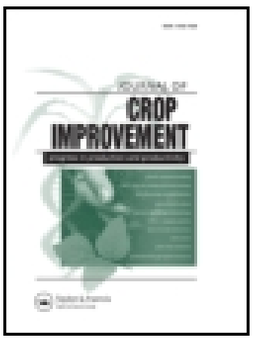

Journal of Crop Improvement

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/wcim20

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To cite this article: Maria Sanchez , Thomas R. Sinclair & Deepti Pradhan (2020): Transpiration response to vapor pressure deficit and soil drying among quinoa genotypes (*Chenopodium quinoa* Willd.), Journal of Crop Improvement, DOI: 10.1080/15427528.2020.1817221

To link to this article: https://doi.org/10.1080/15427528.2020.1817221

Published online: 13 Sep 2020.

JOURNAL OF CROP IMPROVEMENT
https://doi.org/10.1080/15427528.2020.1817221

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Transpiration response to vapor pressure deficit and soil drying among quinoa genotypes (*Chenopodium quinoa* Willd.)

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ABSTRACT

Water-deficit conditions limit increasing crop yield around the world. In order to improve crop yield it has been proposed to decrease water use early in the season so more water will be available later in the season to support seed growth during reproductive development. To achieve this, there are two water-conservation traits of special interest: partial stomatal closure under high vapor pressure deficit (VPD) and early in the soil drying cycle. Quinoa (*Chenopodium quinoa* Willd.) is well known for its ability to grow in poor soils and extreme climatic environments. Therefore, quinoa may especially benefit from expression of water-conservation for water-limited conditions. These traits have not been previously studied in quinoa. This study reported the response of eight quinoa genotypes. Genotypes Red head, CICA-17, Salcedo, Ollague, Good Afternoon, and Pasankalla expressed a VPD breakpoint (BP) but Titicaca and French Vanilla not. All genotypes expressed a FTSW threshold with soil drying as expected. French Vanilla had the highest threshold, so it would be a candidate as a water-conserving genotype. The results of this study can be applied directly in field tests comparing cultivars under water-deficit conditions, and selection of genotypes to be used in breeding for improved cultivars specifically for drought.

ARTICLE HISTORY
Received 13 August 2020
Accepted 27 August 2020

KEYWORDS
Quinoa (*Chenopodium quinoa* Willd.); transpiration response; soil drying; vapor pressure deficit; water-deficit

Drought, commonly the most yield-limiting environmental stress, impacts negatively agriculture despite efforts to improve crop yield under water-deficit conditions (Cattivelli et al. 2008). Due to climate change over the 21st century, it is likely that droughts will increase as a result of more infrequent rain events and less total precipitation (IPCC, Climate Change 2014: Synthesis Report 2014).

Madadgar et al. (2017) found during dry growing seasons that precipitation and soil moisture deficit reduced the average annual yield of the five largest crops in Australia by 25–45% relative to the wet growing seasons. Hence, it has been proposed to develop drought-tolerant plants that consume limited-water during the early growing season so that later in season

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conserved soil-water could be used to sustain plant productivity during seed filling (Sinclair 2018). Two approaches to achieving early-season water conservation have been suggested both involving partial stomatal closure resulting in limited transpiration rate (TR) and hence, conserved soil water (Sinclair 2017). One approach is partial stomatal closure under elevated vapor pressure deficit (VPD), which usually occurs during midday, and the second approach is partial stomatal closure early in the soil drying cycle.

However, partial stomatal closure as a result of either elevated atmospheric VPD or soil drying will impact negatively the immediate CO_2 assimilation rate. Hence, a key issue in deploying these water conservation traits is whether early season loss in photosynthetic activity is more than compensated by late-season growth allowed by conserved soil water. That is, does late-season physiological activity overcome early-season loss in carbon accumulation? Of course, resolution of this question depends on the seasonal environment conditions but there is evidence that seed yield increases can be achieved. In an early simulation study of the VPD-response trait, Sinclair, Hammer, and Van Oosterom (2005) found sorghum [*Sorghum bicolor* (L.) Moench] in Australia with the trait that yield was increased in about 75% of the growing seasons. Commercial cultivars have now been developed in maize (*Zea mays* L.) (Gaffney et al. 2015) and soybean (*Glycine max* Merr. L.) (Carter, Todd, and Gillen 2016) for dryland conditions that express the VPD-response trait.

An expanded role for quinoa (*Chenopodium quinoa* Willd.) in dryland conditions may be especially useful. This species, a pseudo-grain belonging to the Amaranthacean family, was cultivated in the Andean Region for the last 7000 years mainly in the current locations of Peru, Bolivia, Ecuador, Chile, Argentina, and Colombia (Vega-Gálvez et al. 2010). This crop has a high nutritional value with seed protein content between 140 and 180 mg g^{-1} of protein. In addition, the seeds contain all the essential amino acids, trace elements and vitamins, and is gluten free (Gallego Villa et al. 2014). Quinoa has the plasticity to adapt to different environmental conditions such as frost, salinity, and drought; it has been reported to have exceptional physiological adaptations for high water-use efficiency under stomatal closure (Lutz and Bascuñán-Godoy 2017). Also, quinoa is remarkably diverse due to its five major ecotypes linked to the geographical region: Altiplano (Peru and Bolivia), Inter-Andean valleys (Bolivia, Colombia, Ecuador, and Peru), Salt lands (Bolivia, Chile, and Argentina), Yunga (Peru, Bolivia, and Argentina) and Coastal (Chile) (Lutz and Bascuñán-Godoy 2017).

Although there have been studies on quinoa response to soil water deficit, these have been agronomic reporting the impact on yield and harvest index (Bunce 2017) or on plant height, root length, and water-use efficiency (Al-Naggar et al. 2017). No study has explored specific physiological traits such as the water-conservation traits for improving quinoa drought resilience.

Quinoa genotypes expressing water conservation could be especially useful in minimizing crop yield loss in future climates (González et al. 2015). The objectives of this study were to differentiate possible differences among eight quinoa genotypes in expression of the two water-conservation traits: (i) partial stomatal closure under elevated VPD levels and (ii) partial stomatal closure at high soil water content.

Materials and methods

Plant material

A preliminary screen of 16 quinoa genotypes was undertaken at North Carolina State University to assess seeds quality. Eventually, eight quinoa genotypes with consistently good seedling establishment were identified for study: CICA-17, Good Afternoon, French Vanilla, Ollague, Pasankalla, Red Head, Salcedo, Titicaca.

Transpiration response to vapor pressure deficit

Three sets of experiments were performed to measure the response of the eight quinoa genotypes to a range of VPD levels (Table1). Plants were grown in a growth chamber located in the North Carolina State University Phytotron. The first set, which included three genotypes, was sown on 24 February 2020. The second set, which included another three genotypes, was sown on April 30. The final set of two genotypes was sown on April 30.

Plants were grown in polyvinyl chloride pots (10-cm diameter and 33-cm tall), which had a toilet flange attached to the top of each pot to allow easy attachment of a VPD chamber during measurements. The pots were filled

Table 1. Listing of the eight genotypes and three experiments conducted to investigate the response of transpiration rate to VPD.

Experiment	Genotype	Source	Date of sowing	Dates of experiment
Experiment 1	CICA-17	Brigham Young University	24 February 2020	23 March 2020 to 24 March 2020
	Salcedo	Brigham Young University	24 February 2020	23 March 2020 to 24 March 2020
	Titicaca	Brigham Young University	24 February 2020	23 March 2020 to 24 March 2020
Experiment 2	Pasankalla	Brigham Young University	30 April 2020	13 June 2020 to 14 June 2020
	French Vanilla	Commercial genotypes	30 April 2020	13 June 2020 to 14 June 2020
	Good Afternoon	Commercial genotypes	30 April 2020	13 June 2020 to 14 June 2020
Experiment 3	Ollague	Brigham Young University	30 April 2020	16 June 2020 to 17 June 2020
	Red Head	Brigham Young University	14 May 2020	16 June 2020 to 17 June 2020

with a mixture of 50% Sunshine Redi-Earth Pro Growing Mix (Canadian Sphagnum peat moss 50–65%, vermiculite, dolomitic lime, 0.001% silicon dioxide), and 50% cement sand. Three seeds were sown per pot; after a week, each pot was thinned to a single plant. Five replicate pots were established for each genotype.

The plants were grown under 400 μmol CO_2 mol^{-1} and well-watered conditions at 30°C day/26°C night. The growth chamber had a daylength of 16 h; and the lighting source was metal halide bulbs and high-pressure sodium bulbs. Temperature and relative humidity were measured every 5 min using a data logger (Lascar Electronics). Once the plants had developed five to six fully expanded leaves, which occurred about 4 weeks after seedling emergence, four pots with uniform plants of each genotype were transferred to the transpiration measurement facility. The transpiration measurement facility could accommodate only 12 individual VPD chambers, so each set of experiments involved three or two genotypes with four replicates each

The protocol for measurement of transpiration-rate response to VPD was described by Pradhan, Shekoofa, and Sinclair (2018). Plants were transferred to the transpiration measurement facility 1 day before making measurements, and that evening pots were overwatered and allowed to drain overnight. A 340-mm-diameter lid of a food container (Cambro Manufacturing, Huntington Beach, CA) with the center cut out was loosely attached to the toilet flange of each pot. Aluminum foil was placed on the soil surface around the plant to minimize soil evaporation. The following morning a 21-L clear plastic food container (23-cm diameter, 37-cm tall) was attached to the previously installed lid by placing it inverted over the plant. Each VPD chamber was fitted with 12-V computer box fan (Northern Tool and Equipment, Brunsville, MN) to continuously stir the air inside the chamber. In addition, a data logger (Lascar Electronics, Erie, PA) was mounted through the sidewall of each chamber to record chamber relative humidity and temperature every 1 min. The VPD chambers were illuminated with Spyder LED lights (Fluence, Austin, TX) resulting in 550–600 μmol m^{-2} s^{-1}.

Plants were subjected to VPD within three ranges each day during the 2 days of measurement: low (0.5–1.5 kPa), medium (1.5–2.5 kPa), and high (2.5–3.5 kPa). The different levels of VPD were achieved by adjusting the airflow rate through the chambers and/or the source of the air (ambient or dehumidified). The temperature in the facility was set at 32°C and was maintained throughout the measurements.

Chambers were allowed to stabilize for half an hour at each target VPD, and then each chamber was weighed to record initial weight. After 1 h of being exposed to that VPD condition, plants were reweighed to obtain final weight from which transpiration rate was calculated. Measurements were collected from two consecutive days, and on each day, measurements started

within the lowest VPD range, then the medium VPD, and finally the highest VPD. On the second day after completing measurements, plants were harvested, and leaf area was measured using ImageJ software.

All the data of each genotype was subjected to a two-segment linear regression (PRISM 6.0, graphPad Software Inc, San Diego, CA). In addition to the slopes of the two segments, the key output for determination of expression of the limited transpiration trait was identification of a possible breakpoint between the two linear segments. If the slopes of the two segments were not significantly different ($p > 0.05$), a simple linear regression was applied to all the data.

Transpiration response to soil-drying (dry-down)

The soil-drying experiment (dry-down) was conducted in a greenhouse at the NCSU Method Road Greenhouses, Raleigh, NC (35°47′17.4”N, 78° 41′41.5”W) from February to May 2020. Air temperature and humidity of the greenhouse were recorded every 5 min (Model EL-USB-2-LCD, Lascar Electronics). The extremes in temperature were 11°C to 44°C but generally, the temperature was in the range of 23.3 ± 5.9°C.

Quinoa plants were grown in 2-L plastic pots filled with sandy loam topsoil (69% sand, 18% silt, and 13% clay) to within 2 cm of the top of the pots. Three seeds were sown per pot, and after 1 week each pot was thinned to one plant. Ten replicate pots for each of the eight genotypes were sown on 24 February 2020. Plants were grown under well-watered conditions for 45 d, and were watered with a MaxiGro (10-5-14, N-P_2O_5-K_2O, General Hydroponics) nutrient solution once a week.

Transpiration response to soil-drying was measured in a system similar to that described by Shekoofa et al. (2013). Pots were fully watered the evening before the experiment was initiated (7 or 8 April) and allowed to drain overnight. The following morning pots were enclosed in plastic bags and the bag opening was tied around the base of the stem with a twist tie. An 8-mm diam. x 80-mm long plastic tube was inserted between the base of the plant and the plastic bag to facilitate watering of the plants. Each pot was weighed after bagging and the weight was recorded as the initial pot weight. Afterward, pots were weighed daily between 14:00 and 15:00 Eastern Standard Time. Daily transpiration was calculated as the difference in weight of each pot on successive days.

Eight pots per genotype with uniform plants were selected for the experiment. Three pots of each genotype were selected to be well watered (WW), and five were selected for the soil-drying treatment (SS). WW plants were maintained at 150 g below the initial pot weight by watering each day the amount of water lost. SS plants were watered on any day when water loss was greater than

80 g, although this rarely occurred, so the net water loss for that day was only 80 g. The watering of the SS plants prevented rapid dehydration of the soil.

The transpiration data were subjected to two normalizations. The first normalization was carried out to minimize the influence of environmental variations on daily transpiration rate across days. The daily transpiration ratio for each SS pot was calculated between its transpiration rate divided by the average transpiration rate of the three WW pots within each cultivar. The second normalization was done to facilitate analysis of data from all SS plants within a cultivar. The daily transpiration ratio was divided by the average transpiration ratio of that same pot during the first 3 days of the experiment when the soil of the SS plants was still not limiting. This new ratio was identified as normalized transpiration ratio (NTR). By definition, the value of NTR at the beginning of the experiment for each plant was centered on a value of 1.0. The collection of the data continued for a SS plant until NTR ≤ 0.1, which was defined as the endpoint of transpirable soil water.

The total transpirable soil water available to the plant in each pot was calculated as the difference between the initial and endpoint weight of the pot. To track soil drying, fraction of transpirable soil water (FTSW) was determined on each day for each pot. FTSW was calculated as the difference between daily and endpoint weight divided by the initial and endpoint weight of the pot.

The relationship between NTR and FTSW was analyzed using a two linear-segment regression analysis using GraphPad Prism version 5 (GraphPad Software, 2007). This regression analysis generated the FTSW threshold for the initiation in the decline in NTR.

Results

Transpiration response to VPD

The response of TR to VPD was well described by either the two-segment response (illustrated in Figure 1a) or the linear response (illustrated in Figure 1b). The R^2 for the regressions of the eight genotypes ranged from 0.76 to 0.95 (Table 2). Six genotypes identified as expressing the two-segment linear response with the breakpoint (BP) between segments had BP ranging from 1.98 kPa for Red Head to 2.40 kPa for Pasankalla (Figure 1a). The narrow range of BP among these six genotypes did not result in the identification of differences in BP. Two genotypes, Titicaca (Figure 1b) and French Vanilla, did not express any VPD threshold and were represented by a linear response.

Transpiration response to soil-drying (dry-down)

As expected, the plot of NTR vs. FTSW for all eight genotypes were all represented by the linear, two-segmented model with R^2 greater than 0.91

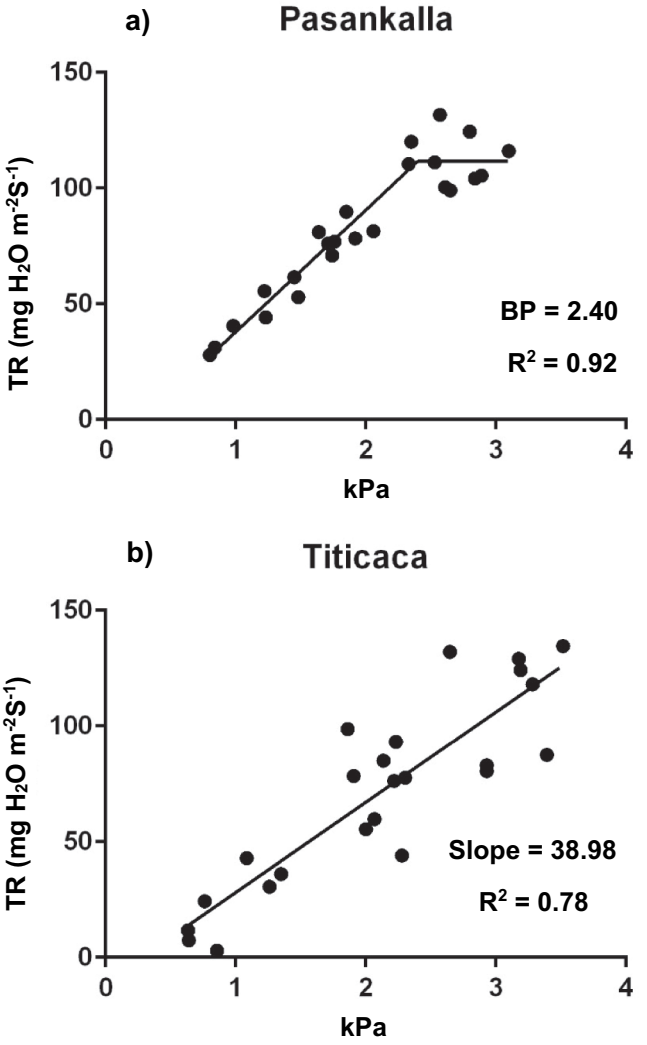

Figure 1. Transpiration rate (TR) response to different levels of vapor pressure deficit (kPa) for cultivars Pasankalla (a) and Titicaca (b) at 32ºC. Results illustrate the two-segment linear response (a) and the single linear response (b).

in all cases (Table 3). The initial phase of soil drying was represented by a plateau followed by a linear decrease below a FTSW threshold. Figure 2 illustrates the results of dry-down experiment for Titicaca and French Vanilla genotypes. The key result for evaluating water conservation was the breakpoint when the decrease in NTR was initiated. Titicaca had the lowest FTSW breakpoint at 0.24 and French Vanilla had the highest FTSW breakpoint at 0.42. The breakpoints of these two genotypes were different as evidenced by no overlap in their 95% confidence intervals (Table 3).

Table 2. Regression results of vapor pressure deficit (VPD) experiment for six quinoa (Chenopodium quinoa Willd.) genotypes: number of values (n), slope 1, Standard Error (SE), breakpoint (BP), 95% confidence interval, slope 2, X–intercept and R^2 that fit a two-segmented model. The results of the linear regression for two genotypes are also presented.

Genotypes	N	Slope 1 ± SE	BP ± SE	95% Confidence interval of BP	Slope 2 ± SE	X–intercept	R^2
Red Head	24	67.98 ± 17.09	1.843 a ± 0.646	0.495 to 3.191	35.55 ± 15.16	−11.520	0.793
Salcedo	21	50.42 ± 15.56	1.903 a ± 0.617	0.601 to 3.205	24.04 ± 6.15	−20.340	0.912
CICA-17	24	48.90 ± 16.73	1.922 a ± 0.796	0.262 to 3.581	26.72 ± 5.65	−23.930	0.916
Ollague	24	64.22 ± 10.92	2.026 a ± 0.322	1.354 to 2.699	26.93 ± 8.855	−13.390	0.881
Good afternoon	24	56.93 ± 5.73	2.346 a ± 0.144	2.046 to 2.645	−6.82 ± 14.84	−8.079	0.947
Pasankalla	24	52.71 ± 4.93	2.400 a ± 0.159	2.068 to 2.731	−0.16 ± 17.84	−14.860	0.921
Titicaca	24	38.98 ± 4.41	linear	-	-	0.279	0.780
French Vanilla	23	40.77 ± 5.06	linear	-	-	0.038	0.756

Table 3. Fraction transpirable soil water (FTSW) of breakpoint (BP) or initiation of decline in normalized ratio (NTR) as determined by two-segment, linear regression analysis. Those thresholds identified with different letters were significantly different between genotypes. Also, presented are the 95% confidence intervals for the BP and R^2 from the regression analysis.

Genotypes	n	Slope 1 ± SE	BP ± SE	Confidence interval of BP	X–intercept	R^2
Titicaca	60	3.96 ± 0.27	0.238 a ± 0.014	0.211 to 0.266	0.019	0.941
Pasankalla	70	3.69 ± 0.15	0.266 ab ± 0.009	0.247 to 0.284	0.038	0.967
CICA-17	69	3.47 ± 0.15	0.274 ab ± 0.010	0.254 to 0.294	0.047	0.971
Red Head	67	3.58 ± 0.21	0.276 ab ± 0.014	0.248 to 0.304	0.019	0.945
Good afternoon	102	3.64 ± 0.24	0.281 ab ± 0.015	0.251 to 0.312	0.027	0.907
Ollague	88	3.30 ± 0.20	0.296 ab ± 0.015	0.266 to 0.327	0.019	0.929
Salcedo	120	3.13 ± 0.11	0.300 b ± 0.009	0.282 to 0.317	0.031	0.959
French Vanilla	91	2.13 ± 0.11	0.418 c ± 0.019	0.380 to 0.456	0.075	0.929

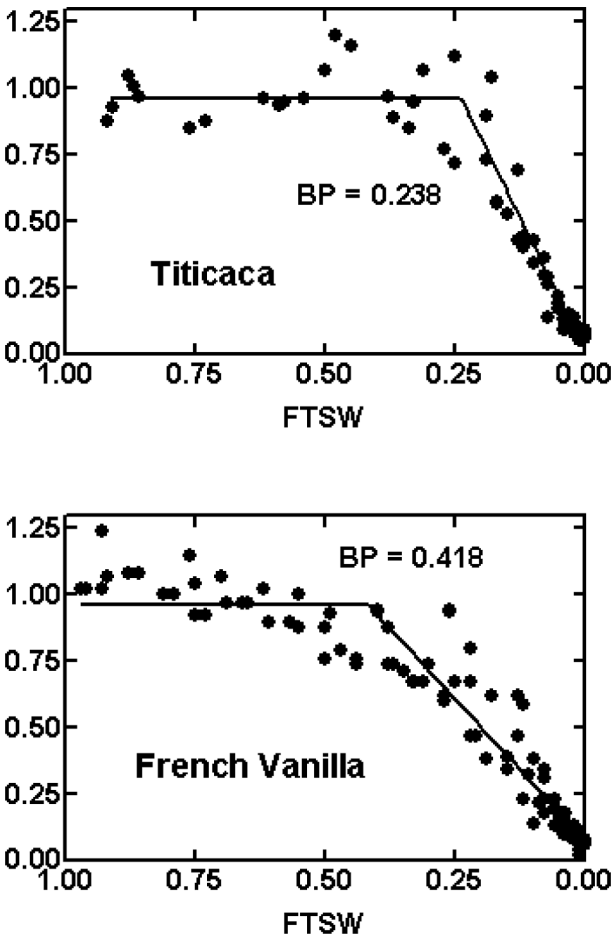

Figure 2. Graphs of normalized transpiration ratio (NTR) vs. fraction transpirable soil water (FTSW) for cultivars Titicaca and French Vanilla. The data were described using two-segmented regression with a breakpoint (BP) for the decline in NTR with further soil drying.

Discussion

Drought is one of the main limitations on crop yield threatening world food security (Farooq et al. 2009). It has been proposed to develop two water-conservation traits that save water in the early stages of crop development so eventually in the seed-filling stage there will be more water to sustain physiological activity during reproductive development. The two plant traits to achieve water conservation examined in quinoa in this study was partial stomatal closure under elevated VPD levels and at early stages of soil drying. The objective of this study were to identify possible genetic diversity among quinoa genotypes for the two water-conservation traits.

Six of eight quinoa cultivars genotypes showed the water conservation trait of a BP in TR with increasing VPD (Table 2). Among these six cultivars, none of the cultivars proved to be superior in the water-conservation trait with all having a BP in the range of 2.0 to 2.4 kPa. However, genotypes with even lower BP might be identified in the quinoa germplasm since genotypes have been identified with BP as low as 1.4 kPa in soybean (Devi et al. 2014) and 1.6 kPa in sorghum (Gholipoor et al. 2010)

There was greater divergence among the quinoa genotypes in the BP in TR with soil drying. The highest BP was at a FTSW of 0.42 for French Vanilla. This result for French Vanilla was somewhat unexpected since French Vanilla was found to have a linear response to increasing VPD. If plant hydraulic conductance limited TR at high FTSW, hypothetically it would be expected that the hydraulic limitation would also be imposed at high VPD. One possibility to explain this apparent contradiction is that there may be two sites of limiting hydraulic conductance that differentially influence water flow in the plant. Water uptake by the plant associated with soil drying might be closely aligned with possible hydraulic limitations in the roots. That is, French Vanilla might have a low root hydraulic conductance so that its BP was expressed at a high FTSW. On the other hand, response to VPD at the leaf level might be associated with hydraulic flow in the leaves. A high hydraulic conductance in the leaves of French Vanilla might impose no limitation on TR with increasing VPD, i.e. a linear VPD response. Of course, resolution of such hypotheses requires further challenging measurements of hydraulic conductance in specific tissues.

The results of this study offer initial information about genetic differences related to the water conservation traits in eight quinoa genotypes. These results identify the genotypes that would be of special interest in field evaluations under water-limited conditions. Clearly, French Vanilla is a candidate for study due to its desired response of limiting water use at high soil FTSW. Several genotypes could be included for a low BP in their response to increasing VPD. Closed canopies of these genotypes could be compared by screening for the onset of wilting once water-limited conditions

are allowed to develop. Those lines that are the last to show wilting are strong candidates for expression of the water-conservation trait in the field. This field evaluation protocol could also be applied to additional genotypes as an initial screen to identify additional quinoa germplasm as candidates expressing one or both of the water conservation traits.

Acknowledgments

The authors gratefully acknowledge the support from the National Agricultural Innovation Program (PNIA) from Peru and Crop and Soils Sciences Department, North Carolina State University (NCSU) for making this collaborative work possible. Also, the authors acknowledge the seed provided by Rick Jellen, Plant & Wildlife Sciences, Brigham Young University, UT.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Peru National Agricultural Innovation Program (PNIA) .

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