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Low stomatal sensitivity to vapor pressure deficit in irrigated common, lima and tepary beans

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ABSTRACT

A limited transpiration rate under high vapor pressure deficit (VPD) could be used to conserve soil water for later use under drought conditions. Many crops show this behavior either as limited transpiration or decreases in stomatal conductance. However, little work has been done in *Phaseolus*. Four experiments evaluated stomatal closure across a range of VPD for well-watered plants, each experiment using varying combinations of genotypes of common (15), lima (6) and tepary beans (7 genotypes). A two-year experiment found genotypic variation in average stomatal conductance, but genotypes only had 14% stomatal closure between a VPD of 1–4 kPa. In comparison, soybean, which is known to close stomata, had a 40% decrease for similar conditions in Davis, CA, USA. In a second field experiment and outdoor pot experiments, genotypes from the three species displayed, on average, a 34, 50–45% increase in stomatal conductance with increasing VPD. Six genotypes were statistically indistinguishable from a 40% decrease, but all had low probability ($p < 0.21$) of having 40% closure, and some showed little closure in other experiments. The VPD range measured in this study was large relative to the range for hot, arid California, thus the results are generalizable: most *Phaseolus* beans are not expected to have appreciable stomatal closure under well-watered conditions. Thus, there is limited evidence that *Phaseolus* has somegenetic diversity in stomatal responses to VPD, relative to that shown in other species. However, there was constitutive genetic variation in species and genotypic stomatal conductance under low VPD conditions.

1. Introduction

A limited transpiration rate at high vapor pressure deficit (VPD) for well-watered conditions has been used as a mechanism to breed water conservative crops (Sinclair et al., 2010; Sinclair et al., 2016). Using the technique of weighing pots under high VPD, many crops have been found to have this behavior, including legumes such as: chickpea (Zaman-Allah et al., 2011), cowpea (Belko et al., 2012), peanut (Devi et al., 2010), and soybean (Sadok and Sinclair, 2009), and other crops like corn (Yang et al., 2012; Gholipoor et al., 2013), sorghum (Gholipoor et al., 2010), tall fescue (Sermons et al., 2012), and wheat (Schoppach and Sadok, 2012). An alternative technique can be used for field evaluations, where measurements of stomatal closure under high VPD would correspond to limited transpiration, and has been applied, for example, to soybean (Gilbert et al., 2011; Medina and Gilbert, 2016) and peanut (Shekoofa et al., 2015). However, little work has determined whether this behavior is found in common bean (*Phaseolus vulgaris* L.) or other domesticated *Phaseolus* species. One greenhouse study did find that varieties of common bean had stomatal closure when exposed to the VPDs at the extreme of those experienced during growth (Comstock and Ehleringer, 1993).

Finding such stomatal closure in beans in the field would be useful, as stomatal closure early in the season would lead to a decrease in water use, and thus soil water conservation for later periods of drought, as evidenced by delayed wilting in soybean (King et al., 2009). Common bean may benefit from conservative water use as they are often grown in drought prone environments (Singh, 2001; Polania et al., 2016). Despite a large quantity of drought related work on *P. vulgaris*, and a dry origin for many genotypes (e.g. Northwestern Mexico and Chile), limited transpiration or stomatal closure behavior remains obscure in this species.

Less drought research has been done on lima bean (*P. lunatus* L.), despite the wide adaptation range of this species (Debouck, 1999; Maquet et al., 1999; Gepts, 2001; Freytag and Debouck, 2002;

Abbreviations: C, common bean; g_{H2O}, stomatal conductance to water vapor; L, lima bean; P, cowpea; T, tepary bean; T_{air}, air temperature; VPD, vapor pressure deficit.

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Delgado Salinas and Gama López, 2015). Tepary bean (*P. acutifolius* A. Gray) is the "archetypal" drought tolerant crop – growing in the agriculture system with the least annual rainfall in the world (Freeman and Station, 1912; Nabhan, 1990; Rainey and Griffiths, 2005). However, tepary drought tolerance may derive from a fast completion of its lifecycle, thereby avoiding soil water deficit. The species may also rely on just one monsoonal rainfall season; this would not allow provision of future rainfall, which water conservative behavior would benefit from. Thus, including the broadly adapted lima bean and the extreme arid environment tepary would increase the chances of finding alternative stomatal behaviors.

The objective was to determine if genotypes and species in domesticated *Phaseolus* had variation in stomatal closure at high evaporative demand under well-watered conditions. The hypothesis was that genotypes/species from arid environments would have the greatest closure under high evaporative demand, conserving the most water. Similarly, the least commercially improved species, tepary bean, would have more drought-adapted traits, such as water conservation and lower stomatal conductance.

2. Materials and methods

Four experiments were undertaken on combinations of species and genotypes (Table 1): Experiment A: a field trial on eight common bean genotypes, and some other selections in 2013 and 2014; Experiment B: an outdoor pot experiment in 2014 on the same eight genotypes as in Experiment A; Experiment C: a parallel pot experiment to B on three genotypes from each of the three bean species; Experiment D: a field trial in 2015 on four to five genotypes from each of the three bean species.

The selection of common bean and lima bean genotypes used for these experiments included representatives of Andean and Mesoamerican centers of domestication and, for common bean, included diverse eco-graphic races from Mexico (Durango and Jalisco). Tepary bean accessions were selected from geographically distinct areas (Table 1), although less is known about tepary diversity (Schinkel and Gepts, 1988, 1989; Blair et al., 2012).

All field trials were performed during the summer on the Plant Sciences Research Station of the University of California Davis (38.53N, -121.78E). This Central Valley site receives no rainfall in the summer (<0.25 cm) due to a hot, arid Mediterranean climate (Csa, Köppen climate classification). The soil type for the 2013 and 2014 field experiments was a Yolo silty loam, fine silty, mixed, nonacid, thermic Mollic Xerofluvents, and in 2015 a similar adjacent Reiff very fine sandy loam.

2.1. Experiment A (field 2013 and 2014)

A field experiment was conducted in 2013 and 2014 on eight diverse genotypes of common bean and some other common and lima bean genotypes in some of the years (Table 1; planted: 5 Jun 2013 and 8 Jun 2014, harvested: 10 Sep 2013 and 12 Sep 2014). The experiment consisted of three blocks/replications of the genotypes planted in random order, a randomized complete block design (RCBD) in 2013, and in 2014 a staggered design was used where initial measurements were done on three well-watered blocks, subsequently the second block was subject to terminal drought starting on 14 Jul 2014. Thus, the two years did not have a consistent blocking design, and block effects were not accounted for. The genotype plots consisted of one single row bed, 6.1 m long, with 0.76 m spacing between rows. A small alley at the end of the plot separated plots (~1 m), otherwise all plots were either bordered by other genotypes, or a five row field border planting. Plants were sampled for gas exchange more than 1m into the plot. The seeds were machine planted, 10 cm apart, flood pre-irrigated, and later maintained with four flood irrigation events. Each flood irrigation brought the rooting volume to field capacity. Pest and diseases were controlled using conventional chemical controls. Gas exchange measurements on well-watered plants were made on all blocks in random order within five days of flood irrigation. Water deficit blocks (2014) were measured on the same days as well-watered plants in random order, alternating between well-watered and water deficit blocks.

2.2. Experiment B (outdoor pots 2014)

Plants were grown in large pots (11.4 L) in an open field at the UC Davis Orchard Park Greenhouse facility during the summer of 2014 in a RCBD. Four blocks were planted with random order of genotypes within the blocks, and each well-watered pot had a water deficit pot adjacent to it. A border, one pot wide, of a common bean genotype (BAT477) was planted around the entire experiment. Eight common bean genotypes from Experiment A were measured in this experiment (Table 1). Pots had a custom mix of sand, topsoil, pumice, fir bark and peat moss, 3:3:2:1:1, by volume. Pots were whitewashed and the grow area covered with 50% shade cloth to prevent pot heating. Three seeds of a genotype were planted per pot along with those of another genotype, BAT477. After emergence, seedlings were thinned so that there was only one seedling per genotype per pot. Measurement of BAT477 acted as a within pot control for variation between pots across space and time. All plants were fertigated with a modified Hoagland solution using a pressure compensating dripper. After establishment (two weeks), two stakes were placed to provide anchorage and support for each plant per pot, and the overhead shade removed when the developing plant canopy was considered to prevent pot overheating. The experiment extended from planting (11 Aug 2014) to harvest of biomass (19 Sep 2014). Manual weeding and pesticides were applied as needed. Water was withheld from water deficit pots for seven days from 22 days after planting, leading to rapid dry-down in comparison to the field experiments.

2.3. Experiment C (outdoor pots 2014)

Plants were grown in the same arrangement and at the same time as described in B, but consisted of a different grouping of genotypes, in this case three genotypes of common, lima and tepary beans (Table 1). Different sampling days and a separate LICOR6400 to the other experiments was used to measure these genotypes (Table 2).

2.4. Experiment D (field 2015)

A field experiment was conducted on four genotypes of common and lima bean, and five of tepary bean selected based on indeterminate growth habit to control for differences among the species (Table 1; planted: 6/21/2015, harvested: 10/22/2015). The experiment consisted of five blocks/replications of the 13 genotypes planted in random order, a RCBD. Genotype plots consisted of two 1.50 m wide and 3.05 m long double row beds, with 0.76 m spacing between rows (i.e. a plot was four rows). The seeds were hand planted, 10 cm apart, sprinkler irrigated for establishment, and later maintained with 20 cm deep, subsurface drip. Each block was split by a two row border and irrigation was withheld from the second plot 30 days after planting. The experiment was surrounded by a two row border (east–west) or 3.05 m long plot (north–south) of varying genotypes. Gas exchange data was only collected from the two middle rows at least 1 m from each end of the row. Pest and diseases were controlled with using conventional chemical controls.