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ORIGINAL ARTICLE

Reproductive fitness in common bean (*Phaseolus vulgaris* L.) under drought stress is associated with root length and volume

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Abstract Common bean (*Phaseolus vulgaris* L.) is an important grain legume crop, and drought stress during its reproductive stages affects flowering and pod-filling process. Mitigating drought stress requires the selection of resilient varieties that withstand drought stress. We hypothesized that drought affects the root system of common bean leading to decreased reproductive success, and a relationship exists between root traits and reproductive success. Objectives are to (1) quantify the effects of drought stress on root and shoot traits and pod set percentage in common bean, and (2) assess whether root traits had a relationship with reproductive success under drought. Seedling root traits were studied in solid agar medium. To understand the influence of drought on the root system of adult plants, the lines were grown in 150-cm columns for 48 days under full irrigation or withholding water for 41 days. Root angles ranged from 32.8° to 60.6°, with Pinto and Lariat having the narrowest (32.8°) and widest (60.6°) root angles, respectively. Drought stress decreased rooting depth (14%), root biomass (29%), total root length (35%), volume (41%), pod set percentage (53%), and pod weight (43%). However, the root: shoot ratio (70%) and *Fo*/*Fm* ratio were (13%) increased in response to drought stress compared to control. A positive relationship between root volume and total root length with pod set percentage ($r^2 \geq 0.80$) and pod weight plant^{-1} ($r^2 \geq 0.35$) was observed. The study identified the genotypes Topaz and Matterhorn as drought tolerant and susceptible, respectively. Topaz had a wider root angle, higher root biomass, root: shoot ratio, total root length, and volume along with higher pod set percentage and pod weight under drought compared to other genotypes. Hence, these traits can be included in the common bean drought stress breeding program.

Keywords Common bean · Drought stress · Root architecture · Thylakoid membrane damage

Introduction

Common bean (*Phaseolus vulgaris* L.) is a widely cultivated grain legume across the world (Beebe et al. 2013). It is a source of dietary protein, complex carbohydrates, and micronutrients for more than 300 million people in parts of Eastern Africa and Latin America (Welch et al. 2000; Beebe et al. 2013). In many areas of the world, common bean is the second most important source of calories after maize (*Zea mays* L.; Broughton et al. 2003). Despite its importance, common bean production potential has not been realized, particularly under stress conditions (Blair et al. 2010). Drought is a major production constraint in common bean. Intermittent drought is common in the semi-arid highlands of the subtropics where the bean is grown in large areas (Urrea et al. 2009). Globally, about 60% of common bean production areas are facing intermittent or terminal drought (Beebe et al. 2013; Singh 2001; Wortmann et al. 1998). Drought stress negatively impacts bean

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yield, with its severity dependent on intensity, timing, type, and duration of the stress (Munoz-Perea et al. 2006). It is predicted that the number of extreme events, such as severe drought and its duration, will increase due to climate change (IPCC 2014). Breeding efforts to improve crop yields under drought stress have focused on aboveground plant traits, while the belowground roots are an underutilized source possibly due to difficulties associated with the reliable measurement of root traits, even though relatively high throughput methods are now available (Wachsman et al. 2015). Given the substantial experimental evidence for roots as reliable adaptive traits under drought, it is imperative to have an in-depth understanding of their role in improving drought tolerance in bean (Rehman et al. 2015)

Historically breeding programs have mainly focused on above ground traits that are easily quantifiable (Paez-Garcia et al. 2015). However, adaptation to drought stress encompasses morphological, physiological, and biochemical mechanisms (Hall 2004), including a deeper root system and water-saving shoot traits (Beebe et al. 2008). Drought tolerance is attributed to the ability of a plant to avoid tissue dehydration, partly through root architecture, such as increased root length, root length density, and rooting depth, that can maximize soil exploration for water uptake (Beebe et al. 2013; Manschadi et al. 2008; Kirkegaard et al. 2007). The magnitude of the available water for crop production depends on water supply from the soil profile explored by the root system, and atmospheric demand. The rooting depth is greatly crop species and genotype-dependent (Manschadi et al. 2008). The roots are crucial for water acquisition and can be targeted as a potential trait to enhance plant productivity under water-limited conditions (Dardanelli et al. 1997). The current challenge for plant breeding based on harnessing root phene variability is the limited by the obvious difficulties associated with reliable phenotyping. Breeding efforts aimed at improved root traits can help identify, water stress-tolerant crops and enhanced capacity for soil exploration and, therefore, better water acquisition. The current approaches for root phenotyping in the laboratory, greenhouse and field encompass simple agar plates to column experiments and labour-intensive root digging (i.e., shovelomics) and soil boring methods, the construction of underground root observation stations and sophisticated computer-assisted root imaging (Dardanelli et al. 1997)

Deep soil moisture extraction late in the season increased the yields of rice (*Oryza sativa* L.; Uga et al. 2011), maize (Hund et al. 2009), sorghum [*Sorghum bicolor* (L.) Moench; Vadez et al. 2013], groundnut (*Arachis hypogaea* L; Jongrungklang et al. 2012), and common bean (Beebe et al. 2011). A larger root system (greater lateral branching and rooting depth) has been associated with increased transpiration, shoot biomass production, and harvest index under terminal drought stress by using more soil moisture (Vadez 2014). However, deeper and more profuse roots alone do not increase grain yields under drought stress (Zaman-Allah et al. 2011). In rice, the mapping population between deep-rooting Azucena and shallow-rooting Bala shows that water-conserving shoot traits from Bala are more important than root traits from Azucena under drought (Price et al. 2002). Similarly, seed yield in chickpea (*Cicer arietinum* L.) under terminal drought had no relationship with rooting depth but had a close association with water-saving shoot traits (Vadez 2014). Some studies have found a close relationship between rooting depth and water extraction pattern (Hund et al. 2009; Vadez et al. 2013), while others found no relationship (Vadez 2014; Ratnakumar and Vadez 2011). Association studies of the whole plant root system with grain yield in wheat (*Triticum aestivum* L.) and chickpea have found a positive (Bishopp and Lynch 2015), negative or neutral association (Vadez 2014; Schoppach et al. 2013; Purushothaman et al. 2017). Understanding this relationship is important because constitutive traits or traits that are closely associated with grain yield under drought stress should be considered as selection criteria rather than grain yield *per se*, as grain yields are prone to large G × E interactions (Ludlow and Muchow 1990).

Palta et al. (2011) used glasshouse and field experiments to examine the relationship between root system size and their functional implication for water capture. Individual root traits for water uptake did not describe a root system as being large or small. However, indirect selection for increased leaf vigour has enlarged the root system through increases in root biomass and length and root length density, which contributes to increased water capture at early growth stages and facilitates the capture of additional water during grain filling. The usefulness of a vigorous root system in increasing yields under water-limited conditions may be greater in rainfed environments, whereas, in the areas where crops rely on stored soil water, a vigorous root system may increase the risk of depleting soil water before completion of grain filling.

Several physiological traits like leaf temperature, photosynthetic rate, stomatal conductance, transpiration rate and thylakoid membrane damage are associated with drought tolerance in common bean (Beebe et al. 2013; Ambachew et al. 2015). The expression of this trait under drought stress is genotype specific (Ambachew et al. 2015). The increase in *Fo*/*Fm* ratio is a characteristic feature of photoinhibition (Lawlor and Cornic 2002). The increase in *Fo*/*Fm* ratio indicates the inactivation of PSII activity and a decrease in the transfer of excitation energy from the light-harvesting complex (LHC) II to photosystem (PS) II, which may be related to the decrease of LHCII content under drought stress (Govindjee 2004). Exposure of common bean to drought stress has resulted in earlier flowering and maturity, and decreased root length, root mass, dry matter production, photosynthate translocation, pod numbers, number of seed pod^{-1}, seed size and seed yield (Ambachew et al. 2015; Asfaw and Blair 2014; Asfaw et al. 2012; Ramirez-Vallejo and Kelly 1998; Sofi et al. 2017). In grain legumes, pod abortion is more common under drought stress during flowering and pod set stages (Leport et al. 2006), due to a reduction in pollen viability and germination and impaired stigma/style function or early embryo abortion (Fang et al. 2010). Drought-stressed pollen grains of common bean had abnormal exines with deeply pitted and smooth regions (Shen and Webster 1986). The impact of drought stress on root, shoot and reproductive traits in common bean has received little attention. To our knowledge, limited information on the association between root traits and reproductive success in common bean under well-watered and water-limited situations is available. This study had the following objectives: (1) to quantify the effects of drought stress on root and shoot traits and pod set percentage, and (2) to assess whether root traits had a relationship with pod set percentage under drought stress. We hypothesized that drought stress affects root growth leading to decreased pod set percentage and a relationship exists between root traits and pod set percentage under drought stress.

Materials and methods

Plant material

Seven determinate varieties of common bean: Lariat, Stampede, Matterhorn, Pinto, Roza, Buster, and Topaz were obtained from North Dakota State University, ND, USA. Lariat, Stampede, Matterhorn, Buster, and Topaz belong to the Durango race, while Roza and Pinto belong to the Jaliso race. An earlier study has shown that these genotypes varied significantly for drought stress response and root traits (Lasley 2013). However, mechanism of drought tolerance or susceptibility based on root traits and reproductive success was not studied in detail.

Experimental details

Experiment 1: Genetic variability for seminal root number and root angle

A controlled environment experiment was conducted in a completely randomized design with four replications. The seeds of seven common bean genotypes were surface sterilized using 10% sodium hypochlorite for 5 min and then washed with deionized water for three times. The seeds were germinated in Petri plates using filter paper (Whatman No. 42) moistened with 5 ml of deionized water for 2 days.

Sterilized agar (Sigma Type A; 2% w/v) was poured into square Petri plates (12 × 12 × 1.7 cm, L × W × H) up to the rim and allowed to solidify. The Petri plates were sealed with cellophane tape (Staples® Invisible Tape, Manhattan, KS). On day 3, uniform seedlings (radicle emerged) were selected and oriented vertically with the radical facing downwards through the cut side of the square Petri plates containing agar and kept for 5 days in an incubator maintained at 25 ± 1 °C (Kirkegaard et al. 2007). After which, root angle data on the first pair of basal roots was measured 3 cm from the seed relative to a vertical line passing through the stem base (Kirkegaard et al. 2007). After measuring the root angle, seedlings were removed from the agar, and the number of basal roots and basal root whorls were counted for each genotype.

Experiment 2: Genetic variability for root and physiological traits and reproductive success

A controlled environment experiment was conducted in a factorial design at the Department of Agronomy, Kansas State University, Manhattan, KS. Plants were grown in polyvinyl chloride (PVC) columns with an inside diameter of 20 cm and height of 150 cm. The columns were filled with an equal quantity of sterilized Turface MVP (PROFILE Products LLC, Buffalo Grove, IL), which had a bulk density of 576.66 ± 32 kg m^{-3}. Turface is a calcined, non-swelling illite and silica clay, which allows easy separation of roots. The rooting medium was fertilized with 10 g of Osmocote (Scotts, Marysville, OH), slow-release fertilizer with 19:6:12 N:P_2O_5:K_2O, per column before sowing and evenly mixed with Turface in the top 2 cm. A systemic insecticide, Marathon 1% G (a.i.: Imidacloprid: 1-[(6-Chloro-3-pyridinyl) methyl]-N-nitro-2-imidazolidinimine; OHP, Inc., Mainland, PA) was applied to the Turface at 1 g per column before sowing to control sucking pests. The seeds were surface sterilized with 10% sodium hypochlorite for 5 min and rinsed with distilled water. Initially, four seeds were sown in each column at 4 cm depth and continuously irrigated till the crop reached the first trifoliate leaf stage. At this stage, one competitive plant was retained per column. Plants were maintained under optimum temperature (28/18 °C, day/night) with a 15 h photoperiod.

Drought stress imposition

From sowing to harvest, the control plants were maintained at 100% field capacity by irrigating water on a daily basis.

For the drought treatment, plants were maintained under 100% field capacity from sowing to the trifoliate stage; then stress was imposed by withholding water till pod development stage (48 days after sowing; DAS). The duration of the drought stress was 41 days. The moisture content of Turface at the end of the drought treatment was 30%, which was quantified on a weight basis (Black 1965).

Root architectural studies

After 48 days, the roots were carefully harvested by gently inverting the columns at about 140° to allow the contents (Turface and plants with entire root system) to slip out. The intact roots were carefully separated from the Turface. The shoots were separated from the roots by cutting at the base of the stem. After removing the shoots, the roots were spread on a flat surface to measure their length (from the base of the stem to the tip of the root system) as an estimate of rooting depth. The root system was then washed with water to remove any adhering Turface, placed between moist paper towels, sealed in Ziploc bags (S.C. Johnson & Sons, Inc. Racine, WI), transported to the laboratory, and stored at 4 °C. For root analysis, the root system of each genotype was stretched and sliced into 30 cm long portions and each portion was submerged in a water and carefully spread (20 × 15 × 2 cm; length × width × height) to maximize root separation and minimize overlap for scanning with an Epson photo scanner (Epson Perfection V700 with 6400 dpi resolution, Epson, Long Beach, CA). The scanned root image for each genotype was analyzed using WinRHIZO Pro image analysis system (Regent Instruments, Inc., Quebec City, QC) to estimate total root length (sum of the lengths of all roots in the root system), total root surface area, root volume, average root diameter, fine root (roots with diameter < 0.5 mm) length, fine root surface area, and fine root volume (McPhee 2005). After scanning, the root system of each genotype was packed in paper bags for drying. The roots and shoots of all the genotypes were dried in an oven at 60 °C for 7 days to determine dry weight (g plant^{-1}).

Chlorophyll index, leaf temperature, and chlorophyll *a* fluorescence

Leaf chlorophyll index, leaf temperature, and PSII quantum efficiency were recorded on 21, 28, and 35 days after the imposition of drought stress. Leaf chlorophyll index was measured in the top fully expanded mature leaves using a self-calibrating soil plant analysis development (SPAD) chlorophyll meter (Spectrum Technologies, Plainfield, IL). Leaf temperature was measured using a FLIR infrared thermal imaging camera (FLIR Systems Inc., Wilsonville, OR). An image of the top fully expanded leaf was taken at a 45° angle and processed using QuickReport 1.2 software (FLIR Systems Inc., Wilsonville, OR). Thylakoid membrane stability (Fo/Fm ratio) was assessed by measuring chlorophyll *a* fluorescence with a pulse-modulated fluorometer (OS 30, OptiScience, Hudson, NH, USA) after 30 min of dark adaptation of leaves. An increase in the Fo/Fm ratio indicates damage to thylakoid membranes (Djanaguiraman and Prasad 2010).

Days to flowering, pod set percentage, and pod weight

Days to flowering was recorded for each genotype as the number of days taken from emergence to the appearance of the first flower. Twenty floral buds (corolla not opened) were randomly tagged with twine on four plants in each water conditions (five flowers per plant or replication). The flowers were tagged on the top third and fourth node of the main stem of each plant. The ability of floral buds to set pods (pod set) was estimated after 10 days (pods > 2 cm long). The pod set percentage was determined from the number of pods formed from the tagged flower buds. Pods > 2 cm long were considered to be fertile. At harvest, the immature pods were harvested from each plant and dried in an oven maintained at 60 °C for 7 days to determine dry weight in g plant^{-1}.

Data analyses

Statistical analyses were performed using the SAS program (SAS Institute 2003). Results on chlorophyll index, leaf temperature, and chlorophyll *a* fluorescence recorded at 21, 28, and 35 days after the imposition of drought stress, separately or in combination of days had similar responses and significance levels for all traits. Therefore, the means of the three data collection days are presented. The root, physiological and reproductive traits were analyzed using PROC GLM procedure in SAS. The standard error is shown as an estimate of variability, and the means of various variables are separated for significance by an LSD test at a probability level of 0.05. The PROC REG procedure in SAS was used for regression analysis. Classification of common bean genotypes for drought tolerance was performed using principal component analysis (PCA) as described by Kakani et al. (2005) by considering the absolute value of root, shoot, and reproductive traits under drought stress. Eigenvectors generated by PCA were used to identify parameters that differentiated common bean genotypes for drought tolerance. The factor loading values of variables and genotypes in PC1 and PC2 were used to classify the variables and genotypes. Genotypes with + PC1 and + PC2 scores were classified as tolerant, + PC1 and − PC2 scores were classified as moderately tolerant, − PC1 and + PC2 scores were classified as moderately susceptible, and − PC1 and − PC2 scores were classified as susceptible.

Results

Experiment 1: Genetic variability for seminal root number and root angle

The seven genotypes varied significantly ($P \leq 0.05$) for basal root whorl number, basal root number, and root angle (Fig. 1a–c). Among the genotypes, Topaz had the highest basal root whorls (3.2) and basal nodal roots (13), followed by Buster (3.0 and 12.3) (Fig. 1a, b). Matterhorn had the least basal root whorls (2.1) and basal nodal roots (8.5) (Fig. 1a, b). Root angles ranged from 32.8° to 60.6°, with Pinto and Lariat having the narrowest (32.8°) and widest (60.6°) root angles, respectively (Fig. 1c).

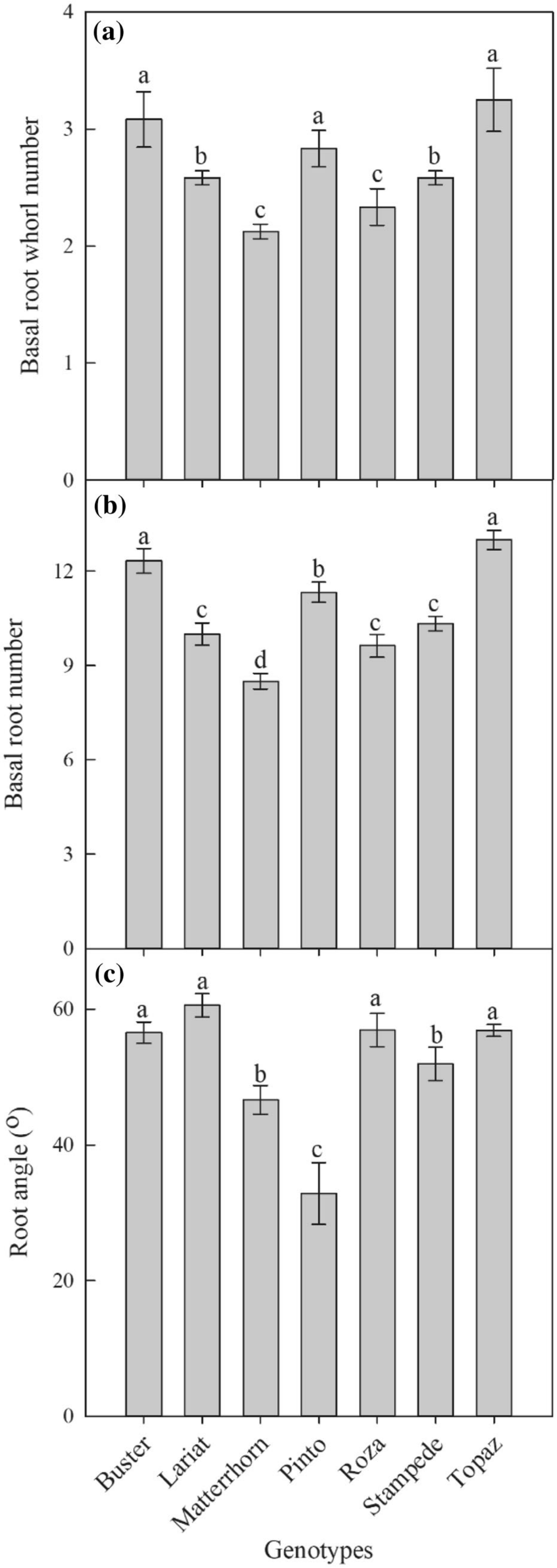
Experiment 2: Genetic variability for root and physiological traits and reproductive success

Plant height, rooting depth, root biomass and root: shoot ratio

Significant ($P \leq 0.05$) differences in plant height (cm), root biomass (g plant^{-1}), rooting depth (cm) and root: shoot ratio were observed for drought stress, genotype, and their interaction (Fig. 2a–d). Across all the genotypes, drought stress reduced plant height (38%), rooting depth (14%), and root biomass (29%) and increased the root: shoot ratio (70%) when compared with the control (Fig. 2a–d). Topaz and Stampede showed no variation in root biomass due to drought stress (Fig. 2b), while Topaz, Stampede, Roza, and Pinto did not vary for rooting depth under drought stress (Fig. 2c). Plant height decreased the most in Roza (48%) followed by Buster (44%) (Fig. 2a). The maximum decrease in rooting depth due to drought stress was observed in Matterhorn (36%), followed by Lariat (22%) and Buster (17%) (Fig. 2c). Drought stress reduced root biomass in Lariat, Matterhorn, and Pinto by 42% (Fig. 2b). The root: shoot ratio increased the most in Roza and Stampede compared to the control (Fig. 2d).

Total root length, total surface area, average root diameter, root volume, root length, and surface area of fine roots (diameter < 0.5 mm)

Significant ($P \leq 0.05$) differences in total root length (cm), total surface area (cm^2), average diameter (mm), root volume (cm^3), fine root length (cm), and fine root surface area (cm^2) were observed for drought stress, genotype, and their interaction (Fig. 3a–f). On average, drought stress



◀**Fig. 1** Genetic variability for seedling traits. **a** Basal root whorl number, **b** basal root number, and **c** root angle among common bean genotypes. Vertical bars denote mean ± S.E. of means. Means with different letter(s) are statistically significant at the $P \leq 0.05$ level

decreased total root length, total surface area, root volume, average root diameter, and fine root length and surface area by 35, 35, 41, 8, 28, and 32%, respectively, compared with the control (Fig. 3a–f). No significant changes in root architecture due to drought stress was observed in Topaz (Fig. 3a–f) However, Matterhorn had the maximum reductions in total root length (53%), total surface area (56%), average diameter (10%), root volume (62%), fine root length (52%), and surface area (55%) (Fig. 3a–f) due to drought stress.

Chlorophyll index, leaf temperature, and thylakoid membrane damage (*Fo*/*Fm* ratio)

Significant ($P \leq 0.05$) differences in leaf temperature, and *Fo*/*Fm* ratio were observed for drought stress, genotype, and their interaction (Fig. 4a–c). Across the genotypes, drought stress decreased chlorophyll index (5%) and increased leaf temperature (12%) and thylakoid membrane damage (13%). Across all genotypes, there was little difference was observed for chlorophyll index (36 vs. 39 SPAD units) and leaf temperature (29.3 to 31.8 °C) under drought stress (Fig. 4a, b). The genotype Topaz (25%) had the highest thylakoid membrane damage followed by Buster (23%) and Roza (11%) (Fig. 4c).

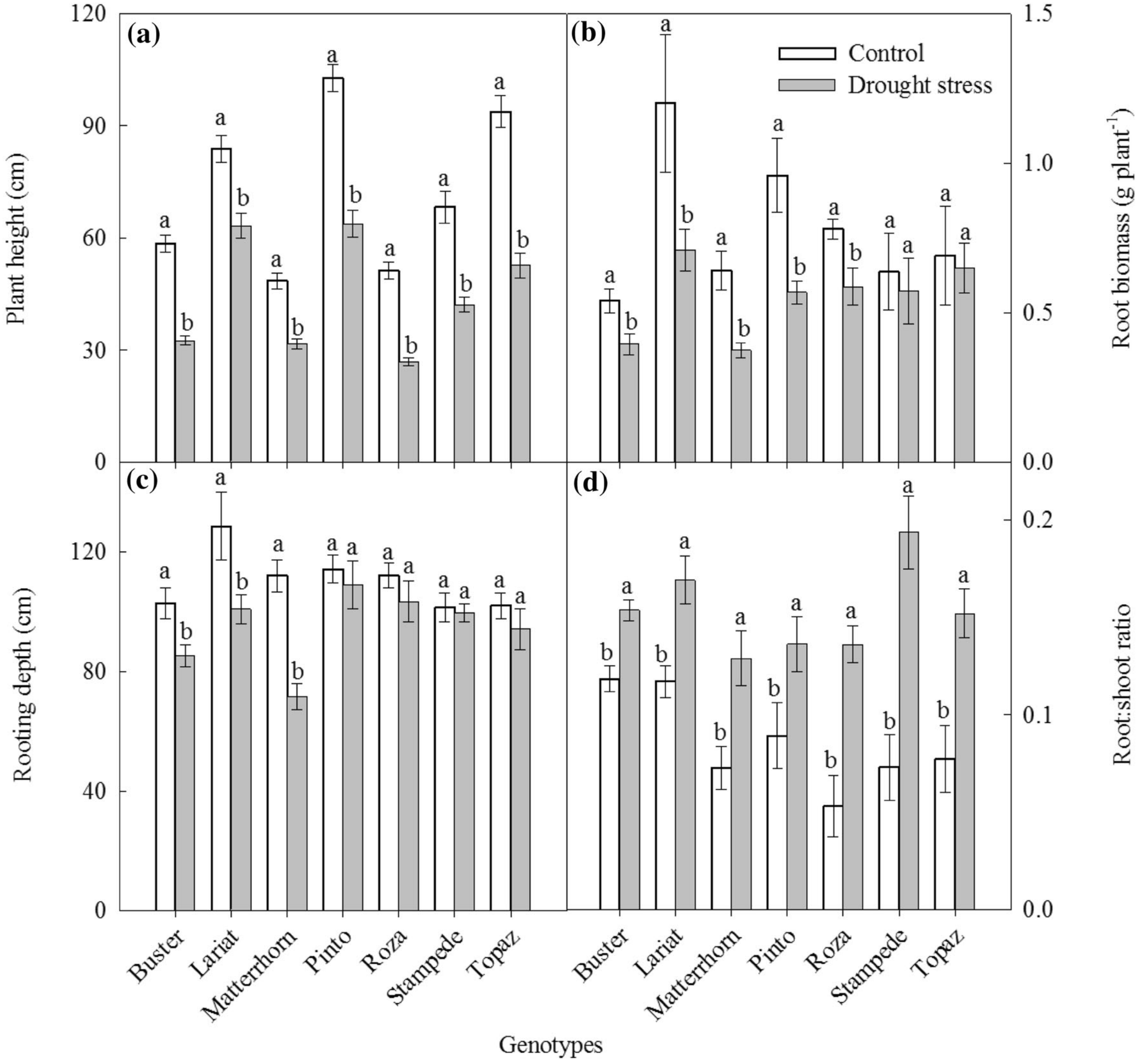


Fig. 2 Genetic variability for shoot and root traits. Interaction effect of drought and genotype on **a** plant height (cm), **b** root biomass (g plant^{-1}), **c** rooting depth (cm), and **d** root: shoot ratio among common bean genotypes. Vertical bars denote mean ± S.E. of means. Control and drought treatments for each genotype were compared for significance at the $P \leq 0.05$ level, and the means with different letter(s) are statistically significant

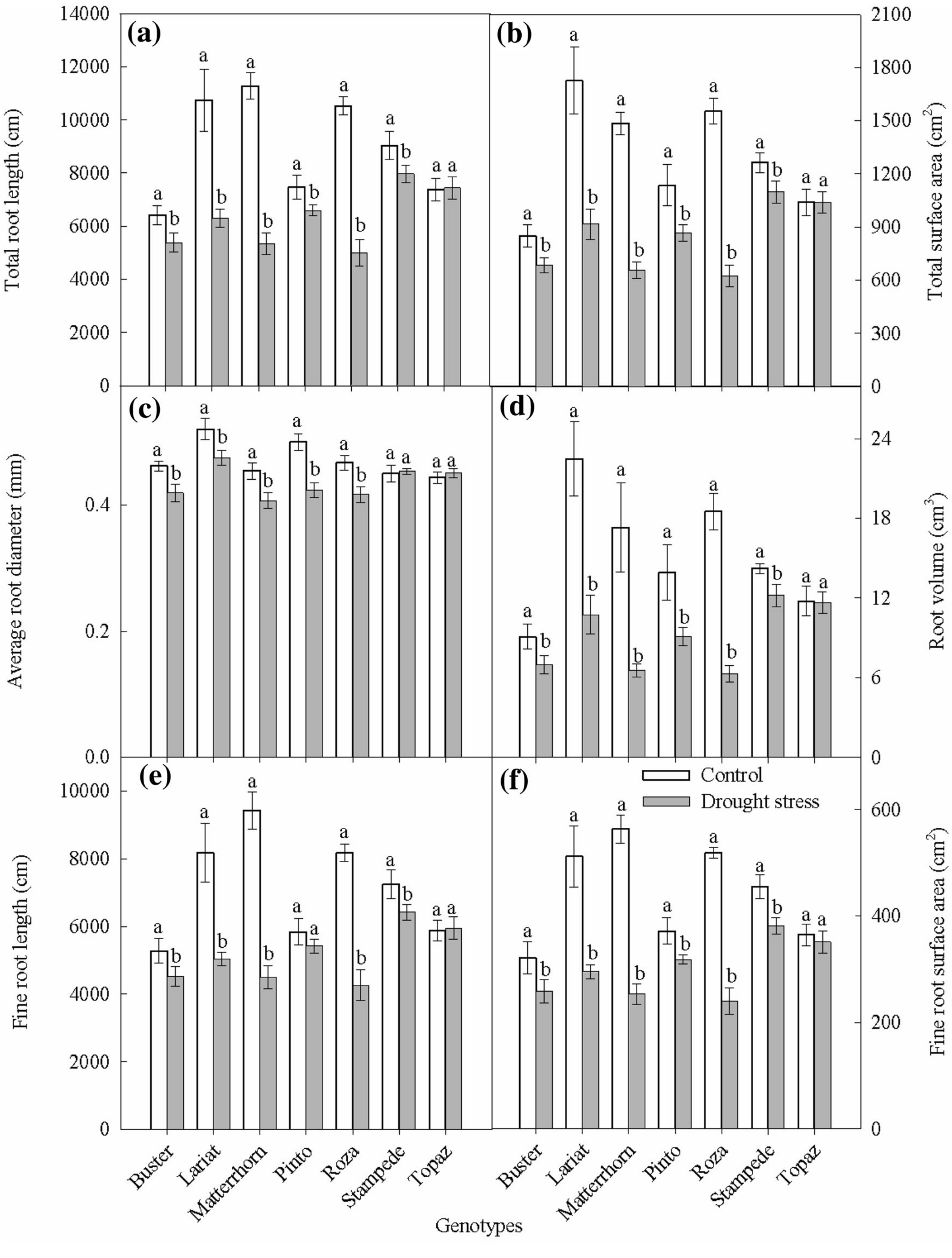
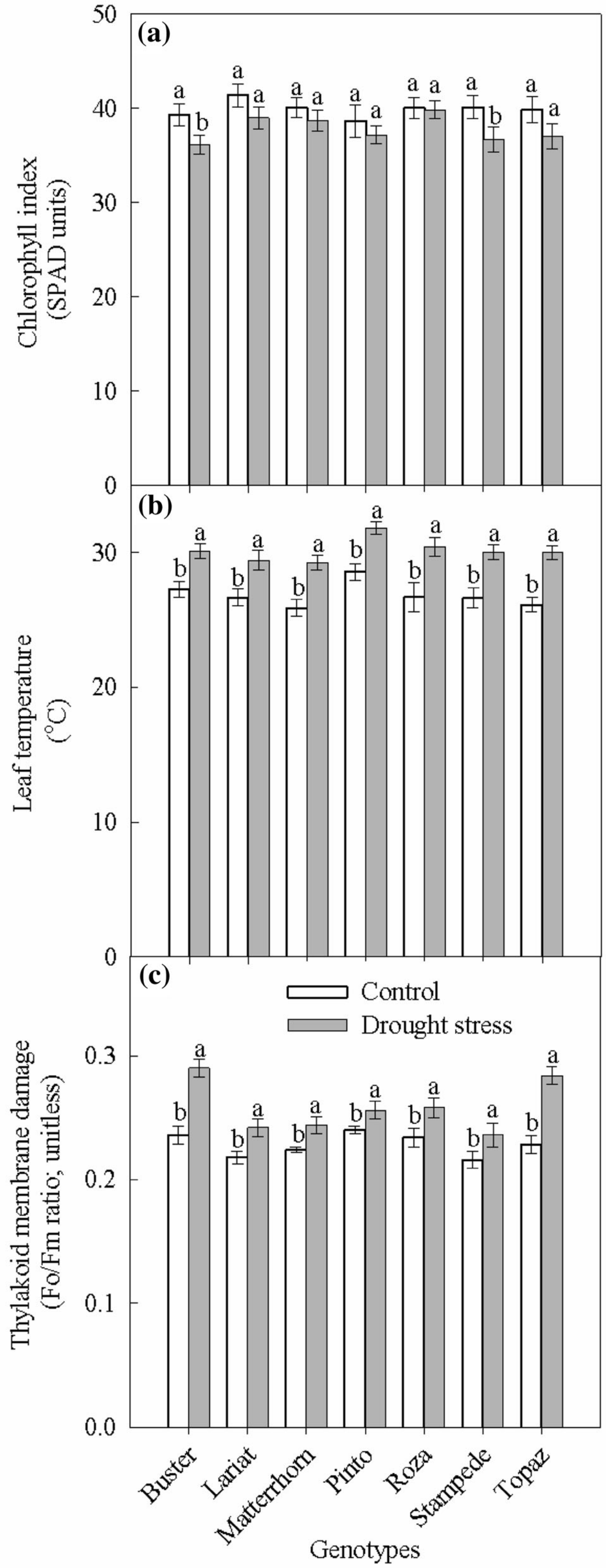


Fig. 3 Genetic variability for root architectural traits. Interaction effect of drought and genotype on **a** total root length (cm), **b** total surface area (cm^2), **c** average root diameter (mm), **d** root volume (cm^3), **e** root length of fine roots (< 0.25 mm class; cm), and **f** surface area of fine roots (< 0.25 mm class; cm^2) among common bean genotypes. Vertical bars denote mean ± S.E. of means. Control and drought treatments for each genotype were compared for significance at the $P \leq 0.05$ level, and the means with different letter(s) are statistically significant



◀**Fig. 4** Genetic variability for physiological traits. Interaction effect of drought and genotype on **a** chlorophyll index (SPAD units), **b** leaf temperature (°C), and thylakoid membrane damage (*Fo*/*Fm* ratio) among common bean genotypes. Vertical bars denote mean ± S.E. of means. Control and drought treatments for each genotype were compared for significance at the $P \leq 0.05$ level, and the means with different letter(s) are statistically significant

Days to flowering, pod set percentage, and pod weight

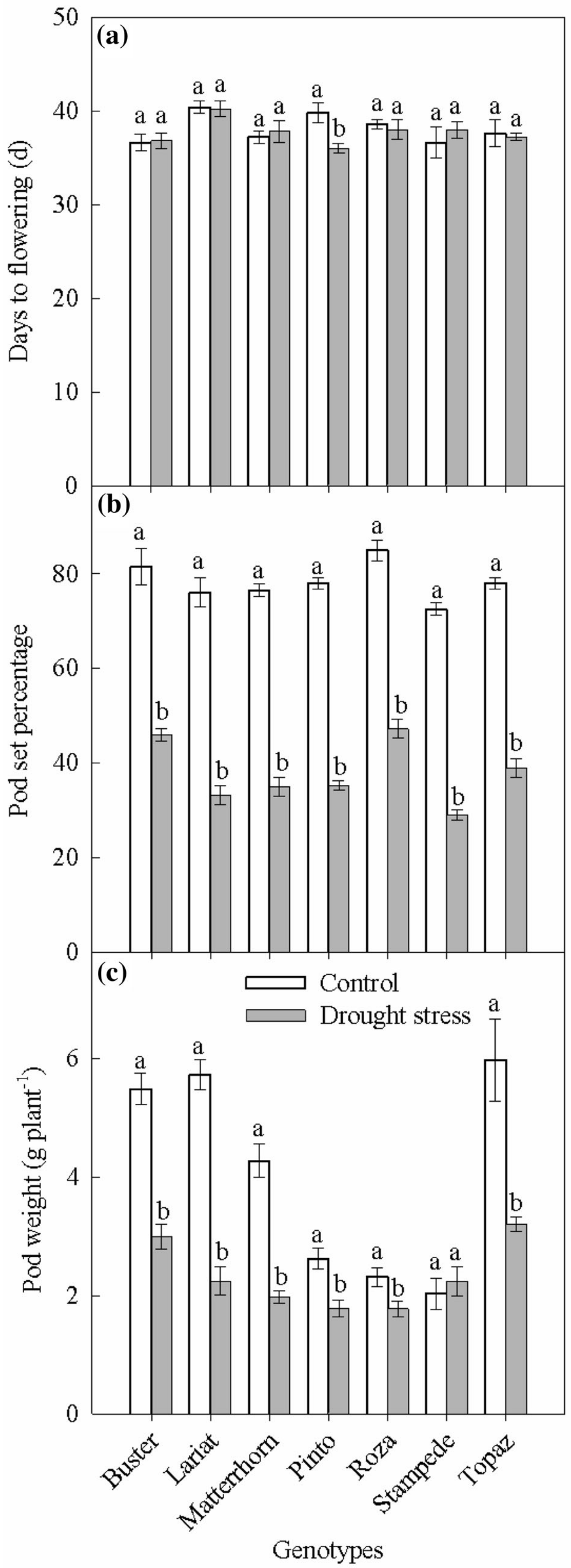
Significant ($P \leq 0.05$) differences in pod set percentage and pod weight were observed for drought, genotype, and their interaction (Fig. 5b, c). However, the only genotypic difference was observed for days to flowering (Fig. 5a). Across the genotypes, the days to flowering ranged from 37 to 40 days (Fig. 5a). Overall, drought stress reduced pod set percentage and pod weight by 53 and 43%, respectively, compared with the control (Fig. 5b, c). Pod set percentage in Buster and Matterhorn declined the most (60 and 57%, respectively; Fig. 5b) and pod weight declined the most in Lariat (61%) followed by Matterhorn (54%; Fig. 5c).

Relationship between root trait and reproductive success

The average root diameter ($r^2 = 0.49$; Fig. 6a), root volume ($r^2 = 0.81$; Fig. 6b) and total root length ($r^2 = 0.81$; Fig. 6c) was positively associated with pod set percentage in common bean. Similarly, a positive relationship was observed between average root diameter ($r^2 = 0.12$; Fig. 6d), root volume ($r^2 = 0.38$; Fig. 6e) and total root length ($r^2 = 0.35$; Fig. 6f) and pod weight was observed.

Principal component analysis

The first two principal component vectors (PC1 and PC2) accounted for 61% of the variability (Fig. 7a). Of the various traits in PC1, the maximum variability was explained by root diameter (21%), followed by root biomass (19%) and root volume (16%). In PC2, the maximum variability was explained by basal root number (28%) followed by days to flowering (18%) (Fig. 7a). Under drought stress, total root length was positively correlated with root volume (r = 0.95), and root diameter was positively correlated with root biomass (r = 0.80) and root volume (r = 0.85). Pod set percentage was positively correlated with root biomass (r = 0.81), and pod weight was positively associated with basal root number (0.79%) (Fig. 7a). Topaz was classified as drought tolerant (+ PC1 and + PC2 score), and Stampede and Lariat were classified



◀**Fig. 5** Genetic variability for pod set percent and pod weight. Interaction effect of drought and genotype on **a** days to flowering (d), **b** pod set percentage, and **c** pod weight (g plant^{-1}) among common bean genotypes. Vertical bars denote mean ± S.E. of means. Control and drought treatments for each genotype were compared for significance at the $P \leq 0.05$ level, and the means with different letter(s) are statistically significant

as moderately drought tolerant (+ PC1 and − PC2 scores) (Fig. 7b). Pinto and Buster were classified as moderately drought susceptible (− PC1 and + PC2 scores), and Matterhorn and Roza were classified as drought susceptible (− PC1 and − PC2 scores) (Fig. 7b).

Discussion

Taken together, the data indicate that (1) drought stress significantly reduced root biomass, rooting depth, total root length, volume, fine root length, and surface area, pod set percentage and pod weight; however, the root: shoot ratio, leaf temperature, and thylakoid membrane damage were increased; (2) a strong positive relationship between total root length and root volume with pod set percentage and pod weight exist in common bean; (3) the genotype Topaz was found to be drought tolerant and Matterhorn and Rosa as drought susceptible; and (4) the drought tolerance ability of Topaz was associated with a wider root angle, higher root biomass, root: shoot ratio, total root length, and volume along with higher pod set percentage and pod weight under drought compared to other genotypes.

Root phenotyping is an important tool for improving drought tolerance (Beebe et al. 2013; Burridge et al. 2016; Rehman et al. 2015), and roots are highly sensitive to moisture gradients (Takahashi et al. 2003). The results indicated that the drought-tolerant genotype Topaz had a wider root angle, and higher total root length, volume, pod set percentage and pod weight plant^{-1} under drought stress than the drought-susceptible genotype Matterhorn (Figs. 1a–c, 3a, d, 5b, c). Lynch (2013) have proposed a wider root angle, higher basal root whorl number, total root length and volume are the influential root traits for better water and nitrogen acquisition in maize. Similar to this ideotype, the genotype Topaz had most of the drought influential root traits along with higher reproductive success. The greater basal root whorl number in Topaz may be associated with more basal roots and longer roots leading to better soil exploration (Lynch and Brown 2001). Shallow roots arising from the uppermost whorls would enable topsoil exploration and phosphorus acquisition, while deeper roots from the lower whorls would be important for water acquisition from drying soil (Miguel et al. 2013). A

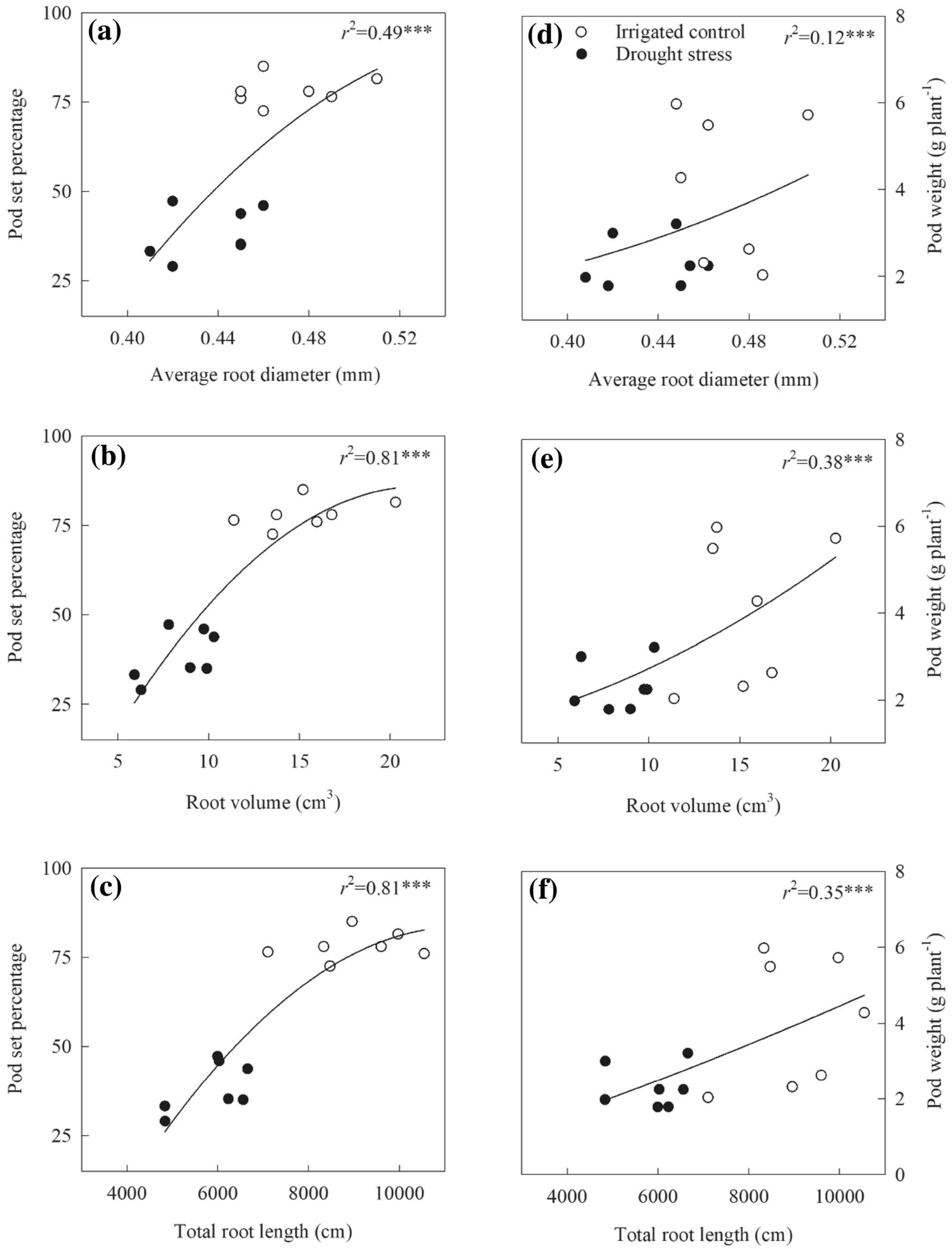


Fig. 6 Relationship between root traits and reproductive success in common bean. **a** average root diameter (mm) with pod set percentage; $y = -2257.24x^2 + 2612.54x - 661.10$; $r^2 = 0.49$; $P < 0.001$; **b** root volume (cm^3) with pod set percentage; $y = -2257.24x^{2-} + 2612.54x - 661.10$; $r^2 = 0.81$; $P < 0.001$; **c** total root length (cm) with pod set percentage; $y = -0.0000013x^2 + 0.03x - 90.37$; $r^2 = 0.81$; $P < 0.001$; **d** average root diameter (mm) with pod weight (g plant^{-1}); $y = 57.77x^2 + 32.69x + 6.09$; $r^2 = 0.12$; $P < 0.001$; **e** root volume (cm^3) with pod weight (g plant^{-1}); $y = 0.0052x^{2-} + 0.09x + 1.29$; $r^2 = 0.38$; $P < 0.001$ and **f** total root length (cm) with pod weight (g plant^{-1}); $y = 0.0000000078x^{2-} + 0.0004x + 0.02$; $r^2 = 0.35$; $P < 0.001$

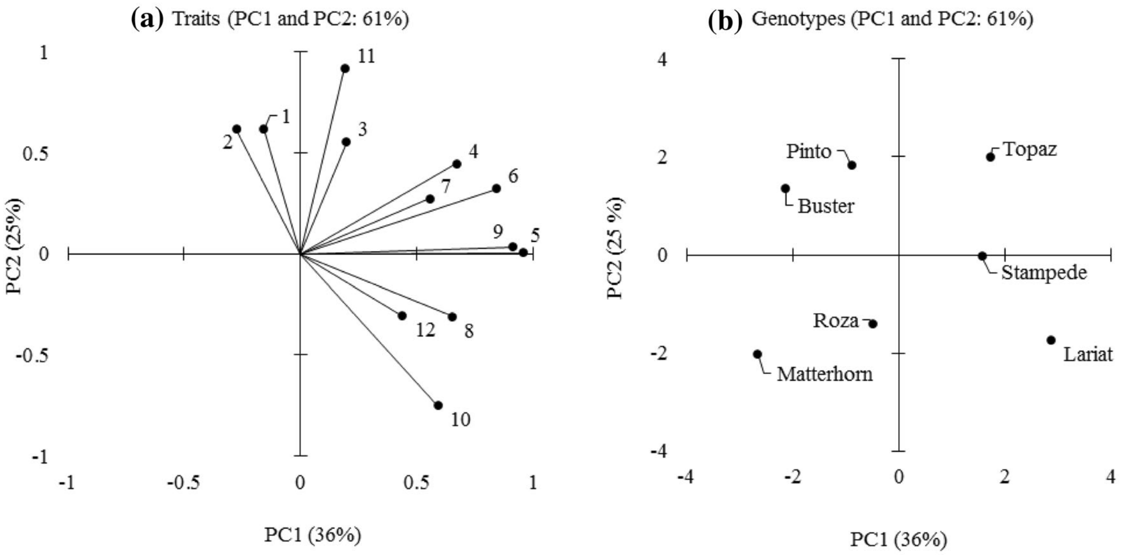


Fig. 7 First and second principal component scores (PC1 and PC2) for identifying traits conferring drought tolerance: **a** the factor loading value for variables is indicated by thick lines radiating from the center showing the direction (angle) and magnitude (length); and **b** classification of common bean genotypes based on the factor scores of first and second principal components. Legend for **a** 1, leaf temperature (°C); 2, thylakoid membrane damage (*Fo*/*Fm* ratio); 3, pod weight (g plant^{-1}); 4, total root length (cm); 5, average root diameter (mm); 6, root volume (cm^3); 7, rooting depth (cm); 8, pod set percentage; 9, root biomass (g plant^{-1}); 10, days to flowering; 11, basal root number; and 12, basal root angle

deeper root system with greater root densities in the deep soil can alleviate the drought stress by increased water uptake (Lynch 2013). In confirmation with this, the study showed a strong positive relationship between total root length and volume with pod set percentage and pod weight plant^{-1} (Fig. 6), suggesting that drought stress effects may be reduced by the deeper root system. In general, the root: shoot ratio increases under drought stress (Asch et al. 2005; Prasad et al. 2008, 2018; Xu et al. 2015) because it enhances soil resource acquisition (Nielsen et al. 2001). Many studies have identified the contribution of deep rooting in water extraction and drought tolerance (Beebe et al. 2013; Ambachew et al. 2015; Bingham 2001; Lynch and Ho 2005; Polania et al. 2009, 2017; Rao et al. 2017).

It was observed that soil dryness significantly affects the capacity of fine roots to grow under drought stress (Bengough et al. 2011; Jin et al. 2015). Fine roots have a high surface area per unit weight. The greater fine root length in the drought-tolerant genotype Topaz offers more opportunity for water absorption (Eissenstat 1992). Under drought stress, the production of more fine roots with a larger surface area per unit mass is a water conservation mechanism to enhance water absorption leading to drought tolerance (Liu et al. 2010; Souza et al. 2016). Having increased fine root growth increases water uptake and yield under drought stress by increasing radial conductivity and root hydraulic conductance (Huang and Eissenstat 2000; Hernandez et al. 2009; Henry et al. 2012). Another important drought adaptation mechanism in Topaz would be to enhance taproot length under drought stress. Taproot length in Topaz (drought tolerant) and Matterhorn (drought susceptible) are decreased by 8 and 40%, respectively, in response to drought stress (data not shown). This indicates that the drought-tolerant ability of Topaz would be a dimorphic-rooted strategy namely increasing basal roots and basal lateral roots and maintaining a longer taproot. This root strategy has been observed in common bean stressed with phosphorus and drought (Ho et al. 2005; Abenavoli et al. 2016). Thus, it is evident that due to increased rooting depth and total root length especially fine roots, the genotype, Topaz had higher pod set percentage and pod weight plant^{-1}.

In this study, root traits like average root diameter, total root length, and root volume showed positive relationships with pod set percentage and pod weight plant^{-1} (Fig. 6). Total root length and volume indicates the distribution of roots in the soil profile and amount of water absorbed (Ludlow and Muchow 1990). Fine roots improve water absorption because of its increases root surface area per unit mass (Eissenstat 1992). The genotypes, with higher total root length, volume, and fine roots had higher reproductive success. Hence, it can be concluded that the increased water uptake through these drought influential traits might have resulted in higher pod set percent and pod weight. Similar to this observation, Polania et al. (2017) have observed a positive association between deeper and vigorous root system with the mobilization of photosynthates to the pod and seed production in common bean.

Darkwa et al. (2015) have observed a significant positive correlation between vertical root pulling resistance force, a proxy of rooting depth and root length with seed yield in common bean.

Drought stress significantly increased leaf temperature and thylakoid membrane damage in all of the genotypes. However, the chlorophyll index was decreased in Buster and Stampede. Chlorophyll is primarily located in the thylakoid membranes, where it forms complexes with the proteins of PSI and PSII (Vach et al. 2007; Darkwa et al. 2015); damage to thylakoid membranes leads to chlorophyll loss. Thylakoid membranes are most sensitive to abiotic stress (Djanaguiraman et al. 2018). The increase in thylakoid membrane damage due to drought stress observed in this study could be due to enhanced photoinhibition of the PSII reaction center and decreased ATP production (Ahmed et al. 2002). Drought stress during the reproductive stage causes pod abortion. In the present study, pod set percentage decreased in all of the genotypes due to drought stress (Fig. 5b). In general, pollen (male) is more sensitive to drought stress than female reproductive structures, although the effects of drought stress on female fertility cannot be overruled (Shen and Webster 1986). In chickpea, the effect of drought stress is greater on female reproductive organs and tissue than male reproductive organs and tissue (Shen and Webster 1986). Drought stress during reproductive development in common bean reduced pollen viability and pollen germination (Shen and Webster 1986). A considerable reduction in pollen viability might affect pod set percent if fewer viable pollen grains are deposited on the receptive stigma (Shen and Webster 1986). However, the mechanism of loss of pollen viability in common bean was not studied in detail. Drought-stress-induced carbohydrate deficiency and impaired ability to use sucrose and starch by developing pollen grains might contribute to pollen grain sterility and abnormal pollen grain development in grain legumes (Farooq et al. 2016). Further studies in the field to validate these findings will provide a better understanding of drought tolerance mechanisms in these genotypes.

Conclusions

Drought stress changed the root architecture in common bean. Drought stress decreased plant height, rooting depth, root biomass, total root length, root volume, average root diameter, pod set percentage, and pod weight, but increased the root: shoot ratio, leaf temperature and the Fo/Fm ratio in most of the common bean genotypes. Pod set percentage and pod weight plant^{-1} was positively and significantly associated with total root length and volume. PCA analysis indicated Topaz and Matterhorn as a drought-tolerant and susceptible genotypes, respectively. The drought tolerance ability of Topaz was associated with wider root angle, higher basal root and root whorl numbers, increased total root length and volume, pod set percentage and pod weight plant^{-1} under drought stress. The traits namely total root length and volume, pod set percent and pod weight plant^{-1} may be useful for drought stress breeding in common bean.

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