

Phenotypic Diversity for Root Traits and Identification of Superior Germplasm for Root Breeding in Watermelon

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Abstract. Root traits are an important component for productive plant performance. Roots offer immediate absorptive surfaces for water and nutrient acquisition and are thus critical to crop growth and response to biotic and abiotic stresses. In addition, roots can provide the first line of defense against soilborne pathogens. Watermelon crop performance is often challenged by inclement weather and environmental factors. A resilient root system can support the watermelon crop's performance across a diverse range of production conditions. In this study, 335 four-day-old watermelon (*Citrullus* spp.) seedlings were evaluated for total root length, average root diameter, total root surface area, and total root volume. Total root length varied from 8.78 to 181 cm (20.6-fold variation), total surface area varied from 2 to 35.5 cm², and average root diameter and total root volume had an 8- and 29.5-fold variation, respectively. Genotypes PI 195927 (*Citrullus colocynthis*) and PI 674448 (*Citrullus amarus*) had the largest total root length values. Accessions PI 674448 and PI 494817 (*C. amarus*) had the largest total root surface area means. Watermelon cultivars (*Citrullus lanatus*) had a relatively smaller root system and significantly fewer fibrous roots when compared with the roots of the other *Citrullus* spp. Positive genetic correlations were identified among total root length, total root surface area, and total root volume. This genetic information will be useful in future breeding efforts to select for multiple root architecture traits in watermelon. Germplasm identified in this study that exhibit superior root traits can be used as parental choices to improve watermelon for root traits.

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Sweet-fleshed (dessert) watermelon (*Citrullus lanatus*) is a lucrative vegetable crop for growers and is consumed by millions of people around the world (FAOSTAT, <http://www.fao.org/faostat/en/>). Cultivated watermelon is related to five other species in the genus *Citrullus*, including *C. amarus* (citron), *Citrullus mucospermus* (egusi watermelon), *C. colocynthis* (desert watermelon), *Citrullus rehmanii*, *Citrullus ecirrhosus*, and *Citrullus naudinianus* (Chomicki and Renner, 2015; Jarret et al., 1997). *C. mucospermus* is native to Western Africa and *C. amarus* originates from Southern Africa. Several of the related species (including *C. amarus*, *C. mucospermus*, *C. colocynthis*, and *C.*

ecirrhosus) can be intercrossed with varying degrees of difficulty with each other and with *C. lanatus* (Jarret et al., 2017). *Citrullus* species contain alleles underlying adaptive (fitness) traits that have been inadvertently lost in the cultivated varieties of *C. lanatus* as a result of repeated cycles of breeding, selection, and evolution (Jarret et al., 2017; Levi et al., 2001).

Breeding and improvement of *C. lanatus* in the past has historically been primarily focused on improving yield and fruit quality traits. These narrowly focused breeding goals have resulted in a significant genetic bottleneck as evidenced by the limited genetic diversity present in the current commercially grown watermelon varieties (Levi et al., 2001). However, the cultivated sweet watermelon has a wide range of geographical distribution and production, which exposes the crop to challenges related to changing weather patterns and climate (Paris, 2015).

Watermelon crop performance is affected by changing weather conditions. The fruit is composed predominantly of water (>90%), therefore water and heat stress can significantly affect fruit yield and quality (Hatfield et al., 2008). Limited soil moisture and elevated temperatures during the growing season can result in inadequate flowering, as well as inability to fend off pests and pathogens, resulting in a marked loss in yield (Krug, 1997; Rubatzky and Yamaguchi, 1997). Given the high moisture content in watermelon, it is vital to identify and develop ideotypes with improved root traits and water-use efficiency.

With the increasing global population and the dwindling availability of arable land, it is critical to develop plant germplasm that can perform optimally under these new crop production constraints (Gilliham et al., 2017). Fluctuating amounts of rainfall and rising temperatures across crop production zones highlight the urgency to develop plant materials that are resilient to these erratic weather patterns (Trenberth et al., 2014).

The root system is the major plant organ involved in water and nutrient acquisition and uptake (Zhu et al., 2011). Root architecture and capacity (number of roots, root volume, length, and surface area) play an important role in water and nutrient acquisition, and in minimizing the negative effects of water and other environmental stresses (Koevoets et al., 2016; Lamaoui et al., 2018). Developing varieties with an improved root system (i.e., that is more robust and efficient) is critical for enhancing plant survival and performance of the watermelon crop during periods of reduced water availability. Identification and quantification of root traits across *Citrullus* spp. can help identify superior genotypes useful for the improvement of watermelon cultivars.

Water-use efficiency, which refers to the ability of plants to convert absorbed water into economic yield, is an important trait to

incorporate into watermelon breeding programs and cultivar development pipelines (Fahad et al., 2017). Development of varieties with an improved root system (e.g., longer roots, more root hairs) is critical for enhancing survival and performance of watermelon plants during periods of reduced water availability. Identification of watermelon genotypes with a robust root network that can potentially perform well under changing climate conditions will be useful in maintaining yields that are profitable to commercial growers.

A resilient root architecture could also be important for protection of the watermelon crop from root pathogens, such as *Verticillium*, *Fusarium*, and root-knot nematodes (Wimer et al., 2015). Watermelon production

can be severely affected by fusarium wilt, whereas genotypes with a branched root system and rich with secondary fibrous roots have an advantage in their ability to minimize or quickly recover from the impact of pathogen damage. Having a robust root system can reduce the damage from soil pathogens, thus allowing the affected plant to grow optimally with minimal reductions in crop yield. Moreover, grafted plants also tend to have an improved performance under both drought and salt stress growth conditions (Yanyan et al., 2018). A survey of root traits across *Citrullus* spp. can help identify genotypes that are uniquely qualified to better tolerate biotic and abiotic stressors.

The exclusion of methyl bromide fumigants from the market in accordance with the

Montreal Protocol on Substances that Deplete the Ozone Layer and the U.S. Clean Air Act (U.S. Environmental Protection Agency, 2012) led to the exploration for new alternatives for the control of soilborne pathogens. One alternative is use of rootstocks resistant to soilborne diseases and nematodes. The use of grafting in watermelon crop production has gained increased popularity over the past decade. The use of disease and pest-susceptible watermelon scions grafted to a resistant rootstock is being used to address the growing burden of soilborne pathogens and the discontinuation of soil fumigants (Davis et al., 2008). Also, it is becoming economically feasible to develop and grow grafted watermelon plants, given the high value of the crops and the potential improvement for increased crop performance in the event of attack from soil pathogens (Keinath and Hassell, 2014; Thies et al., 2010). Successful watermelon grafting requires rootstocks with a robust root system compatible with the selected scions. Previous studies showed that *Citrullus amarus* accessions have a formidable root system resistant to soilborne diseases and root-knot nematodes, and these accessions are likely candidates as rootstocks for grafted watermelon (Levi

Table 1. Phenotypic summary statistics for mean, SD, minimum, and maximum, and fold variation values for four root traits for 335 *Citrullus* germplasm accessions evaluated under greenhouse conditions.

Traits	Mean (\pm SD)	Min.	Max.	Fold variation
TRL (cm)	62.41 (27.69)	8.78	181.02	20.6
TSA (cm ²)	10.31 (5.03)	2.04	35.53	17.4
ARD (mm)	0.54 (0.13)	0.27	2.15	8.0
TRV (cm ³)	0.14 (0.08)	0.02	0.59	29.5

\pm SD refers to the standard deviation of the trait means; fold variation refers to the maximum (Max.) relative to the minimum (Min.) values for each trait. TRL = total root length; TSA = total root surface area; ARD = average root diameter; TRV = total root volume.

Table 2. List of some of the superior genotypes from the 335 *Citrullus* spp. accessions evaluated for root morphological traits under greenhouse conditions.

Accession	Species	Country of origin	Root traits			
			TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 195927	CC	Ethiopia	181.02	29.63	0.53	0.39
PI 674448	CA	Russia	171.58	35.53	0.67	0.59
PI 494528	CM	Nigeria	158.75	28.53	0.57	0.42
PI 306782	CM	Nigeria	151.36	21.83	0.46	0.26
PI 494817	CA	Zambia	145.59	30.19	0.66	0.50
PI 186490	CM	Nigeria	139.73	26.47	0.61	0.40
PI 482338	CA	Zimbabwe	139.38	21.56	0.47	0.27
PI 635691	CL	United States	137.20	19.28	0.45	0.22
PI 254744	CL	Senegal	127.53	19.97	0.50	0.25
PI 482326	CA	Zimbabwe	126.93	24.23	0.61	0.38
PI 560004	CM	Nigeria	124.60	23.69	0.61	0.36
PI 482299	CA	Zimbabwe	124.50	24.95	0.64	0.40
PI 490375	CL	Mali	123.16	17.28	0.45	0.20
PI 482303	CA	Zimbabwe	122.91	20.42	0.53	0.28
PI 674448	CA	Russia	122.68	23.54	0.61	0.36
PI 482259	CA	Zimbabwe	120.29	21.65	0.57	0.31
PI 560002	CM	Nigeria	120.03	23.57	0.63	0.37
PI 482302	CA	Zimbabwe	117.86	15.84	0.48	0.18
PI 494531	CM	Nigeria	116.74	19.06	0.52	0.25
PI 512398	CL	Spain	115.10	17.72	0.49	0.22
PI 482246	CA	Zimbabwe	114.97	15.44	0.43	0.17
PI 500319	CL	Zambia	114.72	19.48	0.55	0.27
PI 482315	CA	Zimbabwe	112.30	20.67	0.59	0.31
PI 270564	CA	South Africa	111.51	15.41	0.45	0.18
PI 482318	CA	Zimbabwe	110.72	19.11	0.55	0.27
PI 482286	CA	Zimbabwe	108.82	21.09	0.62	0.33
PI 482309	CA	Zimbabwe	106.34	18.32	0.55	0.25
PI 482261	CA	Zimbabwe	103.32	12.53	0.39	0.12
PI 212094	CL	Afghanistan	100.97	13.51	0.51	0.15
PI 635631	CL	United States	100.81	17.01	0.54	0.23
PI 379231	CL	Macedonia	21.07	4.78	0.73	0.09
PI 211851	CL	Iran	19.53	2.75	0.45	0.03
PI 635614	CL	United States	18.25	2.99	0.59	0.04
PI 635713	CL	United States	16.05	3.81	0.82	0.08
Allsweet	CL	United States	15.18	2.56	0.55	0.04
PI 635596	CL	United States	9.36	2.04	0.74	0.04
PI 277977	CL	Turkey	8.78	2.76	1.02	0.07
LSD ($\alpha = 0.05$)			24.38	4.19	0.29	0.09

TRL = total root length; TSA = total root surface area; ARD = average root diameter; TRV = total root volume; CC = *Citrullus colocynthis*; CA = *Citrullus amarus*; CM = *Citrullus mucospermus*; CL = *Citrullus lunatus*; LSD = least significant difference.

et al., 2013; Thies and Levi, 2007; Thies et al., 2010; Wechter et al., 2012).

Evaluation of root traits across *Citrullus* spp. is a means to identify superior genotypes useful for the improvement and development of modern watermelon cultivars. Hence, the primary objective of this study was to determine the phenotypic diversity present in the U.S. Department of Agriculture (USDA) *Citrullus* spp. germplasm collection for root traits likely to contribute to enhanced water and nutrient uptake and identify superior genotypes that can be deployed to improve the watermelon crop's ability to remain productive during periods of water shortage and environmental stress. In addition, we sought to determine the genetic relationship among these various root traits across the *Citrullus* spp. germplasm.

Materials and Methods

Plant material and experimental design.

A total of 335 *Citrullus* spp. accessions were evaluated for root traits in this study. The seeds of all accessions were originally obtained from the USDA genebank in Griffin, GA. Individual plants were then self-pollinated for one generation to reduce heterozygosity, which is common in cross-pollinating plant species. The study included 105 *C. amarus*, 14 *C. colocynthis*, 184 *C. lanatus*, and 32 *C. mucospermus* genebank accessions. Most of the genotypes (185) were collected/received from Africa. There were 71 genotypes from Asia, 29 from Europe, and 43 from North America, with the remainder from Central America, South America, and Oceania (Supplemental Table 1). The experiments were performed in the greenhouse as a completely randomized design with four replications.

Plant growth conditions and phenotyping of the root traits. Seeds were sown individually into an 8-cm square pots filled with a mixture of 90% Sungro metro mix and 10% sand (Agawam, MA) and watered as needed to ensure optimal crop growth in the greenhouse. Seedlings were harvested to assay for root traits following germination, on opening of the cotyledon leaves but before the emergence of the first true leaf. In watermelon production, rootstocks are ready for grafting at 7 to 10 d after seed sowing, hence why we used the cotyledon (before emergence of the first true leaf) developmental stage as the time point for root sample collection (Hassell et al., 2008; Mohamed et al., 2014). Samples were harvested in the greenhouse by gently removing them from the pots to minimize root breakage/loss and then gently soaked in water and cleaned to remove any soil from the root surface.

Once harvested and cleaned, the root samples were placed in Ziploc bags with a moist paper towel and kept in a refrigerator (4 °C) for subsequent analysis. The moist towel was used to prevent samples from drying out during the short-term storage. Samples were kept at 4 °C for no longer than 3 d before being evaluated for the root traits.

The roots for each genotype were removed from the Ziploc bags and floated in ≈1 cm of water in a 20 × 25-cm transparent plexiglass tray during image scans. Submersion (floatation) of the roots in water promoted root separation and thus facilitated the accurate scanning of the roots. While in the tray, the roots were scanned on a desk Epson Perfection V800 Photo scanner (Epson America Inc., Long Beach, CA) calibrated with gray-scale scanning and 600-dpi resolution (Costa, et al., 2001). The root morphology traits measured included total root length (TRL), total root surface area (TSA), total root volume (TRV), and average root diameter (ARD). The root phenotypes were quantified via analysis of the scanned images using an established WinRHIZO Pro 2015a Regent instrument software (Regent Instruments Inc., Quebec, Ontario, Canada) previously described by Arsenault et al. (1995). The WinRHIZO software also generated values of TRL, TSA, and TRV for each of the root diameter size categories (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, and >2.5 mm). Most studies delineate fine/secondary roots and

root hairs as those with root diameters less than 0.5 mm (Liu et al., 2018; Polania et al., 2017).

Statistical data analysis. The phenotypic data were analyzed using PROC MIXED in SAS version 9.4 (SAS Institute, 2013) following the statistical model: $Y_{ij} = \mu + G_i + R_j + \epsilon_{ij}$. In this statistical model, Y_{ij} is the measured phenotypic value such as TRL for the i^{th} genotype in the j^{th} replication; μ is the grand mean; G_i is the fixed variable effect of the i^{th} genotype; R_j is the random variable effect of the j^{th} replication; and ϵ_{ij} is the residual error term assumed to be normally distributed with mean = 0. To compare differences among genotypes, mean separation was performed using Fisher's protected least significant difference in SAS version 9.4 (SAS Institute, 2013). Genotypic correlations among the root traits were computed using multivariate restricted maximum likelihood estimation with SAS PROC MIXED as described in Holland (2006). To visually assess trait distribution/variability patterns within the traits data, hist() and boxplot() functions were used to create histograms and boxplots respectively

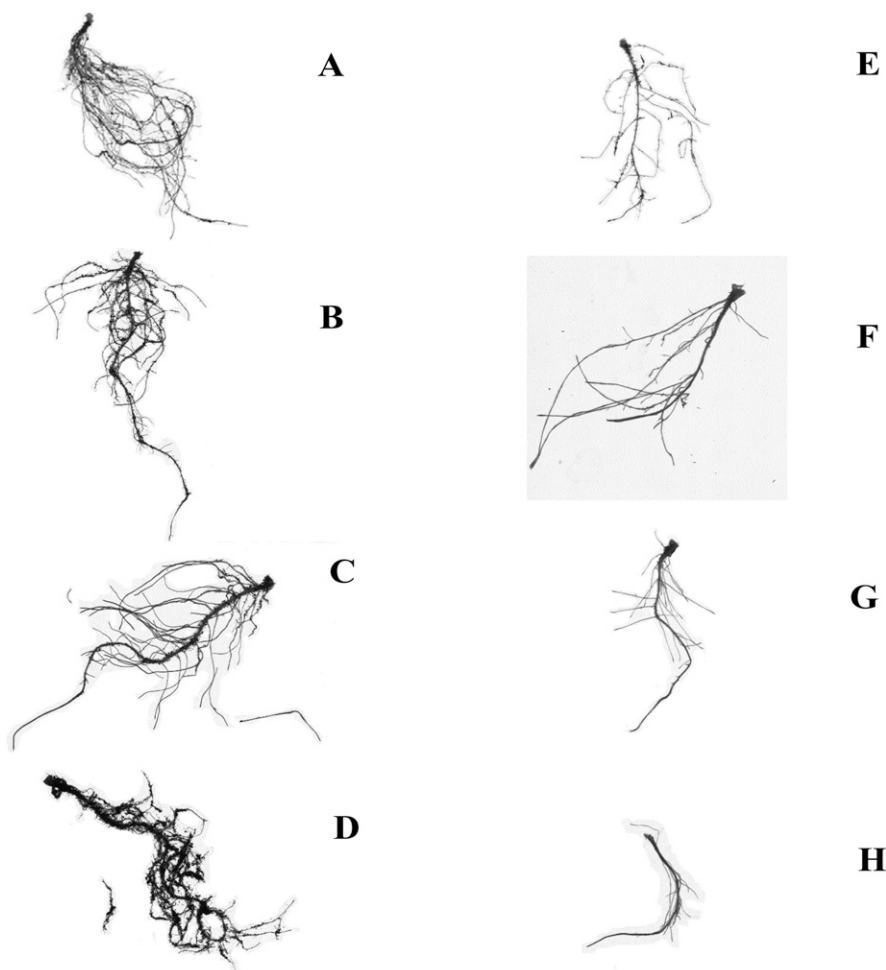


Fig. 1. Images displaying variability in root traits of six *Citrullus* accessions with genotypes A–D exhibiting superior root trait performance, whereas E–H had low root trait means for total root length and total root surface area. A is PI 195927; B is PI 674448; C is PI 494528; D is 494817; E is PI 296341; F is PI 296337; G is PI 635654; and H is Allsweet. Genotypes A and C are *Citrullus colocynthis* and *Citrullus mucospermus*, respectively; genotypes B, D, E, and F are *Citrullus amarus*; G and H are *Citrullus lanatus*.

in the R programming language (R Core Team, 2018).

Results

Genotype effects and descriptive summary statistics. The analysis of variance in SAS showed that there was a significant effect of genotype on all of the evaluated root traits ($P = 0.0001$). TRL ranged 8.78 to 181.02 cm with a 20.6-fold variation. TSA varied from 2.04 to 35.53 cm² with a 17.4-fold change.

ARD ranged from 0.27 to 2.15 mm with an 8-fold variation, and TRV ranged from 0.02 to 0.59 cm³ with a fold change of 29.5 (Table 1).

Genotypes PI 195927 (*C. colocynthis*) collected in Ethiopia, PI 674448 (*C. amarus*) collected in Russia, and PIs 494528 and 306782 (both *C. mucospermus* collected in Nigeria) had the highest TRL values (Table 2; Fig. 1). Genotypes PI 674448 and PI 494817 both *C. amarus* collected in Russia and Zambia, respectively, had the largest

TSA values (Table 2; Supplemental Table 1; Fig. 1).

Most of the accessions with the greatest TRL and TSA values belonged to *C. amarus* (citron) and *C. mucospermus* (egusi) watermelon types (Table 2; Supplemental Table 1). Most of the genotypes with the smallest TRL values belonged to *C. lanatus*, many of which are heirloom cultivars developed in the United States (Supplemental Table 1). *Citrullus lanatus* genotypes PI 269677 and PI 277977 collected in Belize

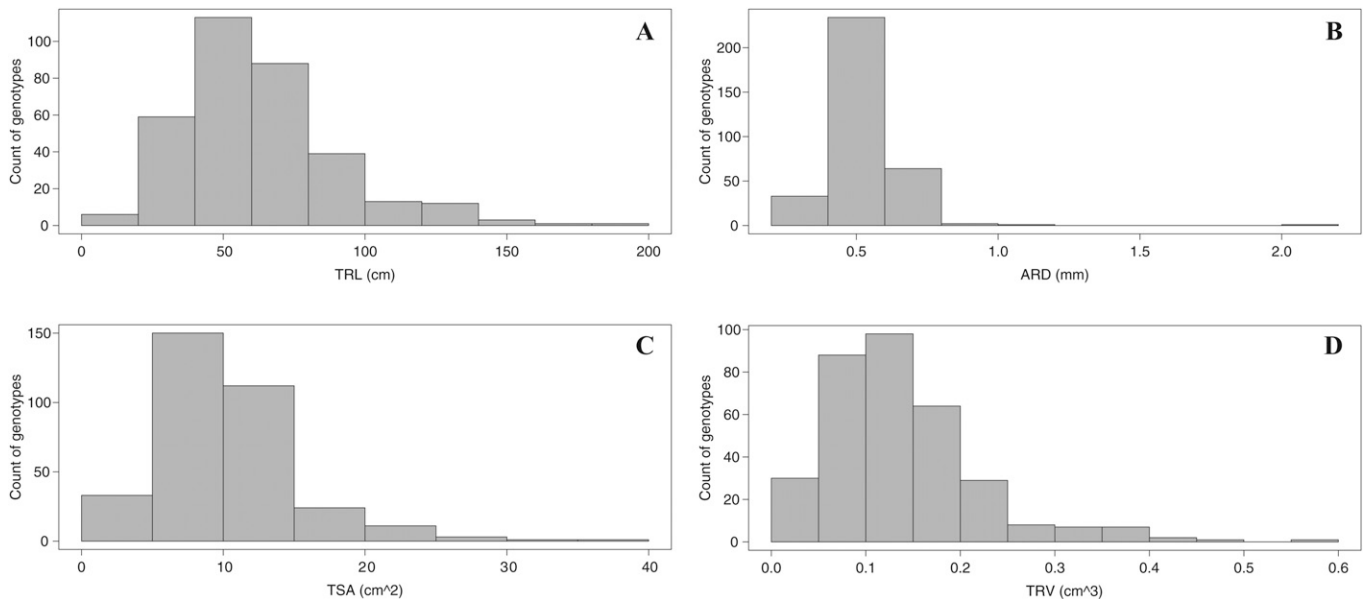


Fig. 2. Histograms showing the distributions of four root morphological traits [(A) total root length (TRL), (B) average root diameter (ARD), (C) total root surface area (TSA), and (D) total root volume (TRV)] across 335 *Citrullus* spp. genbank accessions.

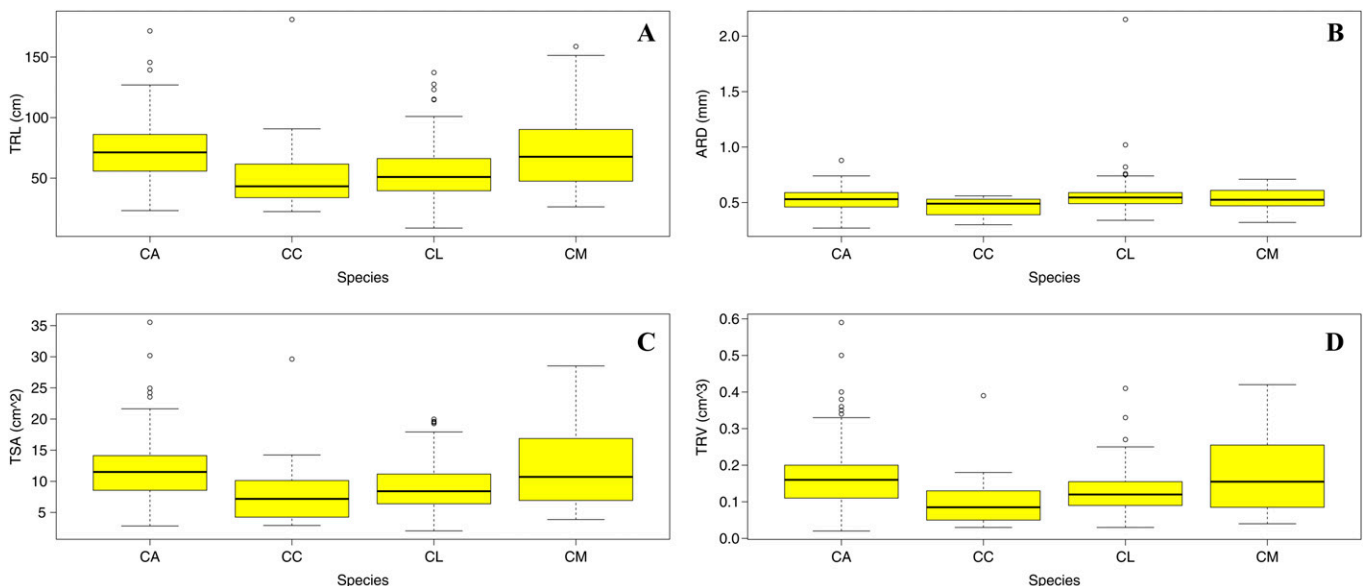


Fig. 3. Boxplot showing the variability of four root morphological traits [(A) total root length (TRL), (B) average root diameter (ARD), (C) total root surface area (TSA), and (D) total root volume (TRV)] across four species of *Citrullus* as evaluated under greenhouse conditions. CA = *Citrullus amarus*; CC = *Citrullus colocynthis*; CL = *Citrullus lanatus*; CM = *Citrullus mucospermus*.

and Turkey, respectively, had the largest ARD values. Genotypes belonging to *C. amarus* and *C. mucospermus* had the smallest ARD (Supplemental Table 1).

Genotypes PI 674448 and PI 494817 collected from Russia and Zambia, respectively, were both *C. amarus* and had the largest TRV values (Supplemental Table 1). Most of the *C. lanatus* genotypes, including PI 379231 (Mrezasto Zelana from Macedonia), PI 635614 (U.S. cv Klondike Striped Blue Ribbon), PI 635713 (Callhoun Gray), PI 635598 (Golden Midget), and Allsweet had smaller TRV values (Table 2; Supplemental Table 1). The histograms for the root traits exhibited continuous distributions (Fig. 2). Variability for TRL, TSA, and TRV was largest within the *C. amarus*, *C. colocynthis*, and *C. mucospermus* accessions, whereas variability in ARD values was largest across the *C. lanatus* accessions (Fig. 3).

Genotypes PI 195927 (*C. colocynthis*) and PI 306782 (*C. mucospermus*) from Ethiopia and Nigeria, respectively, had larger TRL values within the 0- to 0.5-mm-diameter size categories, implying presence of more fine roots and root hairs for these accessions (Table 3). It is worth noting that most of the cultivated sweet watermelon (*C. lanatus*) genotypes had lower TRL values within the 0.1- to 0.5-mm-diameter size class (Table 3; Supplemental Table 2).

These cultivated type genotypes with small TRL scores were from Turkey, Mace-

donia, and the United States. TRL exhibited more variability within the 0- to 0.5-mm-diameter size category compared with the other diameter size classes across the 335 *Citrullus* spp. accessions (Fig. 4). Wide variability for TSA was observed within the 0- to 0.5- and 0.5- to 1.0-mm root diameter classes, whereas TRV was most variable within the 0.5- to 1.0-, 1.0- to 1.5-, 1.5- to 2.0-, and 2.0- to 2.5-mm-diameter sizes (Fig. 4).

Trait correlations. Genotypic correlations among root traits ranged from -0.08 to 0.97 (Table 4). TRL was positively correlated with TSA ($r = 0.95$; $P < 0.0001$) and TRV ($r = 0.85$; $P < 0.0001$) but negatively correlated with ARD ($r = -0.08$; $P = 0.4186$). TSA was positively correlated with both ARD ($r = 0.20$; $P = 0.0380$) and TRV ($r = 0.97$; $P < 0.0001$). ARD was also positively correlated with TRV ($r = 0.39$; $P = 0.0005$) (Table 4). Overall, pairwise genetic correlation between TRL and TSA or TRV showed strong positive correlations ($r \geq 0.79$), whereas the pairwise correlations between ARD and TSA or ARD with TRV showed low positive correlations ($r \leq 0.44$), as shown in Table 4.

Discussion

Variability in root traits is critical in efforts to genetically improve crop performance and adaptation to varying production conditions, including water-limiting stress via modifications to plant root architecture

(Lynch, 2007). Development of crops with robust root phenotypes/architecture is a current goal for numerous crop breeding programs (Comas et al., 2013). Characterization of the native diversity in root traits within and among *Citrullus* species provides a foundation for selection of parental lines that can be used in breeding watermelon for enhanced nutrient and water acquisition, as well as identification of genotypes that might be well suited for use as rootstocks.

Many of the cultivated watermelon (*C. lanatus*) cultivars evaluated in this study had a relatively small root system when compared with accessions of *C. mucospermus* or *C. amarus* (Table 2; Figs. 1 and 3; Supplemental Table 1). This is likely due to a selection sweep resulting from many years of breeding watermelon for desirable fruit qualities, as well as the transition from the cultivation of watermelon genotypes originating from the arid regions in Northern Africa where there are limited water resources to more tropical or humid regions of the world with more abundant water resources and/or irrigation (Jensen et al., 2011; Paris, 2015).

The data reported here indicate that there is a wide variation in overall root system size (TRL and TSA) among accessions of *C. colocynthis* (Fig. 3). This might be expected based on the documented genetic diversity that is known to exist among *C. colocynthis* accessions collected in the desert regions of Northern Africa, the Middle East, and Asia

Table 3. List of some of the superior genotypes from the 335 *Citrullus* spp. accessions for root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) evaluated under greenhouse conditions.

Accession	Species	Country of origin	Root traits		
			TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 195927	CC	Ethiopia	127.30	8.95	0.07
PI 306782	CM	Nigeria	108.43	7.70	0.06
PI 635691	CL	United States	104.34	7.21	0.05
PI 482338	CA	Zimbabwe	101.21	7.81	0.06
PI 494528	CM	Nigeria	100.85	8.90	0.08
PI 674448	CA	Russia	99.73	7.70	0.07
PI 494817	CA	Zambia	94.43	6.37	0.05
PI 490375	CL	Mali	93.40	7.35	0.06
PI 482302	CA	Zimbabwe	93.18	7.16	0.05
PI 254744	CL	Senegal	93.10	6.99	0.06
PI 482303	CA	Zimbabwe	89.58	7.24	0.06
PI 482246	CA	Zimbabwe	88.67	6.27	0.05
PI 186490	CM	Nigeria	86.61	6.44	0.05
PI 482261	CA	Zimbabwe	85.40	7.01	0.06
PI 512398	CL	Spain	85.39	7.36	0.07
PI 270564	CA	South Africa	85.29	7.28	0.06
PI 494531	CM	Nigeria	83.37	6.92	0.06
PI 482326	CA	Zimbabwe	82.11	5.79	0.05
PI 500319	CL	Zambia	81.38	7.07	0.06
PI 212094	CL	Afghanistan	81.32	6.66	0.05
PI 255136	CA	South Africa	80.69	5.76	0.04
PI 560004	CM	Nigeria	80.49	8.14	0.07
PI 601308	CL	United States	15.88	1.01	0.01
PI 211851	CL	Iran	15.32	1.30	0.01
PI 276445	CL	Jordan	15.19	1.39	0.01
PI 635614	CL	United States	12.29	0.96	0.01
Allsweet	CL	United States	10.16	0.83	0.01
PI 379231	CL	Macedonia	9.36	0.98	0.01
PI 635713	CL	United States	8.00	0.65	0.01
PI 635596	CL	United States	6.16	0.54	0.01
PI 277977	CL	Turkey	4.57	0.42	0.01
LSD ($\alpha = 0.05$)			19.65	1.61	0.01

TRL = total root length; TSA = total root surface area; TRV = total root volume; CC = *Citrullus colocynthis*; CA = *Citrullus amarus*; CM = *Citrullus mucospermus*; CL = *Citrullus lanatus*; LSD = least significant difference.

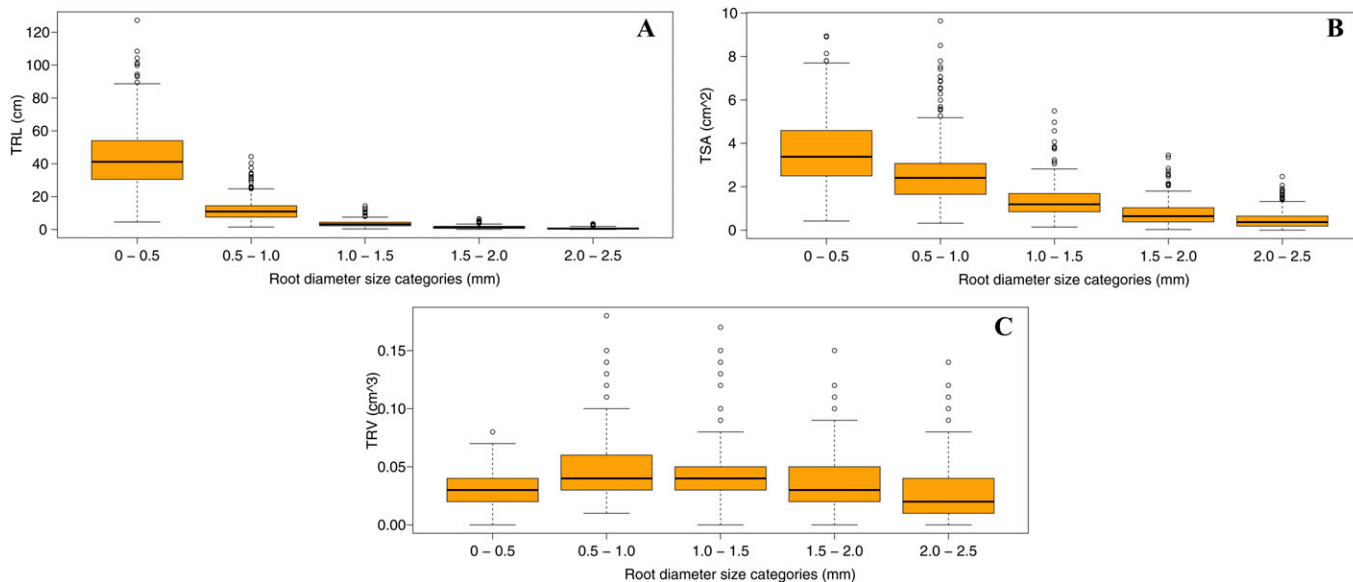


Fig. 4. Boxplot showing the variability of three root traits [(A) total root length (TRL), (B) total root surface area (TSA), and (C) total root volume (TRV)] within five root diameter classes across the 335 *Citrullus* genebank accessions evaluated under greenhouse conditions.

(Levi et al., 2017). Desert plants often have a more elaborate root architecture with longer roots that penetrate deeply into the soil, thus offering larger water and nutrient absorptive surface areas (Sandquist, 2014). In the present study, the African *C. colocynthis* accession (PI 195927) sourced from Ethiopia had a superior average TRL (181.02 cm) and TSA of 29.63 cm² (Table 2). However, it is worth noting that several *C. colocynthis* genotypes exhibited a relatively small root system. Also, in our greenhouse experiments, seeds of *C. colocynthis* accessions were slower to germinate when compared with those of other *Citrullus* species. Many desert plants produce seeds that rapidly germinate on the onset of a rainy season, but may also tend to produce seeds with delayed germination as a survival mechanism by remaining dormant until the water supply is sufficient for seedling survival (Gutterman, 1972).

Root architecture traits like root length, root area, and abundance of secondary roots are often important traits for the plants' response to water stress (drought) and soilborne pathogens (Comas et al., 2013; Thies and Levi, 2007; Wechter et al., 2012). Survey of past literature revealed that some of the accessions from our study with superior TRL, TSA, and proportion of secondary roots (PI 482303, PI 482246, PI 482309, and PI 482302) have also been previously reported to have strong tolerance to seedling wilt induced by water stress (Zhang et al., 2011). Genotypes PI 482246, PI 255136, and PI 270564 with superior root traits performance from this research have also previously exhibited 33% to 56% survival when challenged with *Fusarium oxysporum* f. sp. *niveum* race 2 under greenhouse growth conditions (Wechter et al., 2012). The accessions of PI 482338, PI 482303, and PI 482259 had superior root traits performance and have

also been reported to show reduced root galling and nematode egg production when infected by root-knot nematodes (Thies and Levi, 2007). Genotypes with significant overlap for superior root traits and resistance to water stress and soilborne pathogens based on the present research and the preceding historical studies will be important parental candidates for gene pyramiding of alleles controlling tolerance to both biotic and abiotic stresses in watermelon crop improvement and production.

The continuous distribution of the root traits depicted by the histograms (Fig. 2) suggests presence of quantitative inheritance of the examined root traits and the involvement of multiple loci underlying these traits. Previous studies have reported numerous genetic loci controlling root length and surface area in maize, wheat, and common bean (Bhatta et al., 2019; Ju et al., 2018; Lin et al., 2019; Polania et al., 2017; Wang et al., 2019). The trait distribution patterns generated in this study will serve as a benchmark in future genetic studies seeking to characterize the genetic basis and inheritance of root phenotypes in watermelon.

The *C. amarus* (citron) accessions exhibited the greatest variability for TRL, TSA, and TRV. *C. amarus* has been classified as a sister species to the cultivated sweet watermelon (*C. lanatus*) (Chomicki and Renner, 2015; Jarret et al., 1997; Levi et al., 2013). In addition, a large number of *C. amarus* genotypes have been reported to be resistant/tolerant to root-knot nematodes, fusarium wilt races 1 and 2, and also found to be robust rootstocks for the production of grafted watermelon (Thies and Levi, 2007; Thies et al., 2010; Wechter et al., 2012). *C. amarus* and *C. lanatus* can be readily intercrossed and produce viable hybrids (Levi et al., 2001). Thus, it is feasible to move the

Table 4. Genotypic correlations among the evaluated root traits of the 335 *Citrullus* germplasm accessions grown under greenhouse conditions.

Traits	TRL	TSA	ARD	TRV
TRL	–	0.95**	–0.08 NS	0.85**
TSA		–	0.20*	0.97**
ARD			–	0.39**
TRV				–

TRL = total root length; TSA = total root surface area; ARD = average root diameter; TRV = total root volume.

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

root architecture trait alleles present in *C. amarus* into the cultivated (sweet-fleshed) watermelon genetic background.

The presence of fine (secondary) roots and root hairs is important for nutrient and water uptake in plants as a result of the increased absorptive surfaces that they provide. An abundance of secondary roots can result in better crop performance and resilience when under attack from soilborne pathogens, especially *Fusarium* and root-knot nematode (Thies et al., 2010). Previous studies have indicated that root exudates from secondary roots into the rhizosphere play an important role nutrient acquisition, combating invasive weed species through allelopathy and attraction of beneficial microbes within the root zone that inhibit soilborne pathogens like *Fusarium* and nematodes (Chen et al., 2014; Kerry, 2000; Korenblum et al., 2020; Walker et al., 2003). Fine roots can more easily intercalate into the adjacent soil/root zone allowing the plants to more effectively and efficiently absorb water and nutrients that promote and sustain growth. Fine roots provide a relatively larger surface area for water and nutrient uptake and have a lower carbon

and energy requirement for their function (Lynch, 2011). The *Citrullus* genotypes with a large mass of secondary roots identified in the present study can be used as breeding stocks to increase the number of fine roots present in cultivated watermelon.

Trait correlation analysis is often used to determine positive and negative associations among phenotypes, identify parental combinations useful in cultivar development, and in minimizing trait measurement redundancy (Yan and Fregeau-Reid, 2008). The occurrence of positive correlations among traits suggests that simultaneous selection and improvement of such phenotypes through plant breeding is feasible. The present study findings are in agreement with those of Wasson and coworkers who also reported positive correlations among TRL, TSA, and TRV in wheat (Wasson et al., 2012). This suggests that these phenotypes can be targeted concurrently for watermelon improvement for root architecture traits.

Conclusion

This is the first report on an evaluation of root traits in a collection of *Citrullus* spp. germplasm. The results in this study indicate the presence of great variability in root traits within and among the *Citrullus* spp. accessions. Lower mean values of root traits were observed within the *C. lanatus* genotypes, including cultivars developed in the United States. A high percentage of cultivated watermelon genotypes had a small root system and were generally lacking secondary fibrous roots when compared with *C. lanatus* landraces or accessions of other *Citrullus* spp. This significant reduction in fibrous roots is likely to be a result of many years of cultivation and selection for watermelon ideotypes having desirable fruit quality traits and adaptation to geographical regions with moist soil conditions different from those in the arid areas present at the centers of origin of *Citrullus* spp. in Southern and Northern Africa. The identification of *Citrullus* genotypes with extensive root systems and trait associations will be useful in future genetic studies of root traits and in breeding programs seeking to improve the root system architecture of watermelon.

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Supplemental Table 1. Evaluation of root traits performance across the 335 *Citrullus* sp. accessions grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 596653	<i>Citrullus amarus</i>	South Africa	51.79	6.57	0.41	0.07
PI 596659	<i>C. amarus</i>	South Africa	58.66	10.72	0.58	0.16
PI 596662	<i>C. amarus</i>	South Africa	76.32	15.13	0.64	0.24
PI 596665	<i>C. amarus</i>	South Africa	75.07	10.81	0.46	0.13
PI 596666	<i>C. amarus</i>	South Africa	63.75	11.36	0.58	0.17
PI 596667	<i>C. amarus</i>	South Africa	58.67	9.44	0.52	0.12
PI 596668	<i>C. amarus</i>	South Africa	91.78	14.42	0.50	0.18
PI 596669	<i>C. amarus</i>	South Africa	73.30	14.51	0.64	0.23
PI 596670	<i>C. amarus</i>	South Africa	71.24	13.25	0.59	0.20
PI 596671	<i>C. amarus</i>	South Africa	79.03	9.70	0.40	0.10
PI 596675	<i>C. amarus</i>	South Africa	79.10	14.10	0.58	0.20
PI 596676	<i>C. amarus</i>	South Africa	86.12	15.82	0.58	0.24
PI 596677	<i>C. amarus</i>	South Africa	61.89	11.16	0.58	0.16
PI 225557	<i>C. amarus</i>	Zimbabwe	77.31	14.10	0.59	0.21
PI 596696	<i>C. amarus</i>	South Africa	89.25	14.02	0.50	0.20
PI 532664	<i>C. amarus</i>	Eswatini	59.13	9.47	0.51	0.12
PI 532668	<i>C. amarus</i>	Eswatini	75.18	11.36	0.49	0.14
PI 532670	<i>C. amarus</i>	Botswana	48.99	6.55	0.43	0.07
PI 532659	<i>C. amarus</i>	South Africa	82.82	12.45	0.48	0.15
PI 200732	<i>C. amarus</i>	El Salvador	88.88	13.05	0.47	0.15
PI 270562	<i>C. amarus</i>	South Africa	38.79	4.77	0.38	0.05
PI 270564	<i>C. amarus</i>	South Africa	111.51	15.41	0.45	0.18
PI 674448	<i>C. amarus</i>	Russia	171.58	35.53	0.67	0.59
Grif 15897	<i>C. amarus</i>	Russia	69.19	9.93	0.46	0.11
Grif 17032	<i>C. amarus</i>	United States	43.88	7.76	0.57	0.11
PI 532624	<i>C. amarus</i>	Zimbabwe	71.96	12.15	0.53	0.17
PI 244019	<i>C. amarus</i>	South Africa	63.33	10.55	0.53	0.14
PI 295850	<i>C. amarus</i>	South Africa	48.21	4.72	0.32	0.04
PI 299378	<i>C. amarus</i>	South Africa	45.79	7.64	0.53	0.10
PI 299379	<i>C. amarus</i>	South Africa	82.96	14.20	0.55	0.20
PI 295843	<i>C. amarus</i>	South Africa	71.30	9.86	0.44	0.11
PI 295842	<i>C. amarus</i>	South Africa	71.28	11.00	0.49	0.14
PI 632751	<i>C. amarus</i>	Namibia	37.90	6.73	0.58	0.10
PI 674448	<i>C. amarus</i>	Russia	122.68	23.54	0.61	0.36
PI 542114	<i>C. amarus</i>	Botswana	68.33	12.26	0.57	0.18
PI 606135	<i>C. amarus</i>	Russia	78.35	18.07	0.74	0.34
PI 271769	<i>C. amarus</i>	South Africa	73.19	13.42	0.60	0.20
PI 255137	<i>C. amarus</i>	South Africa	71.07	13.92	0.63	0.22
PI 485581	<i>C. amarus</i>	Botswana	34.36	6.29	0.59	0.09
PI 485583	<i>C. amarus</i>	Botswana	60.52	13.04	0.69	0.23
PI 296334	<i>C. amarus</i>	South Africa	76.81	14.52	0.61	0.23
PI 189225	<i>C. amarus</i>	DR Congo	80.16	11.13	0.44	0.13
PI 244017	<i>C. amarus</i>	South Africa	43.27	5.09	0.40	0.05
PI 271779	<i>C. amarus</i>	South Africa	54.25	8.48	0.48	0.11
PI 271771	<i>C. amarus</i>	South Africa	35.25	6.87	0.64	0.11
PI 271773	<i>C. amarus</i>	South Africa	53.02	5.54	0.34	0.05
PI 482246	<i>C. amarus</i>	Zimbabwe	114.97	15.44	0.43	0.17
PI 532819	<i>C. amarus</i>	China	65.15	12.71	0.63	0.20
PI 379243	<i>C. amarus</i>	Macedonia	47.52	7.32	0.54	0.10
PI 248774	<i>C. amarus</i>	Namibia	23.16	2.83	0.38	0.03
PI 482324	<i>C. amarus</i>	Zimbabwe	76.86	14.12	0.59	0.21
PI 482326	<i>C. amarus</i>	Zimbabwe	126.93	24.23	0.61	0.38
PI 482331	<i>C. amarus</i>	Zimbabwe	69.94	11.69	0.54	0.16
PI 482334	<i>C. amarus</i>	Zimbabwe	71.49	12.85	0.59	0.19
PI 482335	<i>C. amarus</i>	Zimbabwe	57.63	7.09	0.40	0.07
PI 482336	<i>C. amarus</i>	Zimbabwe	52.33	5.63	0.35	0.05
PI 482338	<i>C. amarus</i>	Zimbabwe	139.38	21.56	0.47	0.27
PI 482342	<i>C. amarus</i>	Zimbabwe	77.20	14.76	0.61	0.23
PI 482355	<i>C. amarus</i>	Zimbabwe	65.24	14.00	0.68	0.24
PI 482257	<i>C. amarus</i>	Zimbabwe	55.83	10.33	0.62	0.16
PI 482361	<i>C. amarus</i>	Zimbabwe	91.50	19.94	0.69	0.35
PI 482259	<i>C. amarus</i>	Zimbabwe	120.29	21.65	0.57	0.31
PI 482379	<i>C. amarus</i>	Zimbabwe	86.13	14.67	0.55	0.20
PI 482261	<i>C. amarus</i>	Zimbabwe	103.32	12.53	0.39	0.12
PI 482265	<i>C. amarus</i>	Zimbabwe	73.65	11.67	0.51	0.15
PI 482276	<i>C. amarus</i>	Zimbabwe	55.74	8.21	0.47	0.10
PI 482277	<i>C. amarus</i>	Zimbabwe	55.84	7.98	0.46	0.09
PI 482282	<i>C. amarus</i>	Zimbabwe	27.02	3.18	0.37	0.03
PI 482283	<i>C. amarus</i>	Zimbabwe	58.16	7.04	0.39	0.07
PI 482286	<i>C. amarus</i>	Zimbabwe	108.82	21.09	0.62	0.33
PI 482288	<i>C. amarus</i>	Zimbabwe	60.71	11.46	0.59	0.18
PI 482293	<i>C. amarus</i>	Zimbabwe	67.44	10.23	0.49	0.13
PI 482298	<i>C. amarus</i>	Zimbabwe	49.64	6.74	0.44	0.08
PI 482299	<i>C. amarus</i>	Zimbabwe	124.50	24.95	0.64	0.40

(Continued on next page)

Supplemental Table 1. (Continued) Evaluation of root traits performance across the 335 *Citrullus* sp. accessions grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 482300	<i>C. amarus</i>	Zimbabwe	69.85	12.05	0.55	0.17
PI 482302	<i>C. amarus</i>	Zimbabwe	117.86	15.84	0.48	0.18
PI 482303	<i>C. amarus</i>	Zimbabwe	122.91	20.42	0.53	0.28
PI 482307	<i>C. amarus</i>	Zimbabwe	77.11	10.85	0.46	0.12
PI 482308	<i>C. amarus</i>	Zimbabwe	74.81	10.43	0.45	0.12
PI 482309	<i>C. amarus</i>	Zimbabwe	106.34	18.32	0.55	0.25
PI 482311	<i>C. amarus</i>	Zimbabwe	77.01	11.42	0.47	0.14
PI 482312	<i>C. amarus</i>	Zimbabwe	60.25	11.50	0.61	0.18
PI 482315	<i>C. amarus</i>	Zimbabwe	112.30	20.67	0.59	0.31
PI 482316	<i>C. amarus</i>	Zimbabwe	58.33	9.02	0.50	0.12
PI 482318	<i>C. amarus</i>	Zimbabwe	110.72	19.11	0.55	0.27
PI 482319	<i>C. amarus</i>	Zimbabwe	86.79	10.48	0.38	0.10
PI 482321	<i>C. amarus</i>	Zimbabwe	81.96	9.02	0.35	0.08
PI 482252	<i>C. amarus</i>	Zimbabwe	80.76	12.51	0.50	0.16
PI 255136	<i>C. amarus</i>	South Africa	98.88	12.52	0.40	0.13
PI 270563	<i>C. amarus</i>	South Africa	30.08	8.18	0.88	0.18
PI 296337	<i>C. amarus</i>	South Africa	31.02	3.16	0.32	0.03
PI 296339	<i>C. amarus</i>	South Africa	66.31	8.56	0.41	0.09
PI 296341	<i>C. amarus</i>	South Africa	39.61	3.27	0.27	0.02
PI 296342	<i>C. amarus</i>	South Africa	53.75	8.63	0.52	0.12
PI 296343	<i>C. amarus</i>	South Africa	36.05	6.92	0.61	0.11
PI 512385	<i>C. amarus</i>	Spain	67.60	13.28	0.64	0.21
PI 512854	<i>C. amarus</i>	Spain	78.86	13.74	0.56	0.19
PI 494817	<i>C. amarus</i>	Zambia	145.59	30.19	0.66	0.50
PI 500308	<i>C. amarus</i>	Zambia	87.28	13.19	0.48	0.16
PI 500331	<i>C. amarus</i>	Zambia	76.07	12.97	0.55	0.18
PI 500332	<i>C. amarus</i>	Zambia	90.55	14.00	0.49	0.17
PI 500334	<i>C. amarus</i>	Zambia	65.34	14.12	0.67	0.25
PI 500335	<i>C. amarus</i>	Zambia	46.30	9.18	0.63	0.15
PI 500354	<i>C. amarus</i>	Zambia	44.85	7.12	0.51	0.10
PI 500355	<i>C. amarus</i>	Zambia	86.23	11.42	0.42	0.12
PI 386014	<i>Citrullus colocynthis</i>	Iran	22.39	2.91	0.38	0.03
PI 386018	<i>C. colocynthis</i>	Iran	32.80	3.68	0.36	0.03
PI 525080	<i>C. colocynthis</i>	Egypt	28.86	4.25	0.48	0.05
PI 386024	<i>C. colocynthis</i>	Iran	57.90	10.71	0.55	0.18
PI 386025	<i>C. colocynthis</i>	Iran	61.60	10.12	0.52	0.13
PI 386026	<i>C. colocynthis</i>	Iran	33.89	5.91	0.56	0.09
PI 269365	<i>C. colocynthis</i>	Afghanistan	51.45	8.06	0.52	0.11
PI 195927	<i>C. colocynthis</i>	Ethiopia	181.02	29.63	0.53	0.39
PI 374216	<i>C. colocynthis</i>	Afghanistan	42.06	6.44	0.49	0.08
PI 432337	<i>C. colocynthis</i>	Cyprus	66.14	8.02	0.39	0.08
PI 220778	<i>C. colocynthis</i>	Afghanistan	40.36	5.93	0.48	0.07
PI 549161	<i>C. colocynthis</i>	Chad	42.17	3.98	0.30	0.04
PI 388770	<i>C. colocynthis</i>	Morocco	90.69	14.23	0.49	0.18
PI 537277	<i>C. colocynthis</i>	Pakistan	44.31	7.91	0.56	0.12
PI 185636	<i>Citrullus lanatus</i>	Ghana	80.63	12.07	0.49	0.15
PI 234603	<i>C. lanatus</i>	New Zealand	80.63	14.38	0.59	0.21
PI 255139	<i>C. lanatus</i>	South Africa	74.37	13.34	0.58	0.19
PI 270545	<i>C. lanatus</i>	Sudan	62.23	11.85	0.60	0.18
PI 346787	<i>C. lanatus</i>	Serbia	54.83	8.71	0.53	0.11
PI 459074	<i>C. lanatus</i>	Botswana	50.65	9.29	0.57	0.14
PI 506439	<i>C. lanatus</i>	Moldova	76.98	14.17	0.59	0.21
PI 525084	<i>C. lanatus</i>	Egypt	67.78	13.01	0.61	0.20
PI 331106	<i>C. lanatus</i>	Uruguay	62.86	8.88	0.46	0.10
PI 525086	<i>C. lanatus</i>	Egypt	93.86	19.62	0.67	0.33
PI 525083	<i>C. lanatus</i>	Egypt	79.29	13.06	0.53	0.18
PI 113326	<i>C. lanatus</i>	China	77.05	14.26	0.58	0.22
PI 165448	<i>C. lanatus</i>	Mexico	44.43	9.11	0.66	0.15
PI 165451	<i>C. lanatus</i>	Mexico	58.94	8.60	0.47	0.10
PI 542617	<i>C. lanatus</i>	Algeria	50.27	11.43	0.73	0.21
PI 169237	<i>C. lanatus</i>	Turkey	39.57	6.80	0.63	0.11
PI 368524	<i>C. lanatus</i>	Montenegro	67.61	8.96	0.43	0.10
PI 368526	<i>C. lanatus</i>	Montenegro	44.61	6.28	0.45	0.07
PI 172786	<i>C. lanatus</i>	Turkey	47.14	6.67	0.45	0.08
PI 172798	<i>C. lanatus</i>	Turkey	81.41	11.21	0.44	0.13
PI 193963	<i>C. lanatus</i>	Ethiopia	43.84	7.31	0.57	0.10
PI 193964	<i>C. lanatus</i>	Ethiopia	75.49	10.24	0.43	0.11
PI 164665	<i>C. lanatus</i>	India	72.70	9.77	0.43	0.11
PI 176494	<i>C. lanatus</i>	Turkey	68.15	9.90	0.49	0.13
PI 195562	<i>C. lanatus</i>	Ethiopia	60.75	9.53	0.50	0.12
PI 197416	<i>C. lanatus</i>	Ethiopia	32.05	5.40	0.54	0.08
PI 212094	<i>C. lanatus</i>	Afghanistan	100.97	13.51	0.51	0.15
PI 217939	<i>C. lanatus</i>	Pakistan	49.64	9.31	0.60	0.14

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Supplemental Table 1. (Continued) Evaluation of root traits performance across the 335 *Citrullus* sp. accessions grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 219691	<i>C. lanatus</i>	Pakistan	49.68	8.43	0.56	0.12
PI 253174	<i>C. lanatus</i>	Serbia	31.51	6.35	0.65	0.11
PI 246559	<i>C. lanatus</i>	Senegal	25.76	3.59	0.43	0.04
PI 507867	<i>C. lanatus</i>	Hungary	32.26	6.04	0.61	0.09
PI 249010	<i>C. lanatus</i>	Nigeria	51.41	6.12	0.38	0.06
PI 254744	<i>C. lanatus</i>	Senegal	127.53	19.97	0.50	0.25
PI 181742	<i>C. lanatus</i>	Lebanon	59.99	10.89	0.58	0.16
PI 181868	<i>C. lanatus</i>	Syria	69.92	11.77	0.53	0.16
Allsweet	<i>C. lanatus</i>	United States	15.18	2.56	0.55	0.04
PI 526238	<i>C. lanatus</i>	Zimbabwe	47.09	8.61	0.59	0.13
PI 526233	<i>C. lanatus</i>	Zimbabwe	55.61	8.03	0.46	0.10
PI 512398	<i>C. lanatus</i>	Spain	115.10	17.72	0.49	0.22
PI 512404	<i>C. lanatus</i>	Spain	45.11	8.44	0.60	0.13
PI 270144	<i>C. lanatus</i>	Greece	65.39	10.25	0.50	0.13
PI 193490	<i>C. lanatus</i>	Ethiopia	73.56	12.43	0.54	0.17
PI 227203	<i>C. lanatus</i>	Japan	63.62	10.95	0.55	0.16
PI 518606	<i>C. lanatus</i>	Russia	34.22	5.80	0.53	0.08
PI 556995	<i>C. lanatus</i>	United States	43.39	6.33	0.47	0.08
PI 601062	<i>C. lanatus</i>	United States	39.55	6.82	0.57	0.10
PI 635586	<i>C. lanatus</i>	United States	58.94	10.23	0.55	0.14
PI 179233	<i>C. lanatus</i>	Turkey	36.79	6.21	0.54	0.08
PI 635713	<i>C. lanatus</i>	United States	16.05	3.81	0.82	0.08
PI 271985	<i>C. lanatus</i>	Somalia	39.94	7.47	0.62	0.12
PI 635642	<i>C. lanatus</i>	United States	43.69	7.60	0.56	0.11
PI 385964	<i>C. lanatus</i>	Kenya	49.47	7.56	0.49	0.09
PI 635688	<i>C. lanatus</i>	United States	54.44	7.76	0.45	0.09
PI 357656	<i>C. lanatus</i>	Macedonia	40.68	7.94	0.67	0.13
PI 512332	<i>C. lanatus</i>	China	44.55	7.96	0.59	0.12
PI 635691	<i>C. lanatus</i>	United States	137.20	19.28	0.45	0.22
PI 612464	<i>C. lanatus</i>	Korea, South	56.27	8.16	0.48	0.10
PI 612145	<i>C. lanatus</i>	United States	34.00	5.71	0.54	0.08
PI 635731	<i>C. lanatus</i>	United States	56.17	8.95	0.51	0.11
PI 296332	<i>C. lanatus</i>	South Africa	66.92	9.82	0.46	0.13
PI 269677	<i>C. lanatus</i>	Belize	27.92	5.52	2.15	0.41
PI 288232	<i>C. lanatus</i>	Egypt	42.70	7.61	0.57	0.11
PI 593346	<i>C. lanatus</i>	China	45.88	6.76	0.47	0.08
PI 635596	<i>C. lanatus</i>	United States	9.36	2.04	0.74	0.04
PI 525098	<i>C. lanatus</i>	Egypt	61.85	10.45	0.54	0.15
PI 629108	<i>C. lanatus</i>	United States	35.65	7.47	0.67	0.13
PI 192937	<i>C. lanatus</i>	China	52.48	7.65	0.47	0.09
Grif 1734	<i>C. lanatus</i>	China	30.07	5.87	0.62	0.10
PI 635600	<i>C. lanatus</i>	United States	88.68	13.35	0.48	0.16
PI 226459	<i>C. lanatus</i>	Iran	62.26	10.03	0.52	0.13
PI 635603	<i>C. lanatus</i>	United States	80.18	14.13	0.56	0.20
PI 635741	<i>C. lanatus</i>	United States	40.83	6.40	0.50	0.08
PI 276445	<i>C. lanatus</i>	Jordan	23.29	5.11	0.76	0.10
PI 438677	<i>C. lanatus</i>	Mexico	98.69	17.92	0.58	0.27
PI 179881	<i>C. lanatus</i>	India	57.96	9.91	0.55	0.14
PI 490375	<i>C. lanatus</i>	Mali	123.16	17.28	0.45	0.20
PI 635606	<i>C. lanatus</i>	United States	26.38	4.53	0.57	0.06
PI 536449	<i>C. lanatus</i>	Maldives	47.59	8.46	0.57	0.12
PI 536459	<i>C. lanatus</i>	Maldives	80.32	12.91	0.51	0.17
PI 536464	<i>C. lanatus</i>	Maldives	70.47	11.62	0.53	0.16
PI 635609	<i>C. lanatus</i>	United States	40.04	5.97	0.52	0.07
PI 635703	<i>C. lanatus</i>	United States	35.58	7.21	0.70	0.12
PI 635614	<i>C. lanatus</i>	United States	18.25	2.99	0.59	0.04
PI 180426	<i>C. lanatus</i>	India	58.34	8.82	0.49	0.11
PI 169290	<i>C. lanatus</i>	Turkey	47.50	6.23	0.42	0.07
PI 532813	<i>C. lanatus</i>	China	68.76	11.94	0.56	0.17
PI 601101	<i>C. lanatus</i>	United States	55.55	10.63	0.59	0.17
PI 228238	<i>C. lanatus</i>	Israel	52.17	7.22	0.44	0.08
PI 270525	<i>C. lanatus</i>	Israel	74.33	11.28	0.52	0.15
PI 487476	<i>C. lanatus</i>	Israel	45.48	8.14	0.57	0.12
PI 226445	<i>C. lanatus</i>	Israel	76.90	11.24	0.47	0.13
PI 635616	<i>C. lanatus</i>	United States	46.40	7.54	0.52	0.10
PI 179878	<i>C. lanatus</i>	India	59.17	8.08	0.45	0.09
PI 254716	<i>C. lanatus</i>	Sudan	48.36	7.49	0.49	0.09
PI 345544	<i>C. lanatus</i>	Ukraine	42.57	7.06	0.55	0.10
PI 162667	<i>C. lanatus</i>	Argentina	31.38	3.62	0.37	0.04
PI 635630	<i>C. lanatus</i>	United States	62.96	9.37	0.47	0.11
PI 601307	<i>C. lanatus</i>	United States	26.43	4.20	0.57	0.06
PI 601308	<i>C. lanatus</i>	United States	23.92	4.50	0.64	0.07
PI 675114	<i>C. lanatus</i>	United States	39.35	7.29	0.58	0.11

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Supplemental Table 1. (Continued) Evaluation of root traits performance across the 335 *Citrullus* sp. accessions grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 490385	<i>C. lanatus</i>	Mali	93.57	11.68	0.44	0.14
PI 518610	<i>C. lanatus</i>	Soviet Union	60.39	11.71	0.62	0.18
PI 379231	<i>C. lanatus</i>	Macedonia	21.07	4.78	0.73	0.09
PI 254623	<i>C. lanatus</i>	Sudan	45.94	6.91	0.48	0.09
PI 212208	<i>C. lanatus</i>	Greece	43.58	7.89	0.58	0.12
PI 270306	<i>C. lanatus</i>	Philippines	45.38	7.96	0.56	0.12
PI 270546	<i>C. lanatus</i>	Ghana	38.41	6.23	0.52	0.08
PI 271981	<i>C. lanatus</i>	Somalia	46.85	7.36	0.50	0.09
PI 277970	<i>C. lanatus</i>	Turkey	44.76	7.53	0.54	0.10
PI 207473	<i>C. lanatus</i>	Afghanistan	57.39	9.64	0.53	0.13
PI 212287	<i>C. lanatus</i>	Afghanistan	29.99	6.21	0.66	0.11
PI 212983	<i>C. lanatus</i>	India	51.27	6.68	0.46	0.07
PI 277987	<i>C. lanatus</i>	Turkey	71.87	12.51	0.56	0.18
PI 183218	<i>C. lanatus</i>	Egypt	41.66	6.39	0.50	0.08
PI 212209	<i>C. lanatus</i>	Greece	40.92	8.43	0.75	0.14
PI 271982	<i>C. lanatus</i>	Somalia	28.72	5.80	0.68	0.10
PI 277996	<i>C. lanatus</i>	Turkey	57.93	10.50	0.58	0.15
PI 211851	<i>C. lanatus</i>	Iran	19.53	2.75	0.45	0.03
PI 273481	<i>C. lanatus</i>	Ethiopia	85.80	13.03	0.49	0.16
PI 278003	<i>C. lanatus</i>	Turkey	36.63	7.92	0.69	0.14
PI 276658	<i>C. lanatus</i>	Russia	38.84	7.24	0.60	0.11
PI 278007	<i>C. lanatus</i>	Turkey	80.65	14.88	0.58	0.23
PI 189316	<i>C. lanatus</i>	Nigeria	54.55	6.63	0.39	0.07
PI 211915	<i>C. lanatus</i>	Iran	30.24	3.38	0.38	0.03
PI 270550	<i>C. lanatus</i>	Ghana	42.61	6.60	0.54	0.09
PI 278020	<i>C. lanatus</i>	Turkey	70.79	12.80	0.57	0.19
PI 270551	<i>C. lanatus</i>	Ghana	42.80	8.68	0.66	0.14
PI 278031	<i>C. lanatus</i>	Turkey	57.61	9.78	0.53	0.13
PI 189317	<i>C. lanatus</i>	Nigeria	51.67	8.51	0.56	0.13
PI 211917	<i>C. lanatus</i>	Iran	32.86	6.15	0.63	0.10
PI 277976	<i>C. lanatus</i>	Turkey	48.03	9.09	0.62	0.14
PI 278041	<i>C. lanatus</i>	Turkey	28.54	5.75	0.67	0.09
PI 277977	<i>C. lanatus</i>	Turkey	8.78	2.76	1.02	0.07
PI 635618	<i>C. lanatus</i>	United States	82.19	14.68	0.57	0.21
PI 534597	<i>C. lanatus</i>	Syria	60.91	11.33	0.59	0.17
PI 345545	<i>C. lanatus</i>	Ukraine	47.47	8.72	0.59	0.13
PI 534587	<i>C. lanatus</i>	Syria	48.44	7.35	0.49	0.09
PI 222137	<i>C. lanatus</i>	Algeria	57.71	8.76	0.49	0.11
PI 635619	<i>C. lanatus</i>	United States	30.61	4.66	0.48	0.06
PI 635662	<i>C. lanatus</i>	United States	36.69	5.73	0.51	0.07
Picnic	<i>C. lanatus</i>	United States	27.34	3.92	0.55	0.05
Princecharles	<i>C. lanatus</i>	United States	30.49	5.68	0.62	0.09
PI 164633	<i>C. lanatus</i>	India	67.13	12.92	0.60	0.20
PI 543211	<i>C. lanatus</i>	Bolivia	62.44	10.93	0.56	0.15
Sangria	<i>C. lanatus</i>	United States	30.02	6.15	0.65	0.10
PI 635654	<i>C. lanatus</i>	United States	27.72	3.11	0.36	0.03
PI 227205	<i>C. lanatus</i>	Japan	29.21	4.69	0.54	0.06
PI 635620	<i>C. lanatus</i>	United States	56.69	10.45	0.61	0.16
PI 635621	<i>C. lanatus</i>	United States	77.01	14.57	0.60	0.22
PI 279459	<i>C. lanatus</i>	Japan	35.30	5.39	0.48	0.07
PI 665007	<i>C. lanatus</i>	United States	31.04	6.05	0.64	0.10
PI 635631	<i>C. lanatus</i>	United States	100.81	17.01	0.54	0.23
PI 635732	<i>C. lanatus</i>	United States	33.08	3.96	0.39	0.04
PI 635716	<i>C. lanatus</i>	United States	24.45	3.30	0.45	0.04
PI 250146	<i>C. lanatus</i>	Pakistan	53.14	8.98	0.57	0.13
PI 182935	<i>C. lanatus</i>	India	55.60	8.15	0.51	0.10
PI 249559	<i>C. lanatus</i>	Thailand	57.24	8.39	0.46	0.10
PI 482332	<i>C. lanatus</i>	Zimbabwe	92.90	15.47	0.52	0.21
PI 482255	<i>C. lanatus</i>	Zimbabwe	62.37	11.46	0.59	0.17
PI 482341	<i>C. lanatus</i>	Zimbabwe	46.20	7.87	0.54	0.11
PI 482362	<i>C. lanatus</i>	Zimbabwe	84.30	13.93	0.51	0.19
PI 482258	<i>C. lanatus</i>	Zimbabwe	45.08	7.68	0.55	0.10
PI 482262	<i>C. lanatus</i>	Zimbabwe	96.67	16.65	0.55	0.23
PI 482264	<i>C. lanatus</i>	Zimbabwe	92.58	14.30	0.49	0.18
PI 482268	<i>C. lanatus</i>	Zimbabwe	49.95	10.80	0.69	0.19
PI 482248	<i>C. lanatus</i>	Zimbabwe	60.23	11.14	0.59	0.17
PI 482287	<i>C. lanatus</i>	Zimbabwe	81.20	13.77	0.54	0.19
PI 269681	<i>C. lanatus</i>	Belize	34.19	4.77	0.45	0.05
PI 512395	<i>C. lanatus</i>	Spain	47.42	7.01	0.48	0.08
PI 512374	<i>C. lanatus</i>	Spain	54.25	9.55	0.56	0.14
PI 635712	<i>C. lanatus</i>	United States	59.84	10.60	0.57	0.15
PI 537267	<i>C. lanatus</i>	Pakistan	27.68	4.98	0.66	0.08
PI 537271	<i>C. lanatus</i>	Pakistan	61.83	9.91	0.51	0.13

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Supplemental Table 1. (Continued) Evaluation of root traits performance across the 335 *Citrullus* sp. accessions grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	ARD (mm)	TRV (cm ³)
PI 381734	<i>C. lanatus</i>	India	78.76	8.38	0.34	0.07
PI 179234	<i>C. lanatus</i>	Turkey	81.39	11.19	0.44	0.13
PI 505586	<i>C. lanatus</i>	Zambia	56.07	10.14	0.57	0.15
PI 500301	<i>C. lanatus</i>	Zambia	56.47	6.85	0.40	0.07
PI 500314	<i>C. lanatus</i>	Zambia	62.69	11.70	0.61	0.18
PI 500319	<i>C. lanatus</i>	Zambia	114.72	19.48	0.55	0.27
PI 500328	<i>C. lanatus</i>	Zambia	60.68	9.87	0.53	0.13
PI 500344	<i>C. lanatus</i>	Zambia	42.33	7.60	0.58	0.11
PI 500350	<i>C. lanatus</i>	Zambia	47.27	8.20	0.56	0.12
PI 260733	<i>C. lanatus</i>	Sudan	44.75	7.15	0.54	0.10
PI 247398	<i>Citrullus mucosospermus</i>	Greece	50.28	8.12	0.52	0.11
PI 164248	<i>C. mucosospermus</i>	Liberia	42.92	6.49	0.49	0.08
PI 184800	<i>C. mucosospermus</i>	Nigeria	72.25	13.61	0.62	0.21
PI 185635	<i>C. mucosospermus</i>	Ghana	52.64	5.36	0.32	0.04
PI 186489	<i>C. mucosospermus</i>	Nigeria	64.70	8.07	0.40	0.08
PI 186490	<i>C. mucosospermus</i>	Nigeria	139.73	26.47	0.61	0.40
PI 186975	<i>C. mucosospermus</i>	Ghana	29.32	4.42	0.48	0.05
PI 189318	<i>C. mucosospermus</i>	Nigeria	26.28	3.87	0.49	0.05
PI 249009	<i>C. mucosospermus</i>	Nigeria	39.65	6.53	0.53	0.09
PI 254737	<i>C. mucosospermus</i>	Senegal	65.58	10.23	0.50	0.13
PI 254740	<i>C. mucosospermus</i>	Senegal	50.84	7.32	0.46	0.09
PI 254741	<i>C. mucosospermus</i>	Senegal	47.27	5.41	0.36	0.05
PI 254742	<i>C. mucosospermus</i>	Senegal	74.65	10.55	0.45	0.12
PI 306782	<i>C. mucosospermus</i>	Nigeria	151.36	21.83	0.46	0.26
PI 326516	<i>C. mucosospermus</i>	Ghana	46.52	9.24	0.64	0.15
PI 490381	<i>C. mucosospermus</i>	Mali	78.67	12.91	0.52	0.17
PI 490386	<i>C. mucosospermus</i>	Mali	47.75	8.73	0.58	0.13
PI 494528	<i>C. mucosospermus</i>	Nigeria	158.75	28.53	0.57	0.42
PI 494531	<i>C. mucosospermus</i>	Nigeria	116.74	19.06	0.52	0.25
PI 532738	<i>C. mucosospermus</i>	DR Congo	46.67	9.77	0.71	0.17
PI 559996	<i>C. mucosospermus</i>	Nigeria	95.11	17.45	0.60	0.26
PI 560001	<i>C. mucosospermus</i>	Nigeria	69.76	15.63	0.70	0.29
PI 560002	<i>C. mucosospermus</i>	Nigeria	120.03	23.57	0.63	0.37
PI 560003	<i>C. mucosospermus</i>	Nigeria	85.90	16.30	0.61	0.25
PI 560004	<i>C. mucosospermus</i>	Nigeria	124.60	23.69	0.61	0.36
PI 560005	<i>C. mucosospermus</i>	Nigeria	86.82	13.36	0.49	0.16
PI 560006	<i>C. mucosospermus</i>	Nigeria	63.36	10.87	0.55	0.15
PI 560008	<i>C. mucosospermus</i>	Nigeria	71.04	11.86	0.53	0.16
PI 560010	<i>C. mucosospermus</i>	Nigeria	70.87	11.67	0.53	0.16
PI 560012	<i>C. mucosospermus</i>	Nigeria	93.50	19.77	0.67	0.34
PI 560020	<i>C. mucosospermus</i>	Nigeria	52.69	6.46	0.39	0.07
PI 248178	<i>C. mucosospermus</i>	DR Congo	46.53	5.14	0.36	0.05
LSD ($\alpha = 0.05$)			24.38	4.19	0.29	0.09

TRL = total root length; TSA = total root surface area; ARD = average root diameter; TRV = total root volume; LSD = least significant difference.

Supplemental Table 2. Evaluation of root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) across the 335 *Citrullus* sp. accessions that were grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 596653	<i>Citrullus amarus</i>	South Africa	40.42	3.02	0.03
PI 596659	<i>C. amarus</i>	South Africa	39.75	2.77	0.02
PI 596662	<i>C. amarus</i>	South Africa	46.99	3.46	0.03
PI 596665	<i>C. amarus</i>	South Africa	57.09	4.83	0.04
PI 596666	<i>C. amarus</i>	South Africa	42.13	2.97	0.02
PI 596667	<i>C. amarus</i>	South Africa	40.86	3.29	0.03
PI 596668	<i>C. amarus</i>	South Africa	64.26	5.07	0.04
PI 596669	<i>C. amarus</i>	South Africa	45.14	3.28	0.02
PI 596670	<i>C. amarus</i>	South Africa	45.90	3.29	0.03
PI 596671	<i>C. amarus</i>	South Africa	63.44	4.55	0.03
PI 596675	<i>C. amarus</i>	South Africa	55.88	4.62	0.04
PI 596676	<i>C. amarus</i>	South Africa	53.58	4.66	0.04
PI 596677	<i>C. amarus</i>	South Africa	41.52	2.83	0.02
PI 225557	<i>C. amarus</i>	Zimbabwe	51.93	4.19	0.04
PI 596696	<i>C. amarus</i>	South Africa	68.93	5.35	0.04
PI 532664	<i>C. amarus</i>	Eswatini	40.19	3.12	0.03
PI 532668	<i>C. amarus</i>	Eswatini	53.33	4.27	0.04
PI 532670	<i>C. amarus</i>	Botswana	38.07	3.03	0.02
PI 532659	<i>C. amarus</i>	South Africa	58.19	4.61	0.04
PI 200732	<i>C. amarus</i>	El Salvador	67.90	5.59	0.04
PI 270562	<i>C. amarus</i>	South Africa	32.39	2.40	0.02
PI 270564	<i>C. amarus</i>	South Africa	85.29	7.28	0.06
PI 674448	<i>C. amarus</i>	Russia	99.73	7.70	0.07
Grif 15897	<i>C. amarus</i>	Russia	53.95	4.82	0.04
Grif 17032	<i>C. amarus</i>	United States	29.36	2.61	0.02
PI 532624	<i>C. amarus</i>	Zimbabwe	47.06	3.38	0.03
PI 244019	<i>C. amarus</i>	South Africa	42.82	2.91	0.02
PI 295850	<i>C. amarus</i>	South Africa	40.93	2.57	0.02
PI 299378	<i>C. amarus</i>	South Africa	29.31	2.19	0.02
PI 299379	<i>C. amarus</i>	South Africa	55.90	5.36	0.05
PI 295843	<i>C. amarus</i>	South Africa	55.22	5.07	0.05
PI 295842	<i>C. amarus</i>	South Africa	54.61	5.22	0.05
PI 632751	<i>C. amarus</i>	Namibia	25.36	2.13	0.02
PI 674448	<i>C. amarus</i>	Russia	69.57	6.61	0.06
PI 542114	<i>C. amarus</i>	Botswana	46.30	3.28	0.02
PI 606135	<i>C. amarus</i>	Russia	46.82	3.53	0.03
PI 271769	<i>C. amarus</i>	South Africa	48.16	3.68	0.03
PI 255137	<i>C. amarus</i>	South Africa	38.33	3.52	0.04
PI 485581	<i>C. amarus</i>	Botswana	22.19	1.70	0.01
PI 485583	<i>C. amarus</i>	Botswana	36.36	2.44	0.02
PI 296334	<i>C. amarus</i>	South Africa	50.47	3.57	0.03
PI 189225	<i>C. amarus</i>	DR Congo	62.84	5.55	0.05
PI 244017	<i>C. amarus</i>	South Africa	36.60	2.76	0.02
PI 271779	<i>C. amarus</i>	South Africa	39.65	3.23	0.03
PI 271771	<i>C. amarus</i>	South Africa	20.69	1.54	0.01
PI 271773	<i>C. amarus</i>	South Africa	44.27	3.02	0.02
PI 482246	<i>C. amarus</i>	Zimbabwe	88.67	6.27	0.05
PI 532819	<i>C. amarus</i>	China	40.09	3.45	0.03
PI 379243	<i>C. amarus</i>	Macedonia	35.71	3.01	0.03
PI 248774	<i>C. amarus</i>	Namibia	18.81	1.25	0.01
PI 482324	<i>C. amarus</i>	Zimbabwe	51.42	3.80	0.03
PI 482326	<i>C. amarus</i>	Zimbabwe	82.11	5.79	0.05
PI 482331	<i>C. amarus</i>	Zimbabwe	42.55	3.45	0.03
PI 482334	<i>C. amarus</i>	Zimbabwe	48.32	3.99	0.03
PI 482335	<i>C. amarus</i>	Zimbabwe	45.41	3.87	0.03
PI 482336	<i>C. amarus</i>	Zimbabwe	43.82	3.02	0.02
PI 482338	<i>C. amarus</i>	Zimbabwe	101.21	7.81	0.06
PI 482342	<i>C. amarus</i>	Zimbabwe	50.69	3.59	0.03
PI 482355	<i>C. amarus</i>	Zimbabwe	41.36	2.82	0.02
PI 482257	<i>C. amarus</i>	Zimbabwe	38.42	3.00	0.03
PI 482361	<i>C. amarus</i>	Zimbabwe	54.98	3.90	0.03
PI 482259	<i>C. amarus</i>	Zimbabwe	74.22	6.54	0.06
PI 482379	<i>C. amarus</i>	Zimbabwe	58.69	3.45	0.02
PI 482261	<i>C. amarus</i>	Zimbabwe	85.40	7.01	0.06
PI 482265	<i>C. amarus</i>	Zimbabwe	55.04	5.90	0.05
PI 482276	<i>C. amarus</i>	Zimbabwe	41.03	3.22	0.03
PI 482277	<i>C. amarus</i>	Zimbabwe	42.66	3.49	0.03
PI 482282	<i>C. amarus</i>	Zimbabwe	22.23	1.61	0.01
PI 482283	<i>C. amarus</i>	Zimbabwe	46.47	3.81	0.03
PI 482286	<i>C. amarus</i>	Zimbabwe	63.72	5.52	0.05
PI 482288	<i>C. amarus</i>	Zimbabwe	38.64	2.75	0.02
PI 482293	<i>C. amarus</i>	Zimbabwe	51.30	4.95	0.05
PI 482298	<i>C. amarus</i>	Zimbabwe	37.98	3.25	0.03

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Supplemental Table 2. (Continued) Evaluation of root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) across the 335 *Citrullus* sp. accessions that were grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 482299	<i>C. amarus</i>	Zimbabwe	71.87	5.15	0.04
PI 482300	<i>C. amarus</i>	Zimbabwe	40.96	4.16	0.04
PI 482302	<i>C. amarus</i>	Zimbabwe	93.18	7.16	0.05
PI 482303	<i>C. amarus</i>	Zimbabwe	89.58	7.24	0.06
PI 482307	<i>C. amarus</i>	Zimbabwe	60.99	5.75	0.05
PI 482308	<i>C. amarus</i>	Zimbabwe	58.87	5.10	0.04
PI 482309	<i>C. amarus</i>	Zimbabwe	70.64	6.01	0.05
PI 482311	<i>C. amarus</i>	Zimbabwe	57.80	5.20	0.04
PI 482312	<i>C. amarus</i>	Zimbabwe	38.46	3.77	0.03
PI 482315	<i>C. amarus</i>	Zimbabwe	76.12	5.39	0.04
PI 482316	<i>C. amarus</i>	Zimbabwe	40.13	3.48	0.03
PI 482318	<i>C. amarus</i>	Zimbabwe	74.00	5.88	0.05
PI 482319	<i>C. amarus</i>	Zimbabwe	71.46	5.95	0.05
PI 482321	<i>C. amarus</i>	Zimbabwe	69.46	5.11	0.04
PI 482252	<i>C. amarus</i>	Zimbabwe	64.31	5.66	0.05
PI 255136	<i>C. amarus</i>	South Africa	80.69	5.76	0.04
PI 270563	<i>C. amarus</i>	South Africa	16.40	1.47	0.01
PI 296337	<i>C. amarus</i>	South Africa	27.29	1.99	0.02
PI 296339	<i>C. amarus</i>	South Africa	50.46	3.38	0.03
PI 296341	<i>C. amarus</i>	South Africa	36.68	2.16	0.01
PI 296342	<i>C. amarus</i>	South Africa	37.59	2.80	0.02
PI 296343	<i>C. amarus</i>	South Africa	22.76	1.51	0.01
PI 512385	<i>C. amarus</i>	Spain	42.67	3.86	0.03
PI 512854	<i>C. amarus</i>	Spain	52.26	4.98	0.05
PI 494817	<i>C. amarus</i>	Zambia	94.43	6.37	0.05
PI 500308	<i>C. amarus</i>	Zambia	66.52	6.02	0.05
PI 500331	<i>C. amarus</i>	Zambia	52.59	3.06	0.03
PI 500332	<i>C. amarus</i>	Zambia	64.26	5.50	0.05
PI 500334	<i>C. amarus</i>	Zambia	41.18	3.51	0.03
PI 500335	<i>C. amarus</i>	Zambia	26.67	2.25	0.02
PI 500354	<i>C. amarus</i>	Zambia	31.43	2.44	0.02
PI 500355	<i>C. amarus</i>	Zambia	67.97	5.29	0.04
PI 386014	<i>Citrullus colocynthis</i>	Iran	16.53	1.10	0.01
PI 386018	<i>C. colocynthis</i>	Iran	25.19	1.28	0.01
PI 525080	<i>C. colocynthis</i>	Egypt	19.68	1.37	0.01
PI 386024	<i>C. colocynthis</i>	Iran	39.66	3.01	0.02
PI 386025	<i>C. colocynthis</i>	Iran	42.05	2.86	0.02
PI 386026	<i>C. colocynthis</i>	Iran	21.99	1.80	0.02
PI 269365	<i>C. colocynthis</i>	Afghanistan	35.93	2.87	0.02
PI 195927	<i>C. colocynthis</i>	Ethiopia	127.30	8.95	0.07
PI 374216	<i>C. colocynthis</i>	Afghanistan	30.22	2.32	0.02
PI 432337	<i>C. colocynthis</i>	Cyprus	52.78	3.66	0.03
PI 220778	<i>C. colocynthis</i>	Afghanistan	29.06	2.39	0.02
PI 549161	<i>C. colocynthis</i>	Chad	36.47	2.15	0.01
PI 388770	<i>C. colocynthis</i>	Morocco	64.47	4.51	0.04
PI 537277	<i>C. colocynthis</i>	Pakistan	29.53	2.31	0.02
PI 185636	<i>Citrullus lanatus</i>	Ghana	58.99	4.43	0.04
PI 234603	<i>C. lanatus</i>	New Zealand	51.00	3.96	0.03
PI 255139	<i>C. lanatus</i>	South Africa	47.31	4.90	0.04
PI 270545	<i>C. lanatus</i>	Sudan	36.10	2.94	0.03
PI 346787	<i>C. lanatus</i>	Serbia	39.94	3.51	0.03
PI 459074	<i>C. lanatus</i>	Botswana	34.62	2.31	0.02
PI 506439	<i>C. lanatus</i>	Moldova	53.10	5.46	0.05
PI 525084	<i>C. lanatus</i>	Egypt	46.00	4.71	0.04
PI 331106	<i>C. lanatus</i>	Uruguay	50.91	4.22	0.03
PI 525086	<i>C. lanatus</i>	Egypt	51.45	5.23	0.05
PI 525083	<i>C. lanatus</i>	Egypt	57.12	4.42	0.04
PI 113326	<i>C. lanatus</i>	China	51.93	3.82	0.03
PI 165448	<i>C. lanatus</i>	Mexico	27.55	2.01	0.02
PI 165451	<i>C. lanatus</i>	Mexico	43.46	3.38	0.03
PI 542617	<i>C. lanatus</i>	Algeria	32.26	3.52	0.03
PI 169237	<i>C. lanatus</i>	Turkey	28.21	2.28	0.02
PI 368524	<i>C. lanatus</i>	Montenegro	50.31	3.36	0.02
PI 368526	<i>C. lanatus</i>	Montenegro	34.93	2.73	0.02
PI 172786	<i>C. lanatus</i>	Turkey	36.65	2.65	0.02
PI 172798	<i>C. lanatus</i>	Turkey	62.58	4.55	0.03
PI 193963	<i>C. lanatus</i>	Ethiopia	30.10	2.46	0.02
PI 193964	<i>C. lanatus</i>	Ethiopia	59.66	4.88	0.04
PI 164665	<i>C. lanatus</i>	India	56.22	4.02	0.03
PI 176494	<i>C. lanatus</i>	Turkey	51.85	3.46	0.03
PI 195562	<i>C. lanatus</i>	Ethiopia	44.68	3.78	0.03
PI 197416	<i>C. lanatus</i>	Ethiopia	21.63	1.74	0.01
PI 212094	<i>C. lanatus</i>	Afghanistan	81.32	6.66	0.05

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Supplemental Table 2. (Continued) Evaluation of root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) across the 335 *Citrullus* sp. accessions that were grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 217939	<i>C. lanatus</i>	Pakistan	31.91	2.84	0.03
PI 219691	<i>C. lanatus</i>	Pakistan	34.85	3.05	0.03
PI 253174	<i>C. lanatus</i>	Serbia	20.48	2.21	0.02
PI 246559	<i>C. lanatus</i>	Senegal	18.31	1.32	0.01
PI 507867	<i>C. lanatus</i>	Hungary	21.67	1.99	0.02
PI 249010	<i>C. lanatus</i>	Nigeria	42.30	3.16	0.02
PI 254744	<i>C. lanatus</i>	Senegal	93.10	6.99	0.06
PI 181742	<i>C. lanatus</i>	Lebanon	40.17	3.52	0.03
PI 181868	<i>C. lanatus</i>	Syria	48.12	4.10	0.03
Allsweet	<i>C. lanatus</i>	United States	10.16	0.83	0.01
PI 526238	<i>C. lanatus</i>	Zimbabwe	33.45	3.45	0.03
PI 526233	<i>C. lanatus</i>	Zimbabwe	41.36	3.41	0.03
PI 512398	<i>C. lanatus</i>	Spain	85.39	7.36	0.07
PI 512404	<i>C. lanatus</i>	Spain	30.98	3.14	0.03
PI 270144	<i>C. lanatus</i>	Greece	50.78	5.05	0.04
PI 193490	<i>C. lanatus</i>	Ethiopia	52.25	4.50	0.04
PI 227203	<i>C. lanatus</i>	Japan	45.93	4.38	0.04
PI 518606	<i>C. lanatus</i>	Russia	23.93	2.23	0.02
PI 556995	<i>C. lanatus</i>	United States	31.84	2.62	0.02
PI 601062	<i>C. lanatus</i>	United States	28.43	2.48	0.02
PI 635586	<i>C. lanatus</i>	United States	40.54	3.14	0.03
PI 179233	<i>C. lanatus</i>	Turkey	25.94	2.22	0.02
PI 635713	<i>C. lanatus</i>	United States	8.00	0.65	0.01
PI 271985	<i>C. lanatus</i>	Somalia	24.97	2.49	0.02
PI 635642	<i>C. lanatus</i>	United States	29.03	2.20	0.02
PI 385964	<i>C. lanatus</i>	Kenya	38.18	3.59	0.03
PI 635688	<i>C. lanatus</i>	United States	41.16	3.10	0.02
PI 357656	<i>C. lanatus</i>	Macedonia	24.28	2.17	0.02
PI 512332	<i>C. lanatus</i>	China	31.84	3.06	0.03
PI 635691	<i>C. lanatus</i>	United States	104.34	7.21	0.05
PI 612464	<i>C. lanatus</i>	Korea, South	39.06	2.85	0.02
PI 612145	<i>C. lanatus</i>	United States	25.97	2.78	0.03
PI 635731	<i>C. lanatus</i>	United States	40.62	3.53	0.03
PI 296332	<i>C. lanatus</i>	South Africa	48.99	4.08	0.03
PI 269677	<i>C. lanatus</i>	Belize	21.39	1.64	0.01
PI 288232	<i>C. lanatus</i>	Egypt	29.96	3.01	0.03
PI 593346	<i>C. lanatus</i>	China	34.76	2.73	0.02
PI 635596	<i>C. lanatus</i>	United States	6.16	0.54	0.00
PI 525098	<i>C. lanatus</i>	Egypt	45.91	4.48	0.04
PI 629108	<i>C. lanatus</i>	United States	24.17	1.87	0.02
PI 192937	<i>C. lanatus</i>	China	40.41	3.18	0.03
Grif 1734	<i>C. lanatus</i>	China	18.82	1.41	0.01
PI 635600	<i>C. lanatus</i>	United States	68.84	5.95	0.05
PI 226459	<i>C. lanatus</i>	Iran	44.72	3.85	0.03
PI 635603	<i>C. lanatus</i>	United States	57.58	5.74	0.05
PI 635741	<i>C. lanatus</i>	United States	30.45	2.96	0.03
PI 276445	<i>C. lanatus</i>	Jordan	15.19	1.39	0.01
PI 438677	<i>C. lanatus</i>	Mexico	69.52	5.66	0.05
PI 179881	<i>C. lanatus</i>	India	40.56	3.17	0.03
PI 490375	<i>C. lanatus</i>	Mali	93.40	7.35	0.06
PI 635606	<i>C. lanatus</i>	United States	17.35	1.41	0.01
PI 536449	<i>C. lanatus</i>	Maldives	35.98	3.52	0.03
PI 536459	<i>C. lanatus</i>	Maldives	58.80	5.37	0.05
PI 536464	<i>C. lanatus</i>	Maldives	50.33	4.57	0.04
PI 635609	<i>C. lanatus</i>	United States	29.79	2.49	0.02
PI 635703	<i>C. lanatus</i>	United States	23.86	1.57	0.01
PI 635614	<i>C. lanatus</i>	United States	12.29	0.96	0.01
PI 180426	<i>C. lanatus</i>	India	42.34	3.62	0.03
PI 169290	<i>C. lanatus</i>	Turkey	36.55	2.75	0.02
PI 532813	<i>C. lanatus</i>	China	50.69	5.00	0.05
PI 601101	<i>C. lanatus</i>	United States	36.43	2.44	0.02
PI 228238	<i>C. lanatus</i>	Israel	41.76	3.29	0.03
PI 270525	<i>C. lanatus</i>	Israel	54.15	3.69	0.03
PI 487476	<i>C. lanatus</i>	Israel	30.49	2.49	0.02
PI 226445	<i>C. lanatus</i>	Israel	58.68	5.26	0.04
PI 635616	<i>C. lanatus</i>	United States	27.47	2.50	0.02
PI 179878	<i>C. lanatus</i>	India	46.23	3.81	0.03
PI 254716	<i>C. lanatus</i>	Sudan	34.94	2.98	0.02
PI 345544	<i>C. lanatus</i>	Ukraine	31.12	2.67	0.02
PI 162667	<i>C. lanatus</i>	Argentina	26.40	1.89	0.01
PI 635630	<i>C. lanatus</i>	United States	49.86	4.35	0.04
PI 601307	<i>C. lanatus</i>	United States	18.61	1.39	0.01
PI 601308	<i>C. lanatus</i>	United States	15.88	1.01	0.01

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Supplemental Table 2. (Continued) Evaluation of root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) across the 335 *Citrullus* sp. accessions that were grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 675114	<i>C. lanatus</i>	United States	24.81	1.80	0.01
PI 490385	<i>C. lanatus</i>	Mali	77.91	4.73	0.03
PI 518610	<i>C. lanatus</i>	Soviet Union	41.17	3.88	0.03
PI 379231	<i>C. lanatus</i>	Macedonia	9.36	0.98	0.01
PI 254623	<i>C. lanatus</i>	Sudan	35.54	3.28	0.03
PI 212208	<i>C. lanatus</i>	Greece	28.79	2.70	0.03
PI 270306	<i>C. lanatus</i>	Philippines	33.73	3.56	0.03
PI 270546	<i>C. lanatus</i>	Ghana	28.60	2.76	0.02
PI 271981	<i>C. lanatus</i>	Somalia	34.27	3.04	0.03
PI 277970	<i>C. lanatus</i>	Turkey	32.63	3.14	0.03
PI 207473	<i>C. lanatus</i>	Afghanistan	42.12	3.57	0.03
PI 212287	<i>C. lanatus</i>	Afghanistan	18.64	1.71	0.01
PI 212983	<i>C. lanatus</i>	India	40.37	2.96	0.02
PI 277987	<i>C. lanatus</i>	Turkey	51.44	5.04	0.04
PI 183218	<i>C. lanatus</i>	Egypt	30.90	2.50	0.02
PI 212209	<i>C. lanatus</i>	Greece	23.71	2.23	0.02
PI 271982	<i>C. lanatus</i>	Somalia	17.53	1.86	0.02
PI 277996	<i>C. lanatus</i>	Turkey	38.65	4.23	0.04
PI 211851	<i>C. lanatus</i>	Iran	15.32	1.30	0.01
PI 273481	<i>C. lanatus</i>	Ethiopia	65.01	5.96	0.05
PI 278003	<i>C. lanatus</i>	Turkey	24.07	2.05	0.02
PI 276658	<i>C. lanatus</i>	Russia	25.89	2.62	0.02
PI 278007	<i>C. lanatus</i>	Turkey	54.09	5.64	0.05
PI 189316	<i>C. lanatus</i>	Nigeria	44.06	3.38	0.02
PI 211915	<i>C. lanatus</i>	Iran	24.65	1.67	0.01
PI 270550	<i>C. lanatus</i>	Ghana	31.49	2.51	0.02
PI 278020	<i>C. lanatus</i>	Turkey	46.76	3.54	0.03
PI 270551	<i>C. lanatus</i>	Ghana	27.99	2.35	0.02
PI 278031	<i>C. lanatus</i>	Turkey	41.68	4.01	0.04
PI 189317	<i>C. lanatus</i>	Nigeria	33.00	2.78	0.02
PI 211917	<i>C. lanatus</i>	Iran	20.10	2.01	0.02
PI 277976	<i>C. lanatus</i>	Turkey	32.27	2.73	0.02
PI 278041	<i>C. lanatus</i>	Turkey	17.82	1.56	0.01
PI 277977	<i>C. lanatus</i>	Turkey	4.57	0.42	0.00
PI 635618	<i>C. lanatus</i>	United States	55.57	6.24	0.06
PI 534597	<i>C. lanatus</i>	Syria	40.31	3.29	0.03
PI 345545	<i>C. lanatus</i>	Ukraine	28.14	2.55	0.02
PI 534587	<i>C. lanatus</i>	Syria	36.34	3.02	0.02
PI 222137	<i>C. lanatus</i>	Algeria	44.48	4.10	0.04
PI 635619	<i>C. lanatus</i>	United States	23.68	2.07	0.02
PI 635662	<i>C. lanatus</i>	United States	26.66	2.35	0.02
Picnic	<i>C. lanatus</i>	United States	22.49	1.65	0.01
Princecharles	<i>C. lanatus</i>	United States	19.34	1.39	0.01
PI 164633	<i>C. lanatus</i>	India	45.54	3.33	0.03
PI 543211	<i>C. lanatus</i>	Bolivia	43.25	4.33	0.04
Sangria	<i>C. lanatus</i>	United States	18.30	1.15	0.01
PI 635654	<i>C. lanatus</i>	United States	22.31	1.41	0.01
PI 227205	<i>C. lanatus</i>	Japan	21.54	1.72	0.02
PI 635620	<i>C. lanatus</i>	United States	40.00	4.12	0.04
PI 635621	<i>C. lanatus</i>	United States	51.08	5.56	0.05
PI 279459	<i>C. lanatus</i>	Japan	26.96	2.72	0.02
PI 665007	<i>C. lanatus</i>	United States	19.72	1.61	0.01
PI 635631	<i>C. lanatus</i>	United States	73.45	6.48	0.05
PI 635732	<i>C. lanatus</i>	United States	25.22	1.49	0.01
PI 635716	<i>C. lanatus</i>	United States	18.75	1.21	0.01
PI 250146	<i>C. lanatus</i>	Pakistan	34.37	2.95	0.02
PI 182935	<i>C. lanatus</i>	India	41.85	3.38	0.03
PI 249559	<i>C. lanatus</i>	Thailand	42.79	3.59	0.03
PI 482332	<i>C. lanatus</i>	Zimbabwe	65.19	5.51	0.05
PI 482255	<i>C. lanatus</i>	Zimbabwe	41.73	2.99	0.02
PI 482341	<i>C. lanatus</i>	Zimbabwe	30.70	2.72	0.02
PI 482362	<i>C. lanatus</i>	Zimbabwe	59.74	4.13	0.03
PI 482258	<i>C. lanatus</i>	Zimbabwe	30.72	2.09	0.02
PI 482262	<i>C. lanatus</i>	Zimbabwe	69.12	6.68	0.06
PI 482264	<i>C. lanatus</i>	Zimbabwe	65.05	5.52	0.05
PI 482268	<i>C. lanatus</i>	Zimbabwe	31.25	2.43	0.02
PI 482248	<i>C. lanatus</i>	Zimbabwe	40.15	2.95	0.02
PI 482287	<i>C. lanatus</i>	Zimbabwe	58.00	5.56	0.05
PI 269681	<i>C. lanatus</i>	Belize	25.55	1.91	0.02
PI 512395	<i>C. lanatus</i>	Spain	37.91	3.20	0.03
PI 512374	<i>C. lanatus</i>	Spain	36.23	2.82	0.02
PI 635712	<i>C. lanatus</i>	United States	38.59	3.62	0.03
PI 537267	<i>C. lanatus</i>	Pakistan	18.52	1.48	0.01

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Supplemental Table 2. (Continued) Evaluation of root morphological traits within the 0- to 0.5-mm root diameter size class (secondary roots) across the 335 *Citrullus* sp. accessions that were grown under greenhouse conditions.

Accession	Species	Country of origin	TRL (cm)	TSA (cm ²)	TRV (cm ³)
PI 537271	<i>C. lanatus</i>	Pakistan	42.56	3.71	0.03
PI 381734	<i>C. lanatus</i>	India	66.28	4.98	0.04
PI 179234	<i>C. lanatus</i>	Turkey	63.40	4.51	0.03
PI 505586	<i>C. lanatus</i>	Zambia	40.20	3.96	0.03
PI 500301	<i>C. lanatus</i>	Zambia	47.42	3.57	0.03
PI 500314	<i>C. lanatus</i>	Zambia	42.17	3.81	0.03
PI 500319	<i>C. lanatus</i>	Zambia	81.38	7.07	0.06
PI 500328	<i>C. lanatus</i>	Zambia	48.24	4.76	0.04
PI 500344	<i>C. lanatus</i>	Zambia	30.33	3.03	0.03
PI 500350	<i>C. lanatus</i>	Zambia	35.67	3.64	0.04
PI 260733	<i>C. lanatus</i>	Sudan	33.36	3.14	0.03
PI 247398	<i>Citrullus mucosospermus</i>	Greece	36.64	3.35	0.03
PI 164248	<i>C. mucosospermus</i>	Liberia	30.48	2.24	0.02
PI 184800	<i>C. mucosospermus</i>	Nigeria	49.27	4.22	0.04
PI 185635	<i>C. mucosospermus</i>	Ghana	44.55	3.12	0.02
PI 186489	<i>C. mucosospermus</i>	Nigeria	54.17	4.44	0.04
PI 186490	<i>C. mucosospermus</i>	Nigeria	86.61	6.44	0.05
PI 186975	<i>C. mucosospermus</i>	Ghana	21.83	1.80	0.01
PI 189318	<i>C. mucosospermus</i>	Nigeria	18.13	1.49	0.01
PI 249009	<i>C. mucosospermus</i>	Nigeria	29.73	2.65	0.02
PI 254737	<i>C. mucosospermus</i>	Senegal	48.02	4.06	0.04
PI 254740	<i>C. mucosospermus</i>	Senegal	36.96	2.81	0.03
PI 254741	<i>C. mucosospermus</i>	Senegal	39.35	2.61	0.02
PI 254742	<i>C. mucosospermus</i>	Senegal	57.77	4.67	0.04
PI 306782	<i>C. mucosospermus</i>	Nigeria	108.43	7.70	0.06
PI 326516	<i>C. mucosospermus</i>	Ghana	28.82	1.98	0.01
PI 490381	<i>C. mucosospermus</i>	Mali	55.67	5.02	0.04
PI 490386	<i>C. mucosospermus</i>	Mali	33.76	2.66	0.02
PI 494528	<i>C. mucosospermus</i>	Nigeria	100.85	8.90	0.08
PI 494531	<i>C. mucosospermus</i>	Nigeria	83.37	6.92	0.06
PI 532738	<i>C. mucosospermus</i>	DR Congo	31.20	2.34	0.02
PI 559996	<i>C. mucosospermus</i>	Nigeria	55.58	4.57	0.04
PI 560001	<i>C. mucosospermus</i>	Nigeria	39.62	3.87	0.04
PI 560002	<i>C. mucosospermus</i>	Nigeria	73.94	7.80	0.08
PI 560003	<i>C. mucosospermus</i>	Nigeria	57.82	5.92	0.05
PI 560004	<i>C. mucosospermus</i>	Nigeria	80.49	8.14	0.07
PI 560005	<i>C. mucosospermus</i>	Nigeria	62.43	6.66	0.06
PI 560006	<i>C. mucosospermus</i>	Nigeria	44.16	4.02	0.04
PI 560008	<i>C. mucosospermus</i>	Nigeria	51.65	4.52	0.04
PI 560010	<i>C. mucosospermus</i>	Nigeria	50.00	4.20	0.04
PI 560012	<i>C. mucosospermus</i>	Nigeria	56.62	6.10	0.06
PI 560020	<i>C. mucosospermus</i>	Nigeria	43.57	3.50	0.03
PI 248178	<i>C. mucosospermus</i>	DR Congo	38.20	2.67	0.02
LSD ($\alpha = 0.05$)			19.65	1.61	0.01

TRL = total root length; TSA = total root surface area; TRV = total root volume; LSD = least significant difference.