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Parental effects and provisioning under drought and low phosphorus stress in common bean

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Abstract

Low soil fertility and drought are primary constraints for crop production and food security in many developing nations. Since smallholder farmers often collect seed for the next year's crop from plants grown with abiotic stress, it is important to understand how progeny from a stressed parental environment perform when they are grown under similar stresses. This study investigates the impact of a low phosphorus (P) or drought parental environment on progeny seed and root traits in common bean (*Phaseolus vulgaris*), with the intention of distinguishing impacts of reduced parental provisioning from adaptive responses. Greenhouse, field, and seedling experiments were used to evaluate seed, seedling, and mature root phenotypes in progeny from stressed and nonstressed parental conditions. In addition, progeny from different positions within the pod and pod developmental times were evaluated since they are expected to vary in parental provisioning. Seeds from the peduncular position in the pod had less individual seed weight, fewer basal roots, reduced root dry weight, and smaller taproot diameter than those from the stylar position. Progeny of some genotypes from drought-stressed parents had smaller individual seed weight, fewer basal roots, less total seedling dry weight, shorter seedling basal roots, and smaller basal root diameters. Progeny of some genotypes from a low P parental environment had smaller individual seed P concentration, fewer shoot-borne roots, and greater basal root whorl number. Progeny from drought-stressed parents, progeny from a low P parental environment, and seeds from the peduncular position had root phenotypes that were likely to be related to less parental provisioning. Possible adaptive parental effects were found in both parental drought and parental low P studies. Adequate seed provision under stress merits consideration as a selection target in crop breeding for stressful environments.

KEYWORDS

abiotic stress, common bean, drought, food security, parental effects, parental provisioning, *Phaseolus vulgaris*, phenotypic plasticity, phosphorus stress, root architecture, soil fertility

1 | INTRODUCTION

Several studies have explored how the parental environment impacts progeny traits, independent of the expected genetic contribution of the parent plant. This phenomenon is defined as environmental parental effects. Parental effects have been studied for various abiotic stresses including salinity stress (Amzallaga, 1994), shading (Causin, 2004; Galloway, 2005), low soil fertility (Aarssen & Burton, 1990; Latzel, Janeček, Doležal, Klimešová, & Bossdorf, 2014; Parrish & Bazzaz, 1985; Platenkamp & Shaw, 1993; Sultan, 1996; Wulff, Caceres, & Schmitt, 1994), nitrogen stress (Latzel, Klimešová, Hájek, Gómez, & Šmilauer, 2010; Luzuriaga, Escudero, & Perez-Garcia, 2006), P stress (Austin, 1966; Derrick & Ryan, 1998; Yan, Lynch, & Beebe, 1995), and drought (Aarssen & Burton, 1990; Hill, West, & Hinson, 1986; Meckel, Egli, Phillips, Radcliffe, & Leggett, 1984; Parrish & Bazzaz, 1985; Riginos, Heschel, & Schmitt, 2007). Parental effects may include structural or physiological responses in progeny triggered by the parental environment, where responses may or may not be exaggerated in progeny grown in similar environmental conditions as the parent plant. Phenotypic plasticity is defined as the capability of an organism to alter its phenotype in response to the current environment. In some cases, parental effects impact the level of plasticity of certain traits in the progeny. In other cases, parental effects are constitutive, independent of the current progeny environment. Parental effects may also be dependent on species and genotype.

Parental effects may serve as a mechanism to precondition progeny adaptation to a similar adverse environment as the parent plant. For instance, progeny from parent plants grown under nutrient stress in *Senecio vulgaris* (Aarssen & Burton, 1990) and low nitrogen soil in *Sinapis arvensis* (Luzuriaga et al., 2006) showed delayed germination, a mechanism that is potentially adaptive by allowing progeny to wait for more favorable growth conditions. *Polygonum persicaria* responded to a low parental nutrient environment by increasing the root:shoot ratio and enhancing soil exploration and surface area for nutrient uptake (Sultan, 1996). Latzel et al. (2010), Latzel et al. (2014) found that *Plantago* progeny had the greatest above- and belowground biomass when grown under similar conditions as the parent plant, suggesting progeny may be preconditioned for growth in similar environmental conditions.

Stressful parent environments may reduce parental provisioning of seeds, often resulting in less seed weight and volume. For instance, soybean (*Glycine max*) seed from drought-stressed parents (Hill et al., 1986; Meckel et al., 1984), and *Abutilon theophrasti* seed (Parrish & Bazzaz, 1985) and *Senecio vulgaris* seed (Aarssen & Burton, 1990) from nutrient-stressed parents had less weight. Seed weight was reduced in progeny from P-stressed parent plants in common bean (Yan et al., 1995) and wheat (*Triticum aestivum*) (Derrick & Ryan, 1998). Seeds with less mass often have fewer resources available for seeding growth and establishment, producing less vigorous seedlings (Cheplick & Sung, 1998; Nakamura, 1988) and juvenile plants with shorter root length (Elwell, Gronwall, Miller, Spalding, & Durham Brooks, 2011; Wulff, 1986). The effects of a stressful parental environment on progeny traits may also persist in later life stages (Riginos et al., 2007; Wulff et al., 1994). Progeny with reduced parental provisioning from nutrient-stressed parents had reduced fitness, competitive ability, and seedling vigor (Aarssen & Burton, 1990; Parrish & Bazzaz, 1985; Platenkamp & Shaw, 1993). Poor parental provisioning of seeds from parents grown under P stress produced progeny with less juvenile shoot biomass in watercress (*Rorippa nasturtium aquaticum*) (Austin, 1966) and less root weight in wheat (Derrick & Ryan, 1998) and common bean (Yan et al., 1995). Thus, seeds from stressed parents may contain fewer resources, which may reduce seedling vigor and affect growth in later life stages.

Parental provisioning is also affected by timing of fertilization and position of the ovule. Rocha and Stephenson (1990) and Nakamura (1988) found that seeds from the stylar end (furthest from the petiole) of the pod in *Phaseolus coccineus* and *Phaseolus vulgaris* had greater mass, likely due to primary fertilization of ovules at the stylar end of the pod, conferring a competitive advantage for acquisition of parental resources during seed filling (Rocha & Stephenson, 1991). Seeds that were heavier due to position in the fruit had greater seedling total weight in *Triplasis purpurea* (Cheplick & Sung, 1998) and *P. vulgaris* (Nakamura, 1988) and greater total seedling weight and root length in *Desmodium paniculatum* (Wulff, 1986). In addition to parental growth conditions, timing of ovule fertilization based on seed position within the fruit may impact progeny provisioning due to differences in resource allocation during seed filling.

Root traits have important roles in nutrient and water acquisition. Deeper roots and roots with steeper angles improve water acquisition (Fenta et al., 2014; Lynch, 2013). Traits important for P acquisition in P-deficient soils include lateral root branching density (Postma, Dathe, & Lynch, 2014) and length in maize (Zhu & Lynch, 2004), and shoot-borne roots for topsoil foraging of P (Lynch, 2011; Lynch & Brown, 2008; Miller, Ochoa, Nielsen, Beck, & Lynch, 2003; Walk, Jaramillo, & Lynch, 2006), basal root growth angle (Henry, Kleinman, & Lynch, 2009; Liao et al., 2001a; Miguel, Postma, & Lynch, 2015; Rubio, Liao, Yan, & Lynch, 2003), and basal root whorl number (Liao et al., 2001a; Lynch & Brown, 2008; Miguel, Widrig, Vieira, Brown, & Lynch, 2013; Rubio et al., 2003; Walk et al., 2006) in common bean. Genotypes exhibiting increased development of root traits important for the performance under the same stress as that to which the parents were exposed could be useful in breeding crops with consistently better performance over multiple generations.

Common bean (*P. vulgaris*) is an important source of nutrients in many developing nations, yet produces only 10 to 20 percent of yield potential primarily due to drought and low soil fertility (Beebe, Rao, Devi, & Polania, 2014; Lynch, 2007; Rao, 2014; Wortmann, Kirkby, Eledu, & Allen, 1998). Many farmers in these areas do not have access to fertilizer or irrigation water, resulting in substantial yield reduction due to phosphorus (P) and drought stress. Root architectural and anatomical phenotypes beneficial for water and P acquisition have been identified in common bean, aiding the production of genotypes that thrive in drought or low P soils (Henry et al., 2009; Liao et al., 2001b; Lynch, 2011; Lynch & Brown, 2008; Miguel et al., 2015, 2013; Miller et al., 2003; Rubio et al., 2003; Walk et al., 2006). Genotypes with these phenotypes have been tested for performance in stressful conditions, but performance of the progeny of plants grown under stress has not been formally tested. Since many farmers in developing nations collect seed for the next year's crop from parent plants grown in low P and/or drought, it is important to understand how progeny from a stressed parental environment perform relative to progeny from a nonstressed parental environment.

We investigated the effects of parental phosphorus or drought stress on progeny grown in similar stressful or nonstressful conditions, focusing on seed weight and root traits that have been shown to have important roles under drought and phosphorus stress. Progeny traits were also examined in seeds that developed in different positions within the pod and from pods that developed early or later on the parent plant. While parental provisioning was expected to have important impacts on progeny traits, we also looked for evidence of epigenetic adaptive responses.

2 | MATERIALS AND METHODS

2.1 | Plant material

The following genotypes were used for seed position and pod set timing experiments: DOR364, BAT 477, TLP19, and B98311. These genotypes were previously shown to vary in responses of root traits to low phosphorus (e.g., (Ho, Rosas, Brown, & Lynch, 2005; Liao et al., 2001b; Miguel et al., 2013). All seeds were provided by CIAT (Centro Internacional de Agricultura Tropical, Cali, Columbia), except B98311 which was provided by Dr. James Kelly at Michigan State University. DOR364 and BAT477 have an intermediate erect bush growth habit, TLP19 and B98311 have a type II growth habit (indeterminate upright), and all four genotypes are from the Mesoamerican gene pool.

The following genotypes were used for drought studies: SER118, SER16, and SEA5, from the Mesoamerican gene pool, and eleven RILs (recombinant inbred lines 1, 120, 18, 213, 23, 24, 5, 6, 67, 91, and 96) from the ALB population (SER 16 x (SER 16 x G35346 – 3Q)). The ALB population is an interspecific cross between the small-seeded SER 16 (*P. vulgaris*), developed for drought tolerance, and the large-seeded G35346 – 3Q (*P. coccineus*). All seeds were provided by CIAT (Centro Internacional de Agricultura Tropical, Cali, Columbia). All genotypes were measured for individual seed weight and seedling basal root number. Genotypes were used to measure seedling traits were ALB1, ALB5, ALB6, ALB67, ALB96, SER118, and SER16. Genotypes used in field trials were ALB23, ALB5, ALB6, ALB91, and SER16.

Parent plants were grown under well-watered or moderate drought conditions at the Rock Springs site in 2010. Parent plants grown under terminal drought showed a shoot biomass reduction of 46% significant at $p < .0001$, but did not display differences in basal root number between treatments (Barlow, 2011).

The following BILFA (bean improvement for low fertility in Africa) genotypes were used for phosphorus stress experiments: Bf13572-5, SER15, SER16, SER43, SER55, SER79, SER83, SER85, and Tio Canela 75. BILFA are genotypes selected for tolerance to drought and poor soil nutrition. Parent plants were grown in the field under low and high P at the Russell E. Larson Experimental Farm at Rock Springs, PA in 2010, and seeds were collected from high and low P plots.

2.2 | Greenhouse trials

Pots were filled with media comprised of 50% vermiculite (Whittemore Companies Inc.), 30% medium (0.3–0.5 mm) commercial-grade sand (Quikrete Companies Inc.), and 20% perlite (Whittemore Companies Inc.), by volume. All components were mixed evenly throughout each pot. Pots were fertigated daily through drip irrigation with 2 L of quarter-strength Epstein's nutrient solution, containing (in mM) 1.5 KNO_3, 1 $Ca(NO_3)_2.4H_2O$, 0.25 $MgSO_4.7H_2O$, 0.06 $(NH_4)_2SO_4$, 0.4 $NH_4H_2PO_4$ and (in µM) 50 KCL, 25 H_3BO_3, 2 $MnSO_2{\cdot}H_2O$, 2 $ZnSO_4.7H_2O$, 0.5 $CuSO_4{\cdot}H_2O$, 0.5 $(NH_4)_6MO_7O_{24}.4H_2O$, and 50 Fe-NaEDTA.

Trials were planted in the greenhouses located at The Pennsylvania State University, University Park, PA (40°80'N, 77°51'W). Seeds were weighed individually prior to planting for the pod position and seed development experiments. All seeds were surface-sterilized with 10% bleach solution for one minute and rinsed with deionized water. Two seeds per pot were directly planted into 19-L pot, and one seedling was selected for uniform growth at three days after emergence. High-intensity discharge lamps provided supplemental lights from 0,600 hr to 1,800 hr. There were five replications per genotype per treatment, each placed in randomly selected locations in the greenhouse. Replications were planted at two-day intervals. Plants were harvested, and roots were evaluated as described below.

Greenhouse experiments on phosphorus stress were conducted as above, but with the addition of 1% alumina phosphate (Al-P) providing either low P (0.2 μM) or sufficient P (150 μM) (methodology from Lynch, Epstein, Lauchli, & Weight, 1990) mixed into the growth medium. Pots with low P Al-P were fertigated when necessary through drip irrigation with equal frequency and nutrient concentrations as high P AL-P pots, but with 0.2 mM $(NH_4)_2SO_4$ and without $NH_4H_2PO_4$.

2.3 | Field trials: Rock springs, PA

Trials were located at the Russell E. Larson Experimental Farm at Rock Springs, PA. The soil was a Murrill silt loam 12 (fine-loamy, mixed, semi-active, medic Typic Hapludult). Standard agronomic pest control was implemented when needed.

For drought experiments, we used rain-out shelters covered with clear greenhouse plastic (0.184 mm; Griffin Greenhouse and Nursery Supply) that moved over plants when precipitation was sensed, and reversed direction to expose plots at the end of a rainfall event. Two control plots were located adjacent to rain-out shelters. Both rain-out shelter plots and control plots were 26.8 m × 8.5 m. Each plot contained twenty-four 3 rows by 2-m subplots. There were four subplots per genotype per parental treatment in each plot. Rows were planted 60 cm apart, and plants were planted 10 cm apart. Prior to planting, plots were deep-chiseled, harrowed, and scored in early June. Herbicide was applied one week before planting, and standard agronomic pest control was implemented when needed. Trials were planted on 11 June 2012, and a drip irrigation system was installed on 20 June 2012. Drought treatment was imposed beginning on 25 June 2012 by halting irrigation and employing the rain-out shelters to block precipitation from the plots, while irrigation continued to supply moisture to the control plots to supplement the 36 mm of rain that fell from planting to harvest. Soil moisture was monitored biweekly using a TDR-100 multiplexed time-domain reflectometry system (Campbell Scientific Inc.). Two 20-cm probes were buried directly under a row at 15 cm and 40 cm, in six evenly distributed locations within each plot. Volumetric water content (VWC) averaged 22% in the drought plots and 34% for the well-watered plots between 9 July and 3 August 2012. Shoot biomass reduction for plants under drought stress was 32%. Plants were harvested from 13 to 14 August 2012 following methods of Trachsel, Kaeppler, Brown, and Lynch (2011), and roots were immediately evaluated as described in *Root and Shoot Measurements*.

For P stress experiments, four blocks of high P and four blocks of low P were used and soil was tested for P levels by the Agricultural Analytical Services Lab and The Pennsylvania State University, using Mehlich 3 inductively coupled plasma (ICP) atomic emission spectroscopy, prior to planting. Parent plants were grown in 2010 in low P blocks ranging from 10 to 16 ppm and in high P blocks ranging from 51.5 to 87 ppm. In 2011, progeny were grown in low P blocks ranging from 14 to 15 ppm and high P blocks ranging from 74 to 108 ppm. Each block had one replication per genotype and parental P treatment that consisted of three 2-m rows. Rows were planted 76 cm apart, and plants within rows were planted every 10 cm. A 1-m buffer was planted around the border of each block. Shoot biomass reduction in plants under P stress was 22%. All plots received fertilizers other than phosphorus according to soil test results.

2.4 | Field trials: Ukulima root biological center (URBC), South Africa

Trials were located in a pivot-irrigated field plot at the Ukulima Root Biology Center (URBC) in the Republic of South Africa (RSA) (24°32’S, 28°07’E) in a loamy sandy soil, in 2012. There were two field locations within the pivot, one was used as a drought treatment and the other a well-watered treatment. Each location had four plots with 3 rows by 2-m subplots. Within each plot, there was one subplot per genotype and parental treatment. Rows were planted 76 cm apart, and plants were planted 10 cm apart. Prior to planting, plots were deep-chiseled, harrowed, and scored in early January. Plots were fertilized with complete N-P-K fertilizers before planting. Herbicide was applied one week before planting, and standard agronomic pest control was implemented when needed. Trials were planted on 19–20 January 2012, and drought was imposed starting on 2 February 2012 by halting irrigation to the drought plots. Soil moisture was monitored biweekly using a TDR-100 multiplexed time-domain reflectometry system (Campbell Scientific Inc.). Two 20-cm probes were buried directly under a row at 15 cm and 40 cm, in two randomly distributed locations within each plot. VWC for well-watered and drought plots were both between 10% and 10.5% on 22 February 2012 and between 8% and 9% on 5 March 2012. After irrigation on 5 March 2012, VWC diverged between treatments with well-watered plots averaging 11% and drought plots averaging 8%. Rainfall totaled approximately 174 mm/m^2 from planting to harvest. Shoot biomass reduction for plants under drought stress was 22%. Plants were harvested on 15 March 2012, following methods of Trachsel et al. (2011), and roots were immediately evaluated as described in *Root and Shoot Measurements*.

2.5 | Pod and seed development

Seeds for greenhouse trials at The Pennsylvania State University (University Park, PA) were collected from field sites at the Ukulima Root Biology Center (URBC) in the Republic of South Africa (RSA) (24°32’S, 28°07’E), in 2012. Pods on nonstressed parent plants were tagged and dated at initial pod elongation, that is, pods were 0.5–1 cm long (growth stage R3). Pods were tagged with the date on 17 March 2012, representing early-developing pods, and 30 March 2012, representing late-developing pods. Seeds were collected at the stylar and peduncular position within the pods. Pods were collected at these dates because these were the earliest and latest pod developmental dates that yielded enough seed for greenhouse experiments in the greenhouse. Only seeds from pods with complete filling (all seeds are filled within a pod) and pods with at least four seeds per pod were collected.

2.6 | Root and shoot measurements

Harvested plants from the field and greenhouse were evaluated for seed, shoot, and root traits at flowering (growth stage R2). Representative, young but fully expanded leaves were selected for measurements. During harvest, shoots were separated from the root system and dried for shoot dry weight. Root classes examined included the taproot, basal roots, and shoot-borne roots. Different measurements were performed depending on the root class, including length, density, diameter, number, and weight.

Roots from greenhouse studies were separated from shoots, washed, and stored in 70% ethanol for future evaluation. Roots from field studies were separated from shoots, washed, and immediately evaluated. The taproots were measured for diameter 1 cm from the point of attachment to the stem, and length was measured in greenhouse studies. Basal roots were evaluated for basal root number, basal root whorl number, diameter of a representative basal root 1 cm from the point of attachment to the stem, and length of a representative basal root (greenhouse studies only). Shoot-borne roots were counted, and length of a representative shoot-borne root was recorded (in greenhouse studies only).

For P stress experiments, yield components were measured including pods per plant, seeds per pod, and weight per 100 seeds. Seeds were dried at 60°C for two days, weighed, and ground with a Wiley mill, ashed at 500°C for ten hours, and then dissolved in 100 mM of hydrochloric acid to prepare samples for testing phosphorus concentration. Leaf and seed P concentration was measured using the Murphy–Riley method (Murphy and Riley, 1962) and a Lambda 25 Spectrometer (Perkin-Elmer).

2.7 | Seed and seedling trials

Seeds were weighed, surface-sterilized with 10% bleach solution for 1 min, and rinsed with deionized water. Seeds were then placed two inches apart in 79 lb roll-up germination paper (Anchor Paper Co.) and placed into a 500-mL beaker with 30 ml of 0.5 mM calcium sulfate solution. The roll-ups were placed in a dark germination chamber at 28 C° for 72 hr and then grown for 48 hr under 110 μmol/m^2/s cool-white fluorescent light. Seedlings were preserved in 70% ethanol for further analyses. Seedlings were evaluated for total seedling dry weight, basal root number, basal root whorl number, taproot length, and basal root length. Four seedling replicates were used per genotype per parental treatment for analysis of all traits. Root lengths of the taproot and a representative basal root were measured.

2.8 | Statistical analyses

A randomized complete block design was used in both field and greenhouse studies. Replications in greenhouse studies were blocked in time (to allow time between harvests) and space. Replications in field experiments were blocked in space. Statistical analyses were performed using Minitab 16 Statistical Software (*Minitab for Windows,* Release 16, Minitab Inc.). Data for root traits within genotypes were analyzed for parental (Gen. 0) and progeny (Gen. 1) treatment effects using a two-way ANOVA with a significance level of $p \leq .05$ unless otherwise noted. Data within genotypes for root traits between seed and pod position traits, using pod position and seed development date as factors, were analyzed using a two-way ANOVA with a significance level of $p \leq .05$ unless otherwise noted. Log-transformed data were used if normality assumptions were not met, and if log-transformed data were still not normally distributed, data were analyzed using a Kruskal–Wallis test. Two-sample *t* tests were used for seed weight and seed P concentration analyses.

3 | RESULTS

3.1 | Seed position within the pod and developmental time on the parent plant

Progeny from different positions (stylar and peduncular) within the pod and different pod set dates (early and late) on parent plants were evaluated for seed traits and then grown in the greenhouse. In three of four genotypes, seed weight was greater in seeds that developed in stylar than in peduncular positions within the pod (BAT477 $p < .001$, DOR364 $p = .002$, TLP19 $p = .01$) (Figure 1, Table 1). Seeds from the peduncular position showed a 33% (BAT477), 13% (DOR364), and 9% (TLP19) reduction in seed weight relative to seeds from the stylar position. In three of four genotypes, individual seed weight was greater in seeds from earlier developing pods (DOR364 $p = .054$, B98311 $p = .046$, TLP19 $p = .056$). Seeds from later developing pods showed a 15% (B98311) and 8% (DOR364, TLP19) reduction in seed weight relative to seeds from the stylar position. There were no significant interactions between pod set date and pod position (Table 1).

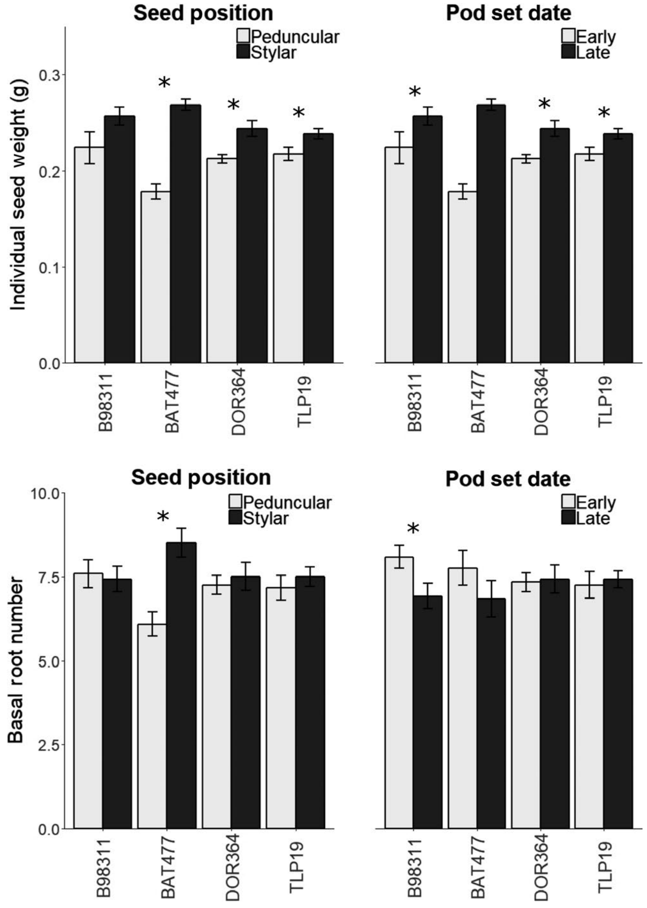

FIGURE 1 Effects of seed position within the pod, stylar (S) or peduncular (P), and pod set date on progeny seed weight and basal root number of progeny plants grown in the greenhouse to R2. Error bars represent standard error of the mean. Asterisks represent significant differences between treatments within genotypes ($p < .05$)

Root dry weight at growth stage R2 was greater in progeny from the stylar position within the pod only in BAT477 ($p = .049$) (Figure 2). Root dry weight was not different between seeds from different pod set dates. Individual seed weight and root dry weight in greenhouse plants at growth stage R2 were correlated in BAT477, and in seeds from the peduncular position within the pod ($R^2 = 46.5\%$, $p = .015$), but not correlated in seeds from the stylar position within the pod. Taproot diameter at growth stage R2 was 16% less in progeny from the peduncular position within the pod in DOR364 ($p = .038$) (Figure 2). Taproot diameters between progeny from early versus late pod set dates were not significantly different (Table 1).

Basal root number was greater at growth stage R2 in seeds that developed in the stylar end of the pod in BAT477 ($p < .001$), and in seeds from earlier developing pods in B98311 ($p = .039$) (Figure 1, Table 1). Seeds from the peduncular position showed a 28% reduction in basal root number in BAT477, and seeds from later developing pods showed a 14% reduction in basal root number in B98311. Despite differences in basal root number, no genotypes showed differences in basal root whorl number between pod positions or pod developmental times (data not shown).

Basal root number and individual seed weight were correlated (all genotypes combined) in seeds from the peduncular position within the pod (R2 = 34.5%, $p < .001$), but not correlated in seeds from the stylar position within the pod. Basal root number and individual seed weight (per seed) were correlated in BAT477 at $p = .174$ in seeds from the peduncular position within the pod (R2 = 17.7%) but were not correlated in seeds from the stylar position within the pod (R2 = 4.6%, $p = .504$). Basal root number and individual seed weight in BAT477 were correlated in seeds from both early-developing pods (R2 = 70.2%, $p = .001$) and late-developing pods (R2 = 46.2%, $p = .015$).

3.2 | Parental effects of drought stress on progeny seed and root traits

Progeny from drought-stressed and well-watered parental (Gen. 0) environments were collected from parent plants grown under well-watered or moderate terminal drought that

TABLE 1 ANOVA table for effect of seed position within the pod and pod set date on seed weight and root traits of plants grown to the reproductive stage in the greenhouse

	Seed weight		Basal root number		Taproot diameter		Root dry weight	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Seed position	1.399	.240	1.299	.258	4.940	.029	0.442	.508
Pod set date	10.010	.002	0.831	.365	2.264	.136	0.525	.471
Genotype	5.614	.002	1.965	.126	0.598	.618	2.899	.040
Seed position × pod set date	1.397	.241	0.026	.872	2.138	.148	0.148	.702
Seed position × genotype	3.139	.030	3.965	.011	2.272	.086	0.217	.885
Pod set date × genotype	1.197	.316	1.905	.136	1.492	.223	0.165	.920
Seed position × pod set date × genotype	1.144	.336	0.121	.947	1.882	.139	0.152	.928

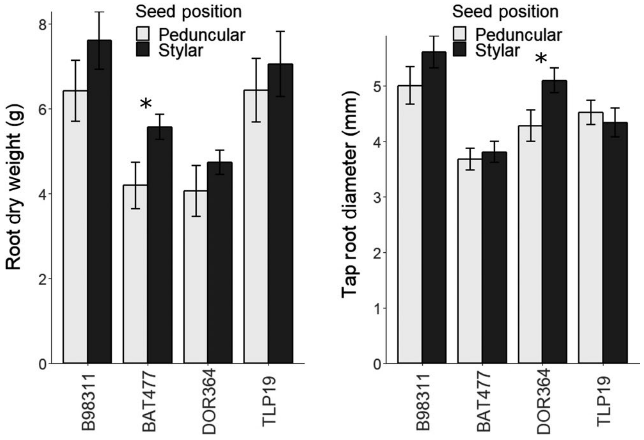

FIGURE 2 Effects of seed position within the pod, stylar (S), or peduncular (P), on root dry weight and taproot diameter of progeny plants grown in the greenhouse to R2. Error bars represent standard error of the mean. Asterisks represent significant differences between treatments within genotypes ($p < .05$)

resulted in a shoot biomass reduction of 46% ($p < .0001$), in the field at the Rock Springs, PA, in 2010 (Barlow, 2011), and used to test the effect of parental environment on seed and seedling traits in roll-ups. All genotypes except ALB67 ($p = .95$) had significantly greater individual seed weight from the well-watered parental environment ($p \leq .038$) (Figure 3, Table 2, note strong main effects and interactions). Reduction in individual seed weight ranged from 0% in ALB67 to 30% in ALB1.

Six out of 14 genotypes displayed significant reduction in seedling basal root number ($p \leq .05$) when collected from drought-stressed parents, ranging from 7% (ALB5) to 26% (ALB120) (Figure 3, Table 2). All genotypes with greater seedling basal root number in progeny from well-watered parents also had greater individual seed weights. However, seven of the 13 genotypes with greater individual seed weights from well-watered parents did not have higher seedling basal root number.

Seedling dry weight was greater in seedlings from a well-watered parental environment in two of the seven genotypes tested, ALB1 ($p = .04$) and ALB67 ($p = .004$, Figure 3). Seedling dry weight was reduced by 28% in seedlings from parental drought in ALB1 and by 47% in ALB67.

In ALB67, seedling taproot length was 52% less in progeny from a drought parental environment ($p < .001$), but other genotypes were unaffected (Figure 3). In three of seven genotypes including ALB67, basal root length was 29%–57% less in seedlings from a parental drought environment ($p \leq .054$). However, in ALB1, seedling basal root length was 37% greater in seedlings from a parental drought environment ($p = .018$, Figure 3).

When three genotypes were grown in the field to R2, there were fewer basal roots in progeny from a drought-stressed parental environment in ALB5 (19% reduction, $p = .001$, when data were averaged over progeny well-watered and drought treatments, Figure 4, Table 3). When parental and progeny treatments were analyzed individually, it was clear that the significant effect resulted from ALB5 progeny grown in well-watered conditions having fewer basal roots when they were from drought-stressed parents ($p = .001$, Figure 4).

Basal root diameter at R2 was 33% smaller in progeny from a drought-stressed parental environment in ALB5 at Rock Springs, PA ($p < .001$, Figure 4, data averaged over progeny well-watered and drought treatments). In the URBC field, basal root diameter at R2 was 15%–23% smaller in progeny from a drought-stressed parental environment in three of five genotypes ($p \leq .006$, Figure 4, Table 3). At the Rock Springs, PA site, taproot diameter at R2 was smaller in progeny from a drought-stressed parental environment in ALB5 ($p = .03$, 12% reduction) and ALB120 ($p < .001$, 45% reduction) (Figure 4). In ALB120, the significant effect resulted from the fact that well-watered progeny grown had a smaller taproot diameter when they were from drought-stressed parents ($p = .001$, data not shown).

3.3 | Parental effects of phosphorus stress on progeny seed and root traits

Progeny from low and high phosphorus (P) parental (Gen. 0) environments were collected from parent plants grown under low or high P in the field at Rock Springs, PA, and grown in the greenhouses under low and high P conditions. Seed P concentration was lower in progeny from a low P parental environment in three of nine genotypes (SER85 $p = .077$, SER16 $p = .01$, SER43 $p = .05$) (Figure 5, Table 4). Reduction in seed P concentration in the low P parental environments ranged from 13% to 21%. There were no significant differences in individual seed weight among progeny from different parental P environments (data not shown).

In the field at Rock Springs, PA, shoot-borne root number was greater in progeny from a high P parental environment in SER16 ($p = .014$, 35% reduction) and Tiocanela75 ($p = .009$, 27% reduction) (Figure 5). Only SER79 showed the opposite trend, at a significance level of $p = .123$, and the Gen. 0 treatment X genotype interaction was significant at 0.095 (Table 4). In the greenhouse, basal root whorl number was 19% greater in progeny from a low P parental environment in Tiocanela75 ($p = .043$, Figure 5), but basal root number was not different between parental treatments in any genotype.

4 | DISCUSSION

4.1 | Parental effects of seed position in the pod and pod developmental time

Parental provisioning of seeds involves the investment of resources including nutrients, carbohydrates, and protein

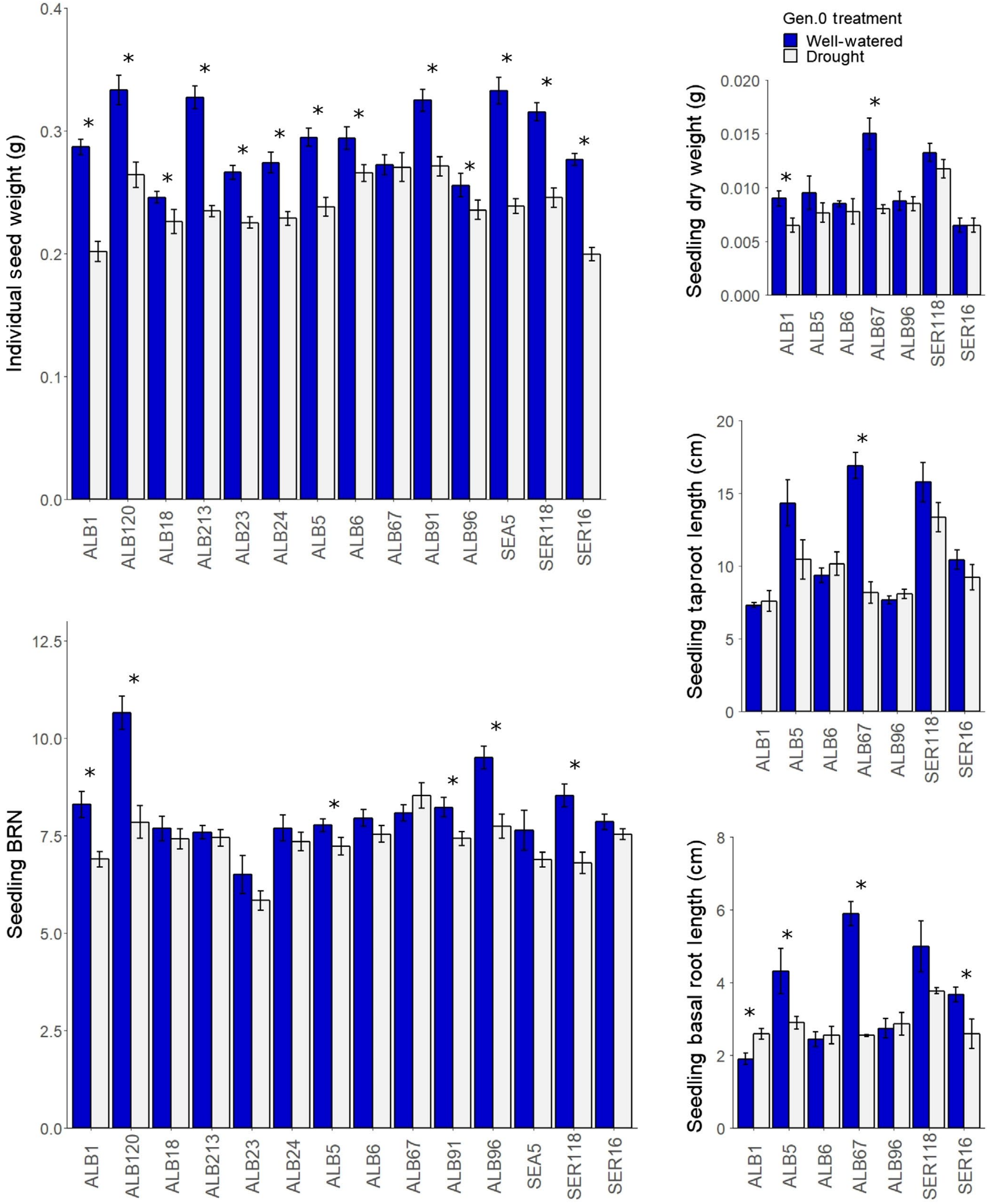

FIGURE 3 Effects of parental drought on progeny seed weight and root traits of 5-d-old seedlings germinated in roll-ups. Error bars represent standard error of the mean. Asterisks represent significant differences between treatments within genotypes ($p < .05$)

TABLE 2 ANOVA table for effect of parental (Gen. 0) drought treatment (TRT) on seed weight and seedling root traits

	Seed weight		Seedling basal root number		Seedling basal root length		Seedling taproot length		Seedling dry weight	
	F	*P*	*F*	*P*	*F*	*p*	*F*	*p*	*F*	*p*
Gen. 0.TRT	336.950	<.001	58.807	<.001	22.968	<.001	19.151	<.001	16.728	<.001
Genotype	15.685	<.001	11.371	<.001	12.319	<.001	17.983	<.001	11.343	<.001
Gen. 0.TRT × Genotype	6.778	<.001	4.276	<.001	8.150	<.001	7.392	<.001	3.544	.006

into seeds by parent plants during seed fill. Allocation of resources from the parent plant to each seed is usually not equal and depends on a variety of factors such as the environment during seed fill, the time of seed development on the parent plant, and the location of the seed on the parent plant (Cheplick & Sung, 1998; Sultan, 1996). In these experiments, seeds from the stylar position in the pod and from earlier developing pods had greater individual seed weight relative to seeds from the peduncular position in the pod and later developing pods in the majority of genotypes tested (Figure 1). Rocha and Stephenson (1990) found that individual seed weight was greater in seeds from the stylar position in a related species, *P. coccineus*. They suggested that seeds from the stylar position in the pod may have had greater mass due to primary fertilization of ovules at the stylar end of the pod. Assuming that the vasculature is similar in *P. vulgaris,* the differences in individual seed weight would suggest weaker partitioning of resources to peduncular seeds relative to stylar seeds due to the order of fertilization within the pod and may explain differences in individual seed weight between seeds from stylar and peduncular positions.

Reduced provisioning in smaller seeds from the peduncular position resulted in significant differences in root traits. Heavier seeds from the stylar position had larger and more numerous roots, including higher basal root number

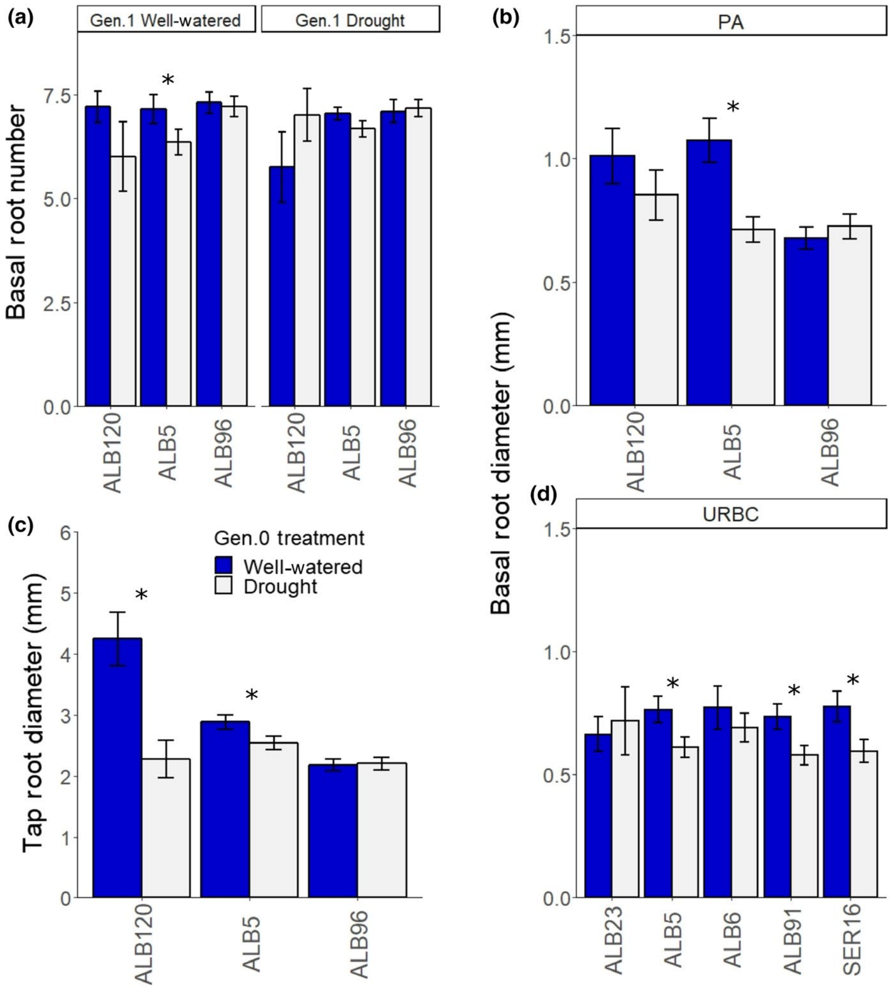

FIGURE 4 Effects of parental drought on root traits of progeny grown in the field to R2 under well-watered or drought conditions, in Rock Springs, PA (a, b, c), or the Ukulima Root Biology Center (URBC), South Africa (d). Error bars represent standard error of the mean. Asterisks represent significant differences between treatments within genotypes ($p < .05$)

TABLE 3 ANOVA table for effect of parental (Gen. 0) and progeny (Gen. 1) drought treatment (TRT) on root traits of plants grown to the reproductive stage in the greenhouse and field

	Basal root number		Taproot diameter		Basal root diameter (URBC)		Basal root diameter (PA)	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Gen. 0 TRT	1.109	.293	26.328	<.001	0.004	.948	0.443	.506
Gen. 1 TRT	0.770	.381	5.680	.018	0.723	.397	1.118	.291
Genotype	0.035	.966	22.314	<.001	0.274	.894	4.357	.014
Gen. 0.TRT × Gen. 1.TRT	1.541	.215	6.710	.010	0.831	.364	0.077	.782
Gen. 0.TRT × Genotype	0.570	.566	13.837	<.001	0.368	.831	1.819	.164
Gen. 1.TRT × Genotype	0.338	.713	4.514	.012	0.261	.903	0.256	.775
Gen. 0.TRT × Gen. 1.TRT × Genotype	0.460	.632	4.980	.007	0.498	.737	0.024	.977

and a larger taproot diameter, compared with seeds from the peduncular position (Figures 1 and 2). Greater differences in seed weight were associated with greater likelihood of differences in root traits. For instance, BAT477 had the greatest difference in individual seed weight between seeds from different pod positions and was also the only genotype with significant differences in basal root number and root dry weight between positions (Figures 1 and 2). Similarly, B98311 had the greatest difference in individual seed weight between seeds from different developmental times on the parent plant and was the only genotype with significant differences in basal root number between development times. Effects of seed position in the fruit on individual seed weight and seedling traits were reported in *Triplasis purpurea*, where heavier seeds from the lower part of the panicle produced seedlings with greater shoot and root dry weight (Cheplick & Sung, 1998). Wulff (1986) also found that individual seed weight in *Desmodium paniculatum* was correlated with seedling root dry weight, total seedling dry weight, and root length, but did not consider seed position within the fruiting body in their study.

Reduced individual seed weight, basal root number, and taproot diameter in seeds from the peduncular position and later developing pods may be in part explained by less allocation of resources into these seeds by parent plants. It is logical that fewer resources in the seed could limit the development and growth of seedling organs that develop soon after germination, such as the taproot and basal roots, and thus overall root biomass. In a few genotypes, root dry weight, basal root number, and taproot diameter were

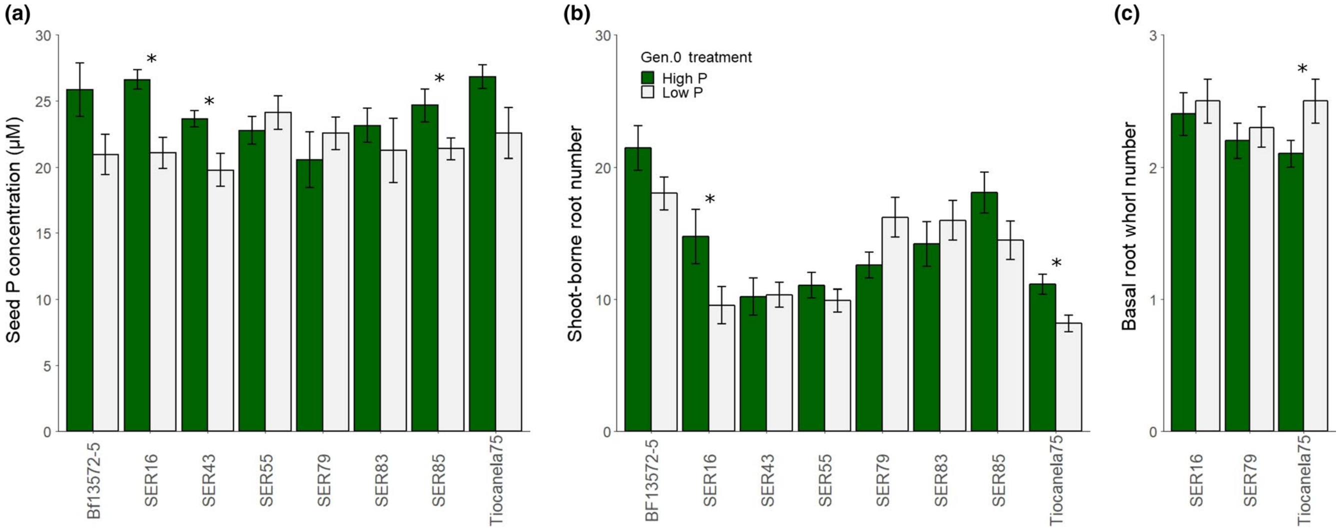

FIGURE 5 Effects of parental low phosphorus (P) stress on seed P concentration (a) and root traits (b, c) of progeny. Shoot-borne root number was assessed in field-grown plants harvested at R2 in Rock Springs, PA (b), while basal root whorl number was assessed in greenhouse-grown plants harvested at R2 (c). Due to space constraints, fewer genotypes were used in the greenhouse. Error bars represent standard error of the mean. Asterisks represent significant differences between treatments within genotypes ($p < .05$)

TABLE 4 ANOVA table for effect of parental (Gen. 0) and progeny (Gen. 1) phosphorus stress treatment (TRT) on seed phosphorus concentration and root traits of plants grown to the reproductive stage in the greenhouse

	Seed P concentration		**Shoot-borne root number**		**Basal root whorl number**	
	F	***p***	***F***	***p***	***F***	***P***
Gen. 0 TRT	16.804	*<.001*	2.956	.087	1.846	.181
Gen. 1 TRT	N/A[a]	N/A[a]	0.558	.456	1.846	.181
Genotype	1.568	.156	4.793	*<.001*	0.308	.737
Gen. 0.TRT × Gen. 1.TRT	N/A[a]	N/A[a]	0.032	.859	2.077	.156
Gen. 0.TRT × Genotype	1.836	.090	1.765	.095	0.462	.633
Gen. 1.TRT × Genotype	N/A[a]	N/A[a]	1.383	.213	0.462	.633
Gen. 0.TRT × Gen. 1.TRT × Genotype	N/A[a]	N/A[a]	0.836	.558	1.615	.209

[a] Seeds tested for seed P concentration were not grown under a Gen. 1 treatment; therefore, no data are available.

reduced at reproductive growth stage R2 in plants that were from the peduncular position on the parent plant, suggesting that the reduction in seed reserves had a prolonged impact on plant growth.

4.2 | Parental effects of drought stress

Relative to parent plants grown under well-watered conditions, drought-stressed parent plants were stunted and had fewer resources available to allocate to yield. Thus, resources available to seeds during seed fill on drought-stressed parent plants were expected to be less relative to seeds from well-watered parents. Hill et al. (1986) and Meckel et al. (1984) found that soybean seeds from drought-stressed parent plants had lower seed weight and volume. Our results confirmed that seeds from parent plants subjected to drought-weighed less, and some genotypes had smaller or fewer roots at the seedling stage and at mature growth stage R2 (Figures 3 and 4). Most seedling traits were negatively impacted by parental drought, and the extent varied considerably with genotype.

Individual seed weight alone did not explain differences in seedling dry weight or taproot and basal root lengths in seedlings from drought-stressed versus well-watered parents. No correlations were found between individual seed weight and total seedling dry weight, taproot length, or basal root length. ALB67 was the only genotype out of fourteen tested that had no difference in individual seed weight, but it showed differences in seedling traits between parental treatments, and ALB6 was the only genotype tested that differed in individual seed weight, but it did not show any differences in seedling traits between parental treatments. Sultan (1996) also observed lower seedling dry weight and shorter root length in *Polygonum persicaria* seedlings from drought-stressed parents, with little to no correlation with seed size. Other factors not tested, including (but not limited to) seed nutrition, carbohydrate, and protein composition, may play roles in growth and development of these traits at early growth stages.

There was a general lack of adaptive responses in root traits to parental drought stress. One exception was that ALB1 had greater seedling basal root length in progeny from parental drought, relative to progeny from well-watered parents. It is possible that fewer but longer basal roots may be a strategy to permit deeper soil exploration for limiting water. Genotypes such as ALB6 that have fewer negative phenotypic impacts from parental stress may be useful for breeding programs focusing on the performance of seedlings under stress through consecutive generations. Genotypic differences in the impact of parental stress may be due to factors such as seed composition and should be tested in future studies. It is noteworthy that phenotypic responses to parental drought in ALB RILs used in this study may not be representative of *P. vulgaris* responses to parental stress since the ALB population is from an interspecific cross with *P. coccineus*. However, *P. coccineus* is an important source of stress tolerance that can be used in breeding programs focused on drought tolerance (Hidalgo, 1991; Wilkinson, 1983).

4.3 | Parental effects of phosphorus stress

Parental phosphorus treatments did not significantly affect individual seed weight in these experiments, in contrast to previous research on parental effects of P stress in common bean, watercress, and soybean (Derrick & Ryan, 1998; Vandamme, Pypers, Smolders, & Merckx, 2016; Yan et al., 1995). P availability was moderately low in parental fields, resulting in shoot dry weight reductions of 15%–35%. This may not have been severe enough to cause differences in individual seed weight but were enough to result in differences in seed P concentration in some genotypes (Figure 5). Despite the lack of difference in individual seed weight in this study, parental phosphorus stress resulted in differences in mature root traits in some common bean genotypes (Figure 5).

Genotypes varied in the extent to which parent plants under P stress produced fewer seeds but with similar mass and equal provisioning (P content). Three of nine genotypes grown under low P produced seeds with lower seed P concentration, relative to seeds produced on parent plants grown under nonstressed conditions, but few negative impacts of reduced P content were observed. An exception was that one of the three genotypes that had lower seed P concentration from parental low P stress, SER16, had fewer shoot-borne roots at R2. In a study on parental drought by Sultan (1996), *Polygonum persicaria* parent plants grown under drought produced fewer offspring, but greater mass per seed. Genotypes capable of maintaining both seed weight and seed P content, such as SER55, SER79, and SER83 (Figure 5), present candidates for breeding programs targeting tolerance to low P across generations. Although these genotypes may produce fewer seeds, each seed would be expected to perform better in a low P field.

Basal root whorl number was greater in progeny from a low P parental environment in Tio Canela 75 (Figure 5). This response may be an adaptation to a low P parental environment since greater basal root whorl number has been found to improve P uptake under low P conditions in common bean (Miguel, 2012; Miguel et al., 2015). Such a response may be controlled by mechanisms such as heritable epigenetic modifications affecting basal root whorl number. Heritable epigenetic modifications in response to stress have been suggested to be adaptive in some cases (Mirouze & Paszkowski, 2011). For instance, *A. thaliana* exposed to heat stress had over five times greater individual seed production when the parent generation was exposed to similar heat stress (Whittle, Otto, Johnston, & Krochko, 2009), and *A. thaliana* progeny from salt-stressed parents had greater global DNA methylation and were more adapted to salt stress, compared to progeny from nonstressed parents (Boyko et al., 2010). In rice, Wang et al. (2011) suggested that drought-induced DNA methylation patterns in rice could reflect an adaptive mechanism to cope with drought, potentially across generations.

5 | CONCLUSIONS

Most of the negative effects on seed, seedling, and root traits assessed in this study could be attributed to weaker provisioning from parent plants grown in a stressful environment or competition from other seeds with a more favorable position or timing of seed development. In nearly every case, individual seed weight was reduced in seeds from the peduncular position within the pod, seeds from late-developing pods, and seeds from parental drought. The greater the difference in individual seed weight between parental treatments, seed position, or pod set timing, the more likely we were to find significant differences in root traits. However, in every experiment, genotypes varied considerably with respect to which, if any, seed, seedling, or mature plant traits were altered by parental provisioning. While this made it difficult to generalize about the responses of root traits to parental provisioning, it does suggest that genotypes could be selected for their ability to maintain seed weight and vigorous root development even when seeds are produced in an unfavorable parental environment.

Parental drought stress most often affected seed weight, but genotypes varied in the extent to which seedling and mature plant root traits were affected. Many genotypes showed no negative impact of parental drought stress on seedling or mature plant phenotypes. Likewise, parental low phosphorus stress most commonly affected seed phosphorus content, but only a few genotypes showed negative impacts on seedling or mature plant phenotypes. Therefore, most of these breeding lines could be used in programs targeting drought and low phosphorus environments without substantial negative impact when seed production occurs in a stress environment.

We observed some responses (e.g., increased seedling basal root length in progeny from ALB1 parents exposed to drought and increased basal root whorl number in progeny from P-stressed Tiocanela75 parents) that would be expected to improve establishment and performance if the progeny were exposed to the same stress. The ability to “remember” previous stress via epigenetic mechanisms has been suggested as a way to improve crop responses to stress (Bilichak & Kovalchuk, 2016; Lämke & Bäurle, 2017). While most research in this area has been on model species, recent work on crops has revealed chromatin changes in crops in response to nutrient, water, and other types of stress (Fortes & Gallusci, 2017; Secco, Whelan, Rouached, & Lister, 2017). Whether these changes are heritable, and whether they are common enough in crops to be useful in breeding, is an open question (Springer & Schmitz, 2017). As more discoveries are made about epigenetic inheritance and methods to exploit it, heritable “stress memory” could become an important tool for breeders (Bilichak & Kovalchuk, 2016; de la Rosa Santamaria et al., 2014).

Plant breeders often evaluate new cultivars for stress tolerance using seed that developed in a well-watered, high-fertility parental environment. Due to the differences in genotypic and phenotypic responses to parental stress, the parental environment should be considered in breeding programs targeting tolerance to stresses such as drought and poor nutrient availability. Genotypes displaying relatively greater reduction in provisioning of progeny in response to parental stress should be avoided in breeding programs with these objectives. Cultivars that maintain provisioning of individual seeds would be beneficial to farmers using seeds from stressed parent plants.

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CONFLICT OF INTEREST

None declared.

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