 experimental environments and utilized subsets of genotypes ($N = 39$ – 182) from the Andean and Mesoamerican gene pools grown at 15 locations, across 5 years (2012–2016), under a variety of abiotic stressors including drought, low fertility, and heat. These field sites spanned latitudes ranging from approximately 50°N to 30°S across three continents. A comprehensive list of all field sites, years, and growing conditions can be found in the supplementary materials (Table S2).

To determine the influence of individual root phenes on seed yield in the field, Pearson's product-moment correlation analysis was used to compare genotypic means of seedling root phenes and seed yield in each environment. The frequency of association between seedling root phenes and seed yield was determined from the proportion of these 51 field sites where statistically significant correlations were found.

To explore the interaction between root phenotypes and environmental stress, GLM and ANCOVA were used. In these analyses, non-stress conditions were set as the reference level and a linear model was created with seed yield as the dependent variable and root phenes as the independent variables with "stress" as an interaction term. For this analysis, mean seed yield for each genotype within each environment was percentile rank transformed to control for differences in the number of accessions grown at each site as well as relative shifts in yield from site to site within each stress.

To classify the genotypes by multiple root phene (integrated root system phenotypes), K-means cluster analysis was performed across all genotypes using the genotypic means of each root phene as measured in seedlings. Within group sum of squares was used to determine the optimal number of cluster assignments. To determine if any of these integrated root system phenotypes contributed to greater seed yield in a given environment, ANOVA and Tukey's HSD test were performed comparing mean seed yield for each genotype across the clusters. To reveal if clustering genotypes by seedling root phenotypes also grouped genotypes by genetic background, a chi-square test of independence was used to explore the distribution of genotypes from each gene pool across the clusters.

To determine if gene pool had a significant effect on seed yield within each stress, ANOVA and Tukey HSD tests comparing seed yield data across gene pools were performed. Percentile rank transformation was used on seed yield data to control for environmental differences between locations where different gene pools were grown.

2.5. Statistics

All statistical analyses were performed using RStudio Version 0.99.903 (RStudio, Inc.). Prior to all statistical tests, the normality and homoscedasticity of the data were determined using the Shapiro-Wilk test and the nonconstant error variance test, respectively. Where data did not meet these assumptions, a box-cox or log transformation was used to help normalize the data. Significant correlations and differences for all data analyses were considered at $\alpha \leq 0.05$ and at $\alpha \leq 0.1$ where noted.

3. Results

3.1. Seedling root phenotypes

A summary of root phenotypes for all genotypes can be found in the supplementary materials (Table S1). Genetic factors explained 52% of phenotypic variation of basal root whorl number, 55% of phenotypic variation in basal root number, 57% of phenotypic variation in adventitious root number, and 52% of phenotypic variation in taproot length in seedlings (Table 1).

Correlation analyses found that the scale of certain root phene states may be allometrically related to seed mass, as basal root number was positively correlated with seed mass in both the Mesoamerican and Durango races (Table 2). Additionally, adventitious root abundance had a positive relationship with seed mass in the Durango race at $\alpha \leq 0.1$.

Differences in root architecture among gene pools and races were identified, suggesting variable strategies for soil resource acquisition in environments from which genotypes in each pool evolved (Fig. 2). The Andean gene pool had the greatest number of basal root whorls and basal roots as well as the longest seedling taproot length (Fig. 2). Genotypes belonging to the Mesoamerican race had fewer basal root whorls and basal root numbers than the Andean gene pool, and had the greatest number of adventitious roots and an intermediate seedling taproot length. Genotypes of the Durango race had the fewest basal roots, basal root whorls, adventitious root abundance, and an intermediate seedling taproot length. Interspecific lines also had few basal roots and basal root whorls, a large number of adventitious roots, and the shortest seedling taproot length.

Statistically significant tradeoffs between investment in different root classes were observed and these relationships were not consistent across gene pools. A positive relationship between taproot length and basal root abundance was identified among genotypes of both the Andean gene pool and Mesoamerican race (Table 3). However, a tradeoff between taproot length and adventitious root number was observed in the Durango and Mesoamerican races where these two traits were negatively correlated. Similarly, basal root and adventitious root

Table 2

Correlation coefficients from Pearson's correlation analysis of basal root whorl number (BRWN), basal root number (BRN), taproot length (Tap; cm), and adventitious root number (ARN) measured in seedlings and seed mass for the Andean gene pool, Mesoamerican race, and Durango race. * Significance at $\alpha \leq 0.1$; ** Significance at $\alpha \leq 0.05$, ***Significance at $\alpha \leq 0.001$, n.s. indicates not significant.

Geno	N	BRWN	BRN	Tap	ARN
Andean	153	n.s.	n.s.	n.s.	NA
Mesoamerican	112	0.61 ***	0.57 ***	n.s.	n.s.
Durango	190	0.22 **	0.23 **	n.s.	0.14 *

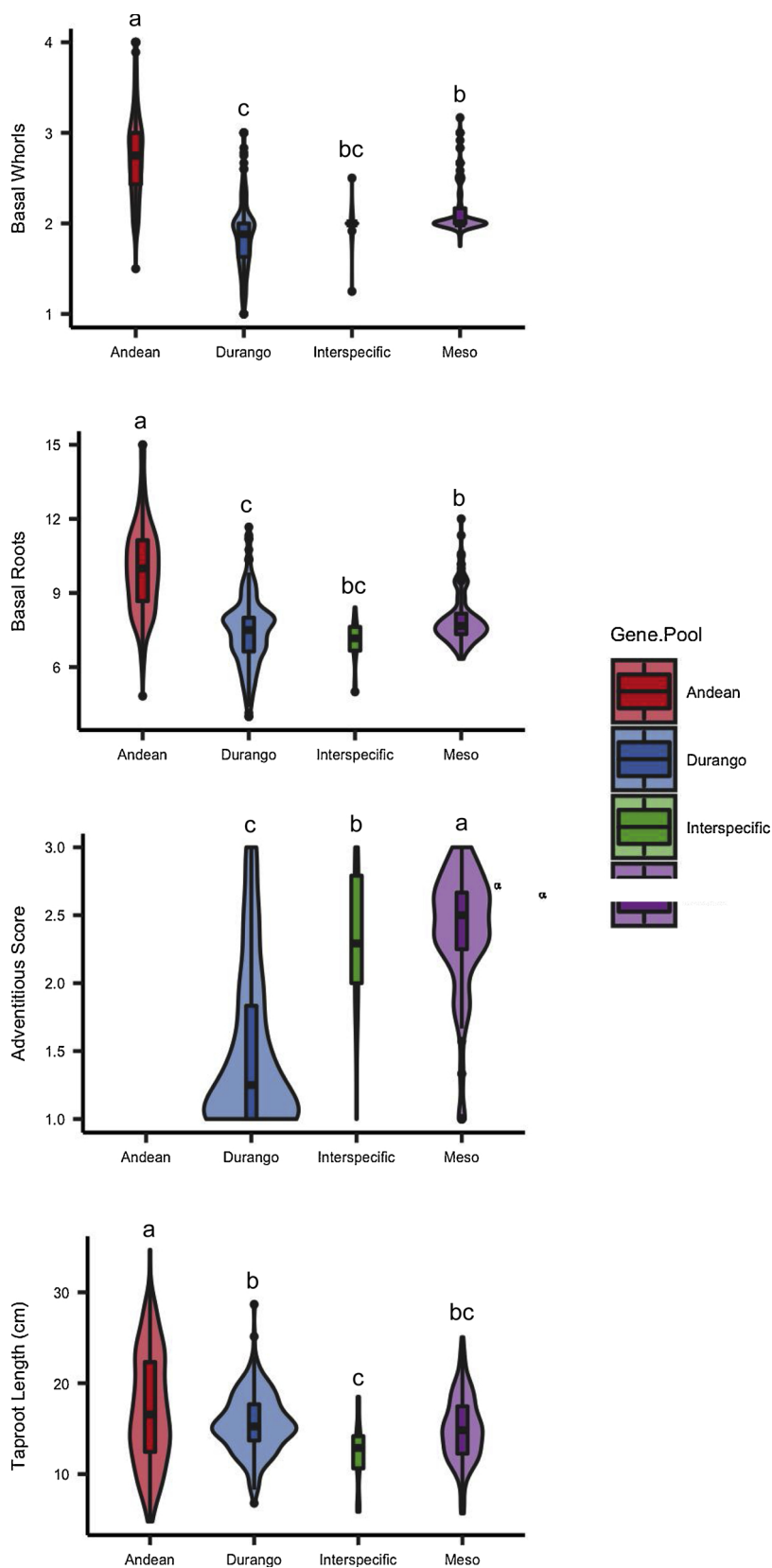


Fig. 2. Violin plots showing median, interquartile range, 95% confidence intervals, and frequency of root phenes within each gene pool. Comparisons are made across gene pools. $n_{\text{Andean}} = 233$, $n_{\text{Durango}} = 210$, $n_{\text{Interspecific}} = 14$, $n_{\text{Meso}} = 127$. Letters within each graph denote significant differences as determined by Tukey's test ($\alpha \leq 0.05$). Data for adventitious root score were not measured for Andean genotypes.

Table 3

Correlation coefficients from Pearson's correlation analysis between basal root number (BRN), taproot length (Tap; cm), and adventitious root number (ARN) measured in seedlings from the Andean gene pool, Mesoamerican race, and Durango race. * Significance at $\alpha \leq 0.1$; ** Significance at $\alpha \leq 0.05$, ***Significance at $\alpha \leq 0.001$, n.s. indicates not significant.

Geno	N	BRN x Tap	ARN x Tap	BRN x ARN
Andean	151	0.26 **	NA	NA
Mesoamerican	110	0.22 **	-0.39 ***	-0.20 **
Durango	188	n.s.	-0.15 **	0.21 **

Table 4

Correlation coefficients from Pearson's correlation analysis of basal root whorl number (BRWN), basal root number (BRN), and adventitious root number (ARN) measured in seedlings and in the field for the Andean (And), Mesoamerican (Meso), and Durango (Dur) genotypes. * Significance at $\alpha \leq 0.1$; ** Significance at $\alpha \leq 0.05$, ***Significance at $\alpha \leq 0.001$, n.s. indicates not significant. Information on sites can be found in supplemental table S2.

Site	Geno	Year	TRT	N	BRWN	BRN	ARN
PAL	Meso	2014-15	Control	77	0.60 ***	0.56 ***	n.s.
PAL	Meso	2014-15	Drought	77	0.48 ***	0.49 ***	0.29 **
PAL	Meso	2015	Control	77	0.51 ***	0.48 ***	n.s.
PAL	Meso	2015	Drought	77	0.51 ***	0.52 ***	n.s.
PAL	Meso	2014	Control	78	0.42 ***	0.50 ***	n.s.
PAL	Meso	2014	Drought	78	0.34 **	0.36 **	0.35 **
DAR	Meso	2016	P Stress	78	0.43 ***	0.49 ***	0.19 *
CHO	Meso	2014	Drought	125	n.s.	n.s.	n.s.
AZ	Meso	2014	Drought	94	-0.22 **	n.s.	0.37 ***
AZ	Meso	2015	Drought	115	0.34 ***	0.38 ***	0.28 **
AZ	Meso	2016	Drought	119	n.s.	n.s.	n.s.
AZ	And	2014	Drought	86	n.s.	n.s.	NA
AZ	And	2015	Drought	66	0.25 **	0.27 **	NA
AZ	And	2016	Drought	38	0.52 ***	0.37 **	NA
AZ	And	2016	Control	45	n.s.	n.s.	NA
OTH	Dur	2015	Drought	153	NA	n.s.	0.24 *
OTH	Dur	2014	Drought	155	NA	0.37 **	n.s.
Frequency of Sig.					67%	65%	46%

abundance were also negatively correlated in the Mesoamerican race, but were positively correlated in the Durango race (Table 3).

3.2. Relationship of seedling phenotypes to field phenotypes

Seedling root phenotypes had significant relationships with mature root phenotypes in diverse field environments including Colombia, Mozambique, and the United States (Table 4). Basal root whorl number in seedlings was positively related to basal root whorl number in the field in 67% of the environments analyzed (Table 4). Basal root number in seedlings was positively correlated with this same measure in the field in 65% of environments examined (Table 4). Adventitious root number in seedlings was correlated with adventitious rooting in the field in 46% of environments (Table 4).

3.3. Seedling root phenotypes and seed yield

Across the 51 experimental environments, basal root whorl number and basal root number measured in seedlings were both positively correlated with seed yield in 14% and 12% of the environments and negatively correlated in 8% and 6% of environments, respectively (Table S3). Both basal root whorl number and basal root number had a significant positive relationship with seed yield in 14% of control, 0% of heat, 7% of drought, and 25% of low fertility trials (Fig. 3A, 3B).

A significant positive relationship between basal root number and seed yield was observed across an aggregate dataset of all trials, with a significant positive interaction between basal root number on seed yield observed under drought and non-stress conditions (Fig. 4A, 4B).

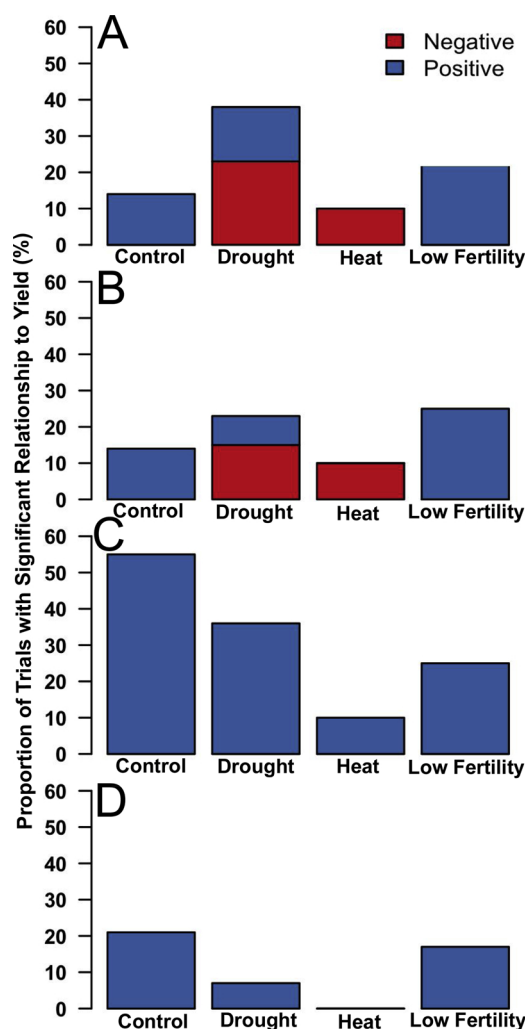


Fig. 3. Proportion of trials where basal whorl number (A), basal root number (B), adventitious root abundance (C), and seedling taproot length (D) had a significant relationship with seed yield. $n_{\text{Control}} = 15$, $n_{\text{Heat}} = 8$, $n_{\text{Drought}} = 13$, $n_{\text{Low Fert}} = 12$.

Across all experiments, adventitious root number from seedlings was positively correlated with seed yield in 35% of the environments (Table S3). Among specific stresses, adventitious root number had a significant positive relationship with seed yield in 55% of control, 13% of heat, 36% of drought, and 25% of low fertility trials (Fig. 3C). A positive relationship between adventitious root number and seed yield was observed across an aggregate dataset of all trials, with significant positive interactions between this trait and seed yield under drought, low fertility, heat stress, as well as non-stress conditions (Fig. 4C).

Across all environments, seedling taproot length was positively correlated with seed yield in 12% of the trials and was never observed to have a negative association with seed yield (Table S3). Seedling taproot length had a significant positive relationship with seed yield in 21% of control, 7% of drought, 0% of heat, and 17% of low fertility environments (Fig. 3D). In an aggregate dataset of all trials, a significant positive interaction between seedling taproot length on seed yield was observed under low fertility (Fig. 4D).

3.4. Cluster analysis

To gain perspective on the fitness of integrated root phenotypes and how phenotypes affect seed yield, unsupervised cluster analysis was performed across all 577 genotypes to group genotypes on the basis of seedling root system architecture. Analysis of within-groups sum of

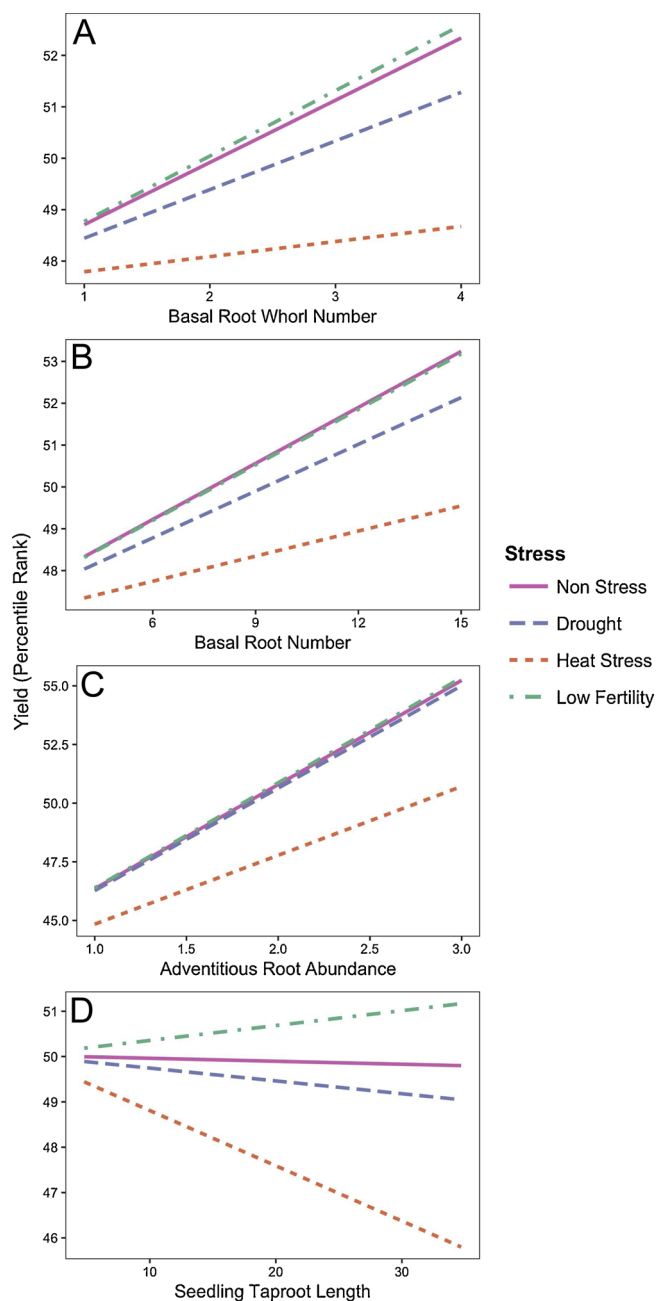


Fig. 4. Interaction plots highlighting the effect of stress on the utility of basal root whorl number (A), basal root number (B), adventitious root abundance (C), and seedling taproot length (D) for seed yield among all genotypes phenotyped.

squares indicated that five clusters were optimal for k-means cluster analysis (Fig. S1). Loadings of the first two principal components that were used for the cluster analyses were dominated by basal root number and taproot length (Fig. 5, Table S4).

A Chi-square test indicated that gene pools were asymmetrically represented across these five clusters, suggesting that gene pools have distinct integrated root phenotypes (Fig. 6). Clusters 1 and 2 were dominated by Andean genotypes, while 3 and 4 were primarily composed of genotypes from the Mesoamerican and Durango races. Cluster 5 hosted interspecific, as well as an equal mix of Andean, Mesoamerican, and Durango genotypes.

ANOVA and Tukey HSD tests pairing each genotype’s cluster assignment with seed yield data found that several clusters had improved seed yields under certain conditions. Cluster 4, consisting primarily of Durango and Mesoamerican genotypes with intermediate seedling

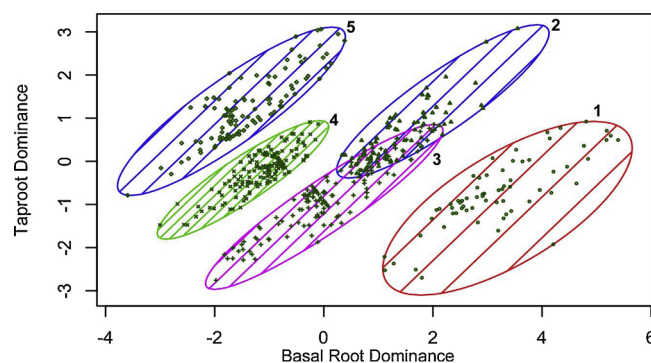


Fig. 5. Principal component plot of K-means clusters derived from seedling root phenotypes. The two principal components primarily influenced by basal root abundance (X axis) and taproot length (Y axis) explained 95% of the genotypic variability in clusters. Ellipses are colored with respect to their density; with increasing density, colors are blue, green, red, and purple (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

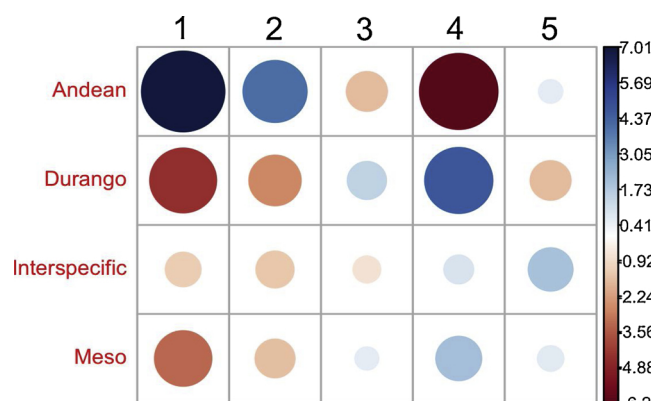


Fig. 6. Plot of residuals from chi-square test of gene pool distribution across clusters. Positive residuals in blue and negative residuals in red specify a positive and negative association, respectively, between a given gene pool and cluster (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

taproot length and few basal roots, was the highest yielding cluster under non-stress, yielded higher than clusters 5 and 1 under drought stress, and had higher seed yields than clusters 1 and 5 along with cluster 3 under low fertility (Figs. 7,8, Table S5).

Because clustering largely separated genotypes by gene pool, ANOVA and Tukey HSD tests comparing seed yield data across gene pools were performed to determine if gene pool was a significant factor in seed yield differences within each stress. Percentile rank transformation was used on seed yield data to control for environmental differences between locations where different gene pools were grown. Under drought, Durango and Mesoamerican genotypes both yielded higher than Andean and Interspecific genotypes (Fig. 9B). Under heat stress, Mesoamerican genotypes yielded higher than Andean genotypes (Fig. 9C). No differences in seed yield were observed between gene pools under non-stress and nutrient stress conditions (Fig. 9A, 9D).

In an effort to further disentangle the connection between higher seed yields of genotypes of Durango and Mesoamerican pedigree, and cluster 4 (dominated by Durango and Mesoamerican genotypes) under drought, comparison of the relative seed yield loss (RYL) from non-stress to drought conditions were made for both clusters and gene pools. Because only a subset of drought trials were grown in parallel with non-stress plots, analysis of RYL utilized a truncated set of environments (N = 11). ANOVA and Tukey HSD tests revealed no differences between clusters for RYL under drought and that Durango genotypes had

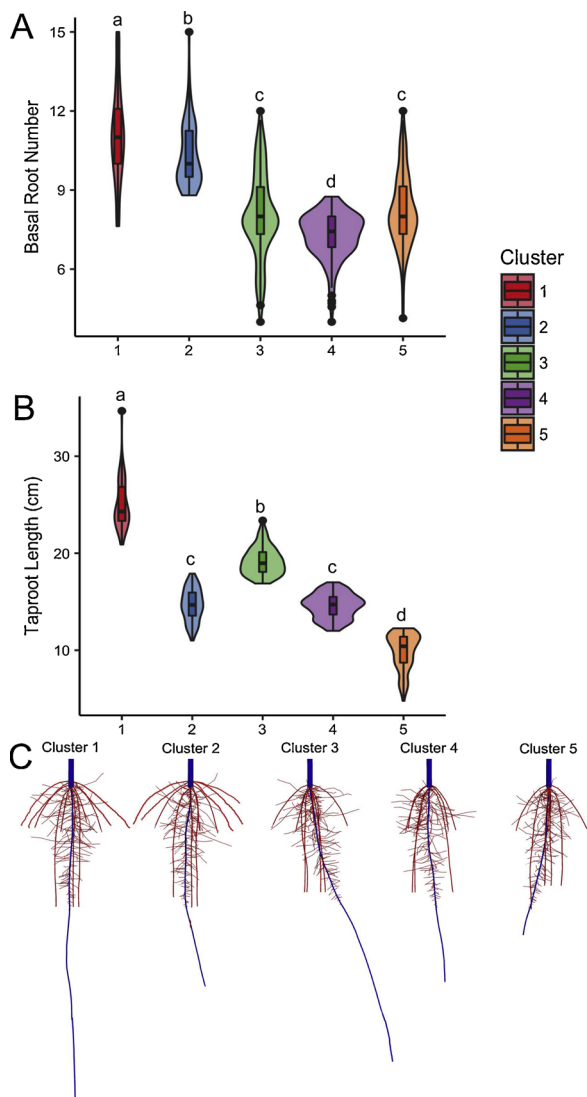


Fig. 7. Violin plots showing median, interquartile range, 95% confidence intervals, and frequency of basal root number (A) and seedling taproot length (B) within each cluster. Comparisons are made across clusters. Graphical representation of integrated seedling root phenotypes for each cluster at nine days after germination created using the functional-structural model SimRoot (C). $n_1 = 67$, $n_2 = 87$, $n_3 = 142$, $n_4 = 175$, $n_5 = 113$.

greater RYL than Mesoamerican genotypes under drought (Table S6).

4. Discussion

In this study we observed that 1) root architectural phenes can be rapidly phenotyped at the seedling stage in common bean (Fig. 1); 2) these architectural phenes are under some degree of genetic control (Table 1); 3) significant genetic variation exists for root architectural phenotypes in common bean and gene pools/ races have distinct root architecture (Figs. 2,5,6); 4) root phenotypes in seedlings have significant relationships with root phenotypes at flowering in the field (Table 4); and 5) root architectural phenotypes are correlated with seed yields in some environments and abiotic stresses (Figs. 3, 4, 8; Table S3).

We found correlations between measures of basal root whorl number, basal root number, and adventitious root abundance in seedlings and in the field (Table 4). These positive correlations between laboratory-based seedling measurements and field-based measurements of mature root phenotypes support the efficacy of using the less labor-

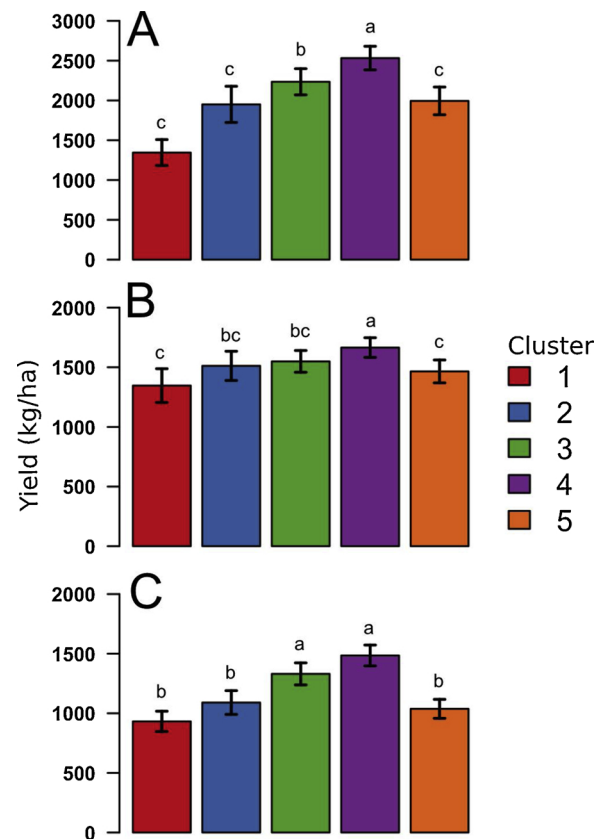


Fig. 8. Mean \pm SE seed yield under non-stress (A) drought (B) and low fertility (C) within each cluster. Comparisons are made across clusters. $n_1 = 67$, $n_2 = 87$, $n_3 = 142$, $n_4 = 175$, $n_5 = 113$.

intensive and higher throughput laboratory-based phenotyping protocol as a tool for breeding programs. Phenotyping at the seedling stage has also been used to rapidly characterize genetic variation for other root phenes such as root hair length and density (Tuberosa et al., 2002; Zhu et al., 2005; Vieira et al., 2007).

Some lack of consistency between laboratory and field measures of root architecture is attributable to environmental influences. In the field, root growth is not only affected by genetic factors, but also by biotic factors such as disease and pests, as well as abiotic factors such as mechanical impedance of root elongation, moisture content, and nutrient availability. These biotic and abiotic factors can act independently or interdependently with significant spatial and temporal variation (Nunez et al., 2016). For example, differences in adventitious root abundance between genotypes may change under field conditions due to water and nutrient content of shallow soil horizons, as it has been shown that P stress stimulates adventitious rooting in a genotypic dependent manner (Miller et al., 2003). This plasticity in adventitious rooting could explain the weak association between seedling and field phenotypes for this phene (Table 4). Unlike adventitious rooting, basal root number is unaffected by P availability (Miguel et al., 2013), although gravitropic responses of this root class have been shown to be significantly modulated by P availability (Bonser et al., 1996; Liao et al., 2001).

Disparities in measures of root phenotypes between the seedling and field are also expected due to biotic pressure from fungal root-rotting pathogens including species of *Fusarium*, *Pythium*, and *Rhizoctonia* that cause the destruction of existing roots as well as the inhibition of new root growth (Nzungize et al., 2011). Herbivorous pests including nematodes and insect larva such as bean stem maggot (*Ophiomyia* spp., Diptera: Agromyzidae) disrupt plant vasculature, which can also affect the longevity and actual abundance of various root classes in the field

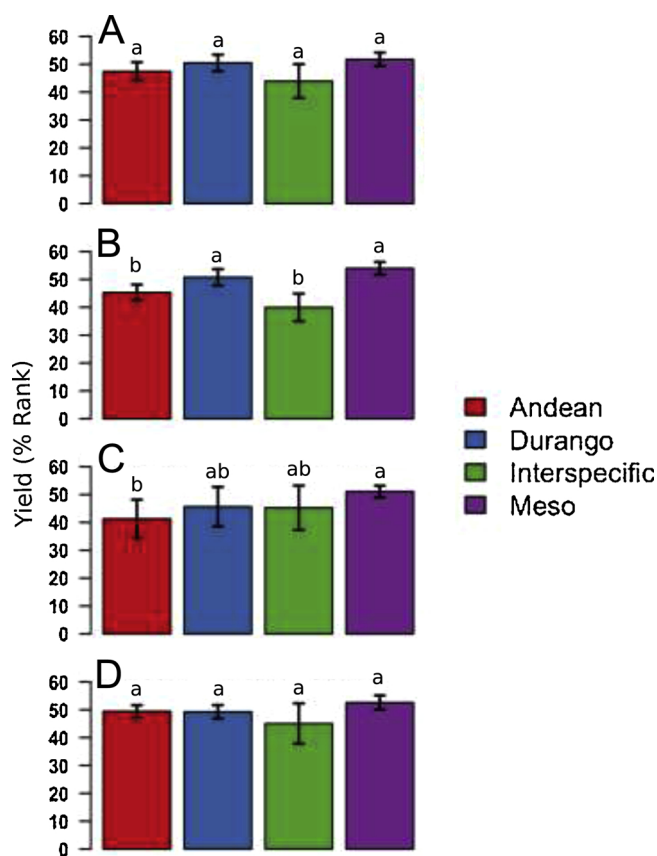


Fig. 9. Mean \pm SE percentile rank transformed seed yield among gene pools and races in non-stress (A), drought (B), heat stress (C), and low fertility (D) environments. Comparisons are made within each stress. $n_{\text{Andean}} = 233$, $n_{\text{Durango}} = 211$, $n_{\text{Interspecific}} = 14$, $n_{\text{Meso}} = 127$.

(Anwar and Van Gundy, 1989; Abate and Ampofo, 1996). Fisher et al. (2002) reports that in *P. vulgaris*, up to 49% of roots can be lost by the pod fill stage due to biological pressure of root herbivores and pathogens. These biotic factors may have contributed to our observations of reduced abundance of basal roots under field conditions compared to measurements in seedlings. In environments where root loss from pathogens and edaphic pests exists, increased root redundancy in genotypes with greater abundance of basal and adventitious roots might help to assist in performance under these pressures.

In addition to the growth inhibition and destruction of roots that occurs under field conditions, edaphic stresses can also affect the allocation of resources between root classes. The relationships among multiple root phenes are of practical interest in breeding programs where simultaneous selection of multiple traits would be desirable (Asfaw et al., 2017), as selection for one trait may cause improvement or deterioration in an associated root phene (Baker, 1986). For example, Walk et al. (2006) found that under some environmental conditions, increased adventitious rooting can reduce allocation of resources to the growth of the taproot and lateral roots arising from basal roots. In the present study, we observed a negative relationship between adventitious rooting and basal root number as well as taproot growth in seedlings (Table 3). These tradeoffs in resource allocation to different root classes during early vegetative growth may have consequences for subsequent vegetative growth and reproduction. Preferential allocation to either adventitious, basal, or taproot classes, coupled with positive feedback between root growth, soil exploration, and resource acquisition, may result in root phenotypes which focus on either shallow or deep soil exploration. This strategy may be ideal in environments either predominately limited by water or P (Lynch and

Brown, 2001; Ho et al., 2005; Lynch, 2013) but may be less optimum under multiple constraints.

Previous reports by Miller et al. (2003); Ochoa et al. (2006) and Walk et al. (2006) on the value of adventitious roots for increased P uptake were validated in the present study, as well as a strong benefit from increased adventitious rooting on seed yields under drought, low fertility, and non-stress conditions (Fig. 3C). The strength of this positive effect from increased adventitious rooting was greatest under non-stressed conditions, low fertility, as well as drought, while greater adventitious root abundance had less effect on improved seed yields under heat stress (Figs. 4C). These positive associations between seedling adventitious root abundance and seed yield are noteworthy considering the weak relationship between measurements of this trait in seedlings and in the field. It may be that adventitious root abundance in seedlings is influenced by seedling vigor, and that seedling vigor and early establishment are important drivers of performance. Greater seedling vigor could contribute to greater nutrient and water acquisition before the onset of weed pressure, terminal drought, or heat stress. Accelerated establishment could subsequently provide an advantage beyond the seedling stage via positive feedback between soil resource acquisition and root growth. The broad success of genotypes with increased capacity for adventitious root development may also result from a risk averse strategy where greater root redundancy affords these genotypes the ability to recover from root loss under drought, heat, and biotic stressors. In environments where root loss is a factor, stimulated growth of adventitious roots, may occur in genotypes with greater capacity for adventitious roots as the excision of roots in bean has been shown to promote the growth of remaining root classes (Rubio and Lynch, 2007).

Our results also support previous reports of the utility of greater basal root whorl number under P stress (Basu et al., 2007; Miguel et al., 2013; Rangarajan et al., 2018) (Fig. 3A, 3B), in addition to showing that more basal root whorls and greater basal root number are related to increased seed yield in non-stress conditions. Not only does greater basal root whorl and basal root number increase topsoil foraging where P has greater availability, but a greater abundance of basal roots increases root redundancy. Root redundancy in basal roots may serve as a means of ensuring that at least some root length explores both shallow and deep soil horizons under conditions of high root mortality or where impenetrable soil zones due to compaction or prohibitive acidity may limit the utility of deep rooting phenes. Under drought stress however, basal root abundance had mixed effects on performance, and under heat stress had entirely negative associations with seed yield (Fig. 3A, 3B). In these conditions, the greater number of basal roots may constitute a metabolic burden as well as provide an avenue for water loss in soil profiles with dry upper horizons through hydraulic lift (Caldwell et al., 1998). This diversion of internal resources from other root classes to basal roots has been reported by Rangarajan et al. (2018) who observed a positive relationship between basal root abundance and carbon consumption, a tradeoff in plant performance between basal root abundance and lateral root branching density, as well as a reduction in rooting depth with increased basal root abundance. Walk et al. (2006) also observed tradeoffs between adventitious and basal root length.

Although no previous studies have explicitly explored the utility of seedling taproot length for plant performance under edaphic stress, results from the present study suggest that increased seedling taproot length provides a benefit under a range of environments (Fig. 3D). Although taproot length is difficult to observe in the field, longer seedling taproot length may be related to greater rooting depth in mature plants. A positive relationship between rooting depth and access to water deep in the soil profile under drought has been well established (Manschadi et al., 2010; Kell, 2011; Wasson et al., 2012; Lynch, 2013; Lynch and Wojciechowski, 2015). In lentil (*Lens culinaris*), taproot length of 35-day-old plants was positively correlated with seed yield under drought (Sarker et al., 2005). In rice, increased root depth leads to increased water uptake and seed yield under rain-fed conditions (Suji

et al., 2012). Kirkegaard et al. (2007) also showed that access to more water at depth increases grain yields in wheat. In common bean, Ho et al. (2005) showed that deeper-rooted genotypes perform better under drought stress. Additionally, comparable to adventitious rooting in seedlings, longer seedling taproot length may also be related to seedling vigor, providing benefit in non-stress and low fertility conditions where plants may be affected by competition with weeds.

While individual root phenes can affect performance, improved seed yield under multiple and variable stress is more appropriately conceptualized as the result of interaction among multiple phenes that constitute an integrated phenotype (Asfaw et al., 2012; York et al., 2013). The concept of an integrated phenotype can be assessed through cluster analysis to provide a valuable new perspective on breeding for edaphic stress tolerance. The asymmetric distribution of Andean, Mesoamerican, Durango, and interspecific genotypes across clusters suggests that gene pools and races have distinct phene aggregates by which they can be defined (Fig. 6). These distinct phene aggregates for each gene pool and race may relate to adaptive strategies tailored to the environments from which they originate.

Cluster 1, dominated by Andean genotypes, had exceptionally long seedling taproot length and the greatest abundance of basal roots compared to other groups. At the other end of the phenotypic spectrum, cluster 5, hosting interspecific, as well as an equal mix of Andean, Mesoamerican, and Durango genotypes, had the shortest seedling taproot length and few basal roots. Although extreme root phenotypes appear to compromise performance in the agricultural settings tested here, these extreme phenotypes may be best adapted to niche edaphic conditions present within the ranges from which these genotypes originate. In contrast to these extreme groups, clusters 3 and 4 had an intermediate combination of phene states and the greatest seed yields under a diversity of conditions (Fig. 7, and Fig. 8). The balanced and risk averse intermediate strategy of clusters 3 and 4 is likely most broadly successful because it does not devote too great or too little resources to a single root class, nor to exploration of shallow and deep soil horizons. It seems that this strategy of “moderation in all things” is not just the most common, but also the most successful strategy for the preponderance of conditions. These observations align with *in silico* results of maize root phenotypes under N stress, where root architectures that are extreme in depth of soil foraging are most beneficial in environments with extreme nitrate stratification, while dimorphic root phenotypes outperform these extreme phenotypes in the majority of environments (Dathe et al., 2013). Rangarajan et al. (2018) also concluded from *in silico* analysis of bean root phenotypes that no single root phenotype is ideal across a range of environmental stresses.

Although higher yielding clusters were dominated by genotypes of the Durango and Mesoamerican races, gene pool had no effect on seed yield in non-stress and low fertility environments, indicating that variation in seed yield under these conditions was a product of the root phenotype defining each cluster rather than pedigree. However, under drought, Durango and Mesoamerican genotypes had inherently greater seed yields than Andean or interspecific genotypes as has been reported by others (Beebe, 2012; Mukeshimana et al., 2014; Polania et al., 2016; Asfaw et al., 2017) making it difficult to credit the superior seed yield of cluster 4 (comprised of Durango and Mesoamerican genotypes) to root phenotype or to other drought tolerance mechanisms present in the Mesoamerican gene pool. Comparison of relative seed yield loss among clusters and gene pools under drought did not aid in disentangling the linkage between gene pools and integrated root phenotype (Table S6). Given that root architectural phenotypes appear to be a defining characteristic of different gene pools and races, further disentanglement of gene pool strategies from root phene aggregates is a topic best suited for targeted physiological studies. Overall, investigation of integrated root phenotypes is an effective strategy in gaining a more comprehensive understanding of how variation in root system architecture affects soil resource acquisition and plant performance under edaphic stress.

5. Conclusion

These results go beyond the conclusions of previous reports on seedling root phenotyping not only by demonstrating the influence of individual seedling root phene states for edaphic stress tolerance in the field, but also by considering the importance of integrated root phenotypes. In the present study we determine that the abundance and length of axial roots among different root classes has important implications for plant performance across a diversity of real-world environments. Additionally, consideration of root phene aggregates as part of an integrated root phenotype reveals differences in soil foraging strategies among gene pools and races, as well as uncovers relationships between integrated root phenotypes and seed yield under stress. Incorporating seedling root phenotyping and the concept of integrated root phenotypes into breeding programs is warranted to help improve common bean performance in marginal environments.

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Declaration of interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fcr.2019.04.012>.

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