HortScience 54(1):38–44. 2019. https://doi.org/10.21273/HORTSCI13333-18

Variation for Salinity Tolerance During Seed Germination in Diverse Carrot [*Daucus carota* (L.)] Germplasm

Adam Bolton
Department of Horticulture, University of Wisconsin – Madison, 1575 Linden Drive, Madison, WI 53706

Philipp Simon[1]
U.S. Department of Agriculture – ARS, Vegetable Crop Unit, Department of Horticulture, University of Wisconsin – Madison, 1575 Linden Drive, Madison, WI 53706

Additional index words. *Daucus carota*, breeding, salinity, diversity

***Abstract*. Global carrot production is limited by the crop's high susceptibility to salinity stress. Not much public research has been conducted to screen for genetic salinity stress tolerance in carrot, and few resources exist to aid plant breeders in improving salinity tolerance in carrot. The objectives of this study were to evaluate the response of diverse carrot germplasm to salinity stress, identify salt-tolerant carrot germplasm that may be used by breeders, and define appropriate screening criteria for assessing salt tolerance in germinating carrot seed. Carrot plant introductions (PIs) (n = 273) from the U.S. Department of Agriculture (USDA) National Plant Germplasm System representing 41 different countries, inbred lines from the USDA Agricultural Research Service (n = 16), and widely grown commercial hybrids (n = 5) were screened for salinity tolerance under salinity stress and nonstress conditions (150 and 0 mM NaCl, respectively) by measuring the absolute decrease (AD) in the percent of germination, inhibition index (II), relative salt tolerance (RST), and salt tolerance index (STI) of germinating seeds. All salt tolerance measurements differed significantly between accessions; AD ranged from −4.2% to 93.0%; II ranged from −8.0% to 100.0%; RST ranged from 0.0 to 1.08; and STI ranged from 0.0 to 1.38. Broad sense heritability calculations for these measurements were 0.87 or more, indicating a strong genetic contribution to the variation observed. Six accessions identified as salt-tolerant or salt-susceptible were evaluated in a subsequent experiment conducted at salt concentrations of 0, 50, 100, 150, 200, and 250 mM NaCl. Variations between mean AD, II, RST, and STI of tolerant and susceptible lines were greatest at 150 mM NaCl, validating the use of 150 mM NaCl concentrations during salt tolerance screening of carrot seed. Wild carrot accessions displayed little tolerance, and PI 256066, PI 652253, PI 652402, and PI 652405 from Turkey were most salt-tolerant.**

Salinity stress is considered one of the most important abiotic factors that limits the productivity of crop plants (Flowers and Yeo, 1995), and the estimated global cost due to salinity is more than $12 billion annually (Qadir et al., 2008). Annually, ≈10 million hectares of land are becoming salinized to a point where the land can no longer sustain adequate crop production. This is due to the extensive use of irrigation and high rates of evapotranspiration, which result in increased salt accumulating in the soil (Rozema and Flowers, 2008). Most crops, including cultivated carrot (*Daucus carota* var. *sativus*), are categorized as glycophytic plants. The growth of glycophytes is greatly reduced in saline soils because they lack physiological mechanisms such as salt glands and bladders that allow halophytes, which are salt-loving plants, to thrive in high salinity (Flowers et al., 2010). One approach to combating the negative effects of salinity stress in glycophytic crops is identifying new genetic sources of tolerance and efficient phenotypic methods to develop salinity-tolerant cultivars (Munns, 2005).

Data collected from many crop species suggest that the level of salinity tolerance is highly dependent on the developmental stage of the plant (Chinnusamy et al., 2005). This life stage-specific tolerance means that a genotype that has tolerance at one life stage may not be tolerant at earlier or later stages. Therefore, to more effectively identify tolerant genotypes, evaluation needs to occur throughout the varying stages of ontogeny of the plant, from germination through the reproductive phase. This type of extensive evaluation is needed to develop varieties that are considered fully tolerant at each developmental stage for carrots.

Screening for salt tolerance at the germination stage is the first step in identifying tolerant genotypes because it is a critical stage for plant development. A number of studies of several crop species, including alfalfa, barley, corn, red kidney bean, and sugar beet (Abel and MacKenzie, 1964), tomato (Cuartero and Fernández-Muñoz, 1998; Foolad and Lin, 1997), grain sorghum (Francois et al., 1984), sugar beet, cabbage, amaranth, and pak choi (Jamil et al., 2006), corn (Maas et al., 1983), cowpea (Ravelombola et al., 2017), and lettuce (Xu and Mou, 2015) have demonstrated that the percent of germination is adversely affected as salinity increases, decreasing the osmotic potential and thus lowering the water potential. Fortunately, screening for salinity tolerance at the germination stage is one of the most rapid and economical stages of development to evaluate a large number of diverse germplasm accessions for tolerance.

Carrot (*Daucus carota* L.; $2n = 2x = 18$) is an economically important root vegetable crop worldwide; every year, 38 million metric tons of carrots are produced on 1.2 million hectares globally. Carrot is widely produced throughout Asia and in the United States, where it is the sixth most consumed fresh vegetable, with more than 80% of U.S. production under irrigation in California (FAO, 2017). Carrot is an important crop for world nutritional security because it is one of the leading dietary sources of provitamin A carotenoids (α-carotene and β-carotene) in the human diet. In the United States, carrots account for 30% of dietary β-carotene and 62% of dietary α-carotene (Simon et al., 2009).

Cultivated carrot (*Daucus carota* var. *sativus*) is one of the most salt-sensitive vegetable crops (Bernstein and Ayers, 1953; Maas and Hoffman, 1977). To date, there have been few evaluations of the salinity tolerance of carrot during the seed germination stage (Kahouli et al., 2014; Rode et al., 2012; Schmidhalter and Oertli, 1991). These studies suggest that carrot seed germination suffers greatly from increased salt concentrations having both total seed germination and rate of germination decrease under salinity stress with these effects becoming more drastic as the concentration of salts increases. The results of these evaluations indicated that concentrations in the range of 125 mM to 150 mM NaCl differentiate the tolerant and sensitive accessions of carrot. In the most expansive evaluation, Kahouli et al. (2014) evaluated 10 carrot accessions from Tunisia. The current lack of information regarding salinity tolerance during the germination stage for carrot suggests the need for a large germplasm evaluation to identify potentially tolerant accessions that could be used for breeding or other studies. The objectives of this study were to evaluate the responses of 294 diverse carrot germplasm accessions, inbred lines, and commercial cultivars to salinity stress during the germination stage, to identify the best measurement for assessing salt tolerance in carrot at the germination stage, and to identify salt-tolerant accessions of carrot to be used in breeding programs and other research.

Received for publication 17 July 2018. Accepted for publication 18 Sept. 2018.
We thank the Global Crop Diversity Trust Project GS14014 for providing financial support. We also thank Kathleen Reitsma and the USDA National Germplasm System for their capable assistance and for providing the plant introduction carrot collection accessions.
[1]Corresponding author. E-mail: psimon@wisc.edu.

Materials and Methods

Germplasm. A total of 294 carrot accessions consisting of 273 accessions (210 cultivated and 63 wild) from the USDA National Plant Germplasm System (NPGS) collection of plant introductions (PIs) in Ames, IA, 16 inbred lines from the USDA carrot breeding program, and 5 widely grown commercial carrot hybrids were included in this analysis. Commercial cultivars were categorized by root color (Supplemental Table 1). The 294 carrot accessions originated from 41 countries and were classified into 14 geographic regions based on their origin (Eastern Africa, Northern Africa, South Africa, North America, South America, Central Asia, Eastern Asia, Southern Asia, Western Asia, Eastern Europe, Northern Europe, Southern Europe, Western Europe, and Oceania). These PIs represented much of the world's genetic diversity for carrot (Iorizzo et al., 2013).

Germination assay. Twenty seeds from each carrot accession were placed on P5 filter paper in 60-×15-mm petri dishes (Fisher Scientific, Waltham, MA). Each petri dish was filled with 7 mL of a 150-mM NaCl solution or deionized water (0 mM NaCl) for the salt stress and control treatments, respectively. Petri dishes were stacked in large plastic bins and placed in complete dark at 23°± 1°. Each accession–treatment combination was present in six total replications in a randomized complete block design, with each bin acting as a replication. The design and conditions were similar to those used in other studies (Maas et al., 1983; Ravelombola et al., 2017).

Evaluation using 150 mM NaCl. Seed germination data were collected for a total of 18 d, with measurements taken 2, 4, 6, 10, 14, and 18 d after sowing. A seed was classified as germinated when the radicle had emerged and was longer than 1 mm. At each measurement time, any seed that had germinated was counted and removed from the petri dish. Standard criteria for determining the performance of carrot accessions under salinity included: 1) final percent of germination under nonstress conditions ($PG_{Control}$); 2) final percent of germination under salt stress (PG_{NaCl}); 3) absolute decrease (AD) due to salt; 4) inhibition index (II); 5) relative salt tolerance (RST); and 6) salt tolerance index (STI) (Ravelombola et al., 2017). These measurements were calculated using the following equations: $AD = PG_{Control} - PG_{NaCl}$; $II = 100 * (PG_{Control} - PG_{NaCl})/(PG_{Control})$; $RST = PG_{NaCl}/PG_{Control}$; $STI = (PG_{NaCl} * PG_{Control})/(PG_{Average})^2$, where $PG_{Average}$ is the average percent of germination of all carrot accessions evaluated under no salt stress.

Evaluations using varying salt concentrations. After the initial germplasm evaluation, a second experiment was conducted to evaluate the germination of a subset of both tolerant and sensitive accessions with a range of NaCl concentrations. Using the same design as described, six carrot accessions (three tolerant and three sensitive) (Table 1) were tested to determine the percent of seed germination using six concentrations of salt (0, 50, 100, 150, 200, and 250 mM NaCl) for 7 d. These concentrations were obtained by dissolving 1.46, 2.92, 4.38, 5.85, and 7.3 g of sodium chloride (Fisher Scientific) in 500 mL of distilled water.

Data analysis. The statistical model used to analyze each of the six measurements was as follows: $Y_{ij} = \mu + R_i + A_j + \varepsilon_{ij}$, where Y_{ij} is the value of the measurements for the *j*th carrot accession in the *i*th replication, where $i = 1, \ldots, 6$ and $j = 1, \ldots, 296$, μ is the total mean (constant), R_i is the effect of the *i*th replication (random effect) on the response measurement, A_j is the effect of the *j*th accession (fixed effect) on the response measurement, and ε_{ij} is the effect of the experimental error associated with *ij*th observation. All analyses were performed using R.3.4.4 (R Core Team, 2018). The analysis of variance (ANOVA) test was performed using the lmer function in the lme4 package (Bates et al., 2018). The least significant difference (LSD) test, with $\alpha = 0.05$, of the mean separation was performed using the LSD test function found in the agricolae package (De Mendiburu, 2014). Pearson rank correlations of measurements were calculated using the cor function found in the stats package (R Core Team, 2018).

The variance values of the among-accession and within-accession measurements were used for calculating broad-sense heritability (H^2), as derived from the work of Falconer and Mackay (1996). $H^2 = (\sigma^2_G/\sigma^2_P) = [\sigma^2_G/(\sigma^2_G + (\sigma^2_E/r) + (\sigma^2_R/r)]$, where σ^2_G = genotypic (accession) variance, σ^2_P = phenotypic variance, σ^2_E = variance due to experimental error, σ^2_R = variance due to replication, and r is the number of replications for each treatment.

Variance components were derived using the following formulas: $\sigma^2_G = (MSA - MSE)/r$, $\sigma^2_E = MSE$, $\sigma^2_R = (MSR - MSE)/n$, where MSA is the mean square accession, MSE is the mean square error, MSR is the mean square replication, r is the number of replications, and n is the number of accessions.

Results and Discussion

Germination assay. The average percent of germination for the 294 carrot accessions under nonstress conditions ranged from 50.0% to 100.0%, with a mean of 81.6% (SD, 12.6%). Germinating seeds in 150 mM NaCl solution reduced the average percent of germination to 37.0% (range, 0.0% to 95.0%; SD, 25.7%) (Fig. 1). These data indicated that salinity stress significantly reduced the percent of germination in most, but not all, carrot germplasm, as indicated by previous studies. For all salt stress-related traits, there was a significant replication effect ($P < 0.0001$) that may have been attributable to human error in phenotyping germination and to variations in the microenvironment within the boxes where the seed was germinated. The average percent of germination varied significantly among carrot accessions under control

Table 1. Three tolerant and three susceptible carrot accessions with the percent of germination without salt stress (Nonstress) using 150 mM salt stress (Stress), relative salt tolerance (RST), absolute decrease (AD), inhibition index (II), and salt tolerance index (STI).

Accession	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI
PI 652402	95.00	93.75	1.25	1.10	0.99	1.37
PI 652403	94.38	91.25	3.13	3.19	0.97	1.32
PI 652405	98.13	95.63	2.50	2.53	0.97	1.44
PI 225869	91.68	5.63	86.05	94.18	0.06	0.08
B2566B	90.00	5.63	84.38	93.03	0.07	0.07
PI 269487	87.47	6.25	81.22	92.25	0.08	0.08

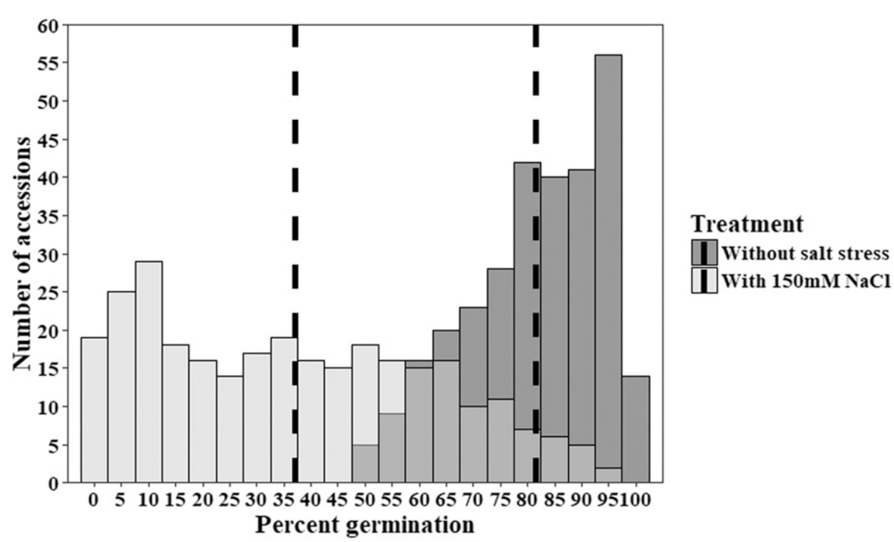

Fig. 1. Distribution and mean (dotted line) percent of seed germination among 294 carrot accessions without salt stress (dark gray) and with salt stress (light gray).

conditions ($F = 8.24$; $P < 0.0001$) (Table 2). PI 632391, PI 642756, PI 643119, and PI 652374 all had the maximum percent of germination values (100.0%), whereas PI 502914, PI 508473, PI 652154, and PI 652253 had the lowest percent of germination (50.0% to 52.2%) under nonstress conditions (Table S1). Percent germination under salt stress also varied significantly among carrot accessions ($F = 12.42$; $P < 0.0001$) (Table 2). Under salt stress conditions, B493B, Nb6526, PI 177381, PI 279764, PI 652344, and PI 652380 all had the lowest percent of germination (0.0%), indicating that they were especially salt-sensitive accessions, whereas PI 652374, PI 652402, and PI 652405 (91.7% to 95.0%) all performed well under salt stress conditions, indicating that they are salt-tolerant accessions.

Interestingly, several cultivated PIs from Turkey displayed the highest level of tolerance. PI 652402, PI 652403, and PI 652405 all had low AD and II values (1.6% to 3.4%), high RST values (0.97 to 0.98), and high STI values (1.28 to 1.38). In fact, most cultivated carrot from Turkey and other countries with low rainfall and, consequently, very reliant on irrigation for carrot production were relatively salt-tolerant. These results suggest that carrot cultivated in more saline soils over time were selected for higher levels of salt tolerance. The most sensitive carrot accessions were wild PIs or inbred lines. Inbred lines B493B and Nb6526B, along with wild carrot from Turkey, Syria, and Libya (PI 177381, PI 279764, PI 652344, and PI 652380), all had 0.0% germination under salt stress; therefore, they had II values of 100.0%, AD values ranging from 56.0% to 83.0%, and the lowest possible RST and STI values (0.0). Many of the most susceptible accessions were wild, which is contrary to what has been observed in many other species in which abiotic stress tolerance has been identified in wild relatives. It should be noted that not all wild carrot types were salt-susceptible. In fact, several wild carrots evaluated were relatively salt-tolerant, perhaps because they were collected from naturally saline nonagricultural land.

The AD measures the decrease in the percent of germination between nonstress conditions and salt stress ($PG_{Control} - PG_{NaCl}$). For the carrot accessions evaluated in this experiment, salt stress reduced the percent of germination from –4.2% to 93.0% (Fig. 2A). AD varied significantly among carrot accessions ($F = 7.87$; $P < 0.0001$) (Table 2). PI 515990 (93.0%) had the highest AD, indicating it is a salt-sensitive accession, and PI 256066 (–4.2%) had the lowest and only negative AD, indicating that salt stress increased the percent of germination.

The II for germination ($100*AD/PG_{Control}$) was significantly different among accessions ($F = 8.51$; $P < 0.0001$) (Table 2) and ranged from –8.0% to 100.0% (Fig. 2B). The six sensitive accessions mentioned all had the highest II values of 100.0%, which followed the same trends as the salt stress percent of germination and AD values, indicating that they were highly salt-sensitive accessions. PI 256066 and PI 652253 had the lowest II values (–8.0% to –1.4%), indicating high levels of salt tolerance during the seed germination stage.

Table 2. ANOVA for six measurements related to seed germination among 294 carrot accessions.

Measurement	Source	DF	Sum of squares	Mean square	F ratio	$P > F$
Germination without salt stress	Rep	5	227.00	45.49	0.40	0.8487
	Accession	293	274,243.00	935.98	8.24	<2.0E-16
	Error	1,446	164,227.00	113.57		
Germination with salt stress	Rep	5	10,805.00	2,161.10	6.86	2.46E-06
	Accession	293	1,146,503.00	3,913.00	12.42	<2.2E-16
	Error	1,446	455,609.00	315.10		
Absolute decrease	Rep	5	13,473.00	2,694.50	6.37	7.42E-06
	Accession	293	975,915.00	3,330.80	7.87	<2.2E-16
	Error	1,446	612,135.00	423.30		
Inhibition index	Rep	5	18,079.00	3,615.90	5.86	2.28E-05
	Accession	293	1,538,453.00	5,250.70	8.51	<2.2E-16
	Error	1,446	892,224.00	617.00		
Relative heat tolerance	Rep	5	1.84	0.37	5.95	1.86E-05
	Accession	293	153.19	0.52	8.46	<2.2E-16
	Error	1,446	89.32	0.06		
Heat tolerance index	Rep	5	1.57	0.31	5.64	3.75E-05
	Accession	293	229.51	0.78	14.04	<2.2E-16
	Error	1,446	80.65	0.06		

DF = degrees of freedom.

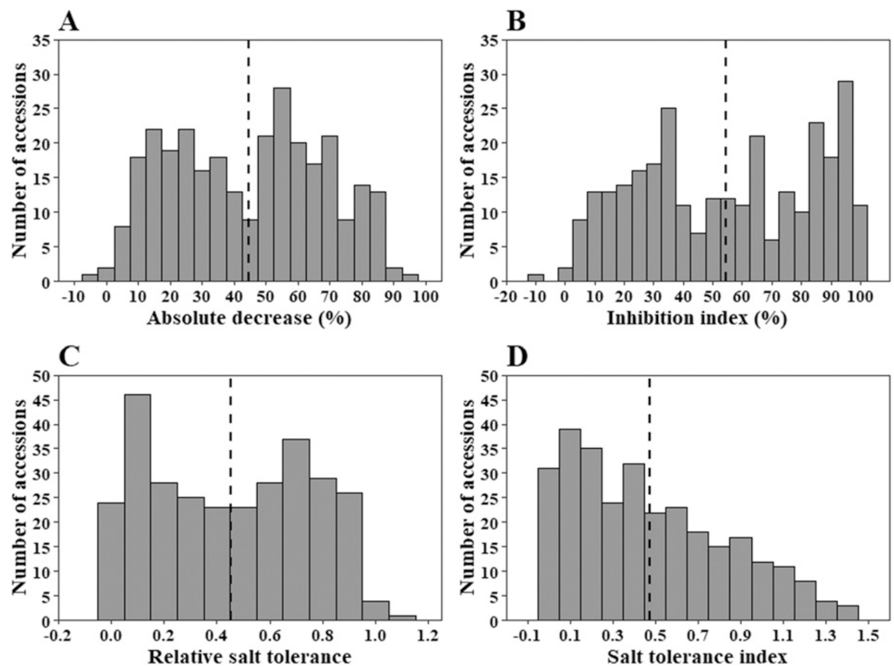

Fig. 2. Distribution and mean (dotted line) percent of seed germination among 294 carrot accessions with four different measures of salt tolerance: (**A**) absolute decrease; (**B**) inhibition index; (**C**) relative salt tolerance; and (**D**) salt tolerance index.

Relative salt tolerance ($RST = PG_{NaCl}/PG_{Control}$) was significantly different among accessions ($F = 8.46$; $P < 0.0001$) (Table 2) and ranged from 0 to 1.08, with a mean of 0.56 (Fig. 2C). The four wild PIs and two inbred lines previously mentioned had the lowest RST value of 0, indicating high salt sensitivity. PI 256066 (1.08) and PI 652253 (1.00) had the highest RST values, indicating that they were salt-tolerant when considering their percent of germination under nonstress conditions.

The STI [$STI = PG_{NaCl}*PG_{Control})/(PG_{Average})^2$] is an important measurement of salt tolerance when comparing the tolerance of one accession to the rest of the collection (Saad et al., 2013). STI in this analysis ranged from 0 to 1.38, with a mean of 0.47 (SD, 0.36) (Fig. 2D), and it was significantly different among accessions ($F = 14.04$; $P < 0.0001$) (Table 2). The six accessions with the lowest RST value also had the lowest STI value of 0, indicating low salt tolerance, whereas the tolerant cultivated accessions from Turkey, PI 652402 and PI 652405, both had the highest STI value of 1.38.

These multiple criteria for quantifying salt tolerance demonstrated wide phenotypic variations in salt tolerance during the seed germination stage among diverse carrot accessions. Exposure to 150 mM salt solution significantly reduced the percent of germination for most of the carrot diversity panel, thus agreeing with the results of similar studies of other species (Abel and MacKenzie, 1964; Cuartero and Fernández-Muñoz, 1998;

Ravelombola et al., 2017) and with smaller studies involving carrots (Rode et al., 2012; Schmidhalter and Oertli, 1991). This evaluation found a wider range of variations for salt tolerance in carrot during the germination stage than did previous studies. For example, Kahouli et al. (2014) identified a percent of germination range of 45.0% to 85.0% at 137 mM NaCl and of 15.0% to 50.0% at 171 mM NaCl for 10 carrot accessions. We observed a range of 0.0% to 95.0% at 150 mM NaCl, thus reinforcing the value of evaluating a large diverse germplasm collection for salt tolerance traits.

Salt tolerance according to geographic origin. Significant differences in the percent of seed germination under nonstress conditions and for all salt tolerance germination measurements were observed among the 14 different regions of carrot accession origin ($P < 0.0001$) (Table 3). When evaluating all cultivated, wild, inbred, and hybrid accessions together, accessions from Southern and Eastern Asia displayed higher salt tolerance during the germination stage. Accessions from Southern Asia had a mean AD of 30.4% (range, –4.2% to 82.4%), a mean II of 40.0% (range, –8.0% to 100.0%), mean RST value of 0.6 (range, 0.00 to 1.1), and mean STI value of 0.56 (range, 0.00 to 1.22). Accessions from Eastern Asia had similar values and ranges as those of Southern Asia, with a mean AD of 33.1% (range, –5.0% to 70.0%), a mean II of 33.5% (range, 6.2% to 95.5%), mean RST value of 0.61 (range, 0.04 to 0.94), and mean STI value of 0.59 (range, 0.04 to 1.12). Oceania and South America each had only one accession, but they were among the most sensitive to salt stress during the germination stage (Table 4). Although accessions from Southern and Eastern Asia were more salt-tolerant than those of other regions, it is still important to note the wide range of variations among accessions from a single geographical region. For example, PI 256065 from Afghanistan and PI 274297 from Pakistan only had 2.5% germination under salt stress. These results reflect the importance of evaluating multiple accessions from within a single region.

When evaluating the cultivated PIs, accessions from Northern Africa, Western Asia, and North America displayed higher tolerance, with mean II and AD values ranging from 19.80% to 20.02%, along with RST and STI values ranging from 0.70 to 0.94. Accessions from Northern Europe, Eastern Africa, and Oceania had lower tolerance, with mean II and AD values ranging from 55.04% to 89.72%, as well as RST and STI values ranging from 0.10 to 0.33 (Table 5). These results suggest that the geographic origin significantly influenced salt tolerance, and it can be speculated that geographic origin is a factor influencing carrot adaptation to sub-optimal growing conditions, as has been seen in other plant species (Baxter et al., 2010; Khoury et al., 2015). Interestingly, although Central Asia is the center of origin of cultivated carrots (Iorizzo et al., 2013), greater diversity has been observed in salinity tolerance in other geographic regions, likely reflecting germplasm response to varying local conditions. To identify salt-tolerant germplasm at later stages of development, and to identify other abiotic stress tolerance traits, it will be critical to screen multiple accessions from diverse geographic regions of the world to best determine the full range of phenotypic variation.

Among wild PIs, accessions from Eastern Asia displayed the highest tolerance, with mean II, AD, RST, and STI values of 33.49%, 24.74% 0.66, and 0.51, respectively. Wild PIs from South America, Western Asia, and Central Asia had low tolerance, with mean

Table 3. ANOVA for six measurements related to seed germination among carrot accessions from 14 geographic regions of origin.

Measurement	Source	DF	Sum of squares	Mean square	F ratio	$P > F$
Germination without salt stress	Replication	5	227.00	45.49	0.19	0.968
	Region	13	16,375.00	1,259.59	5.15	4.52E-09
	Error	1,726	422,095.00	244.55		
Germination with salt stress	Replication	5	10,805.00	2,161.10	2.51	0.02818
	Region	13	118,092.00	9,084.00	10.57	<2.2E-16
	Error	1,726	1,484,021.00	859.80		
Absolute decrease	Replication	5	13,473.00	2,694.50	3.22	6.70E-03
	Region	13	144,831.00	11,140.80	13.32	<2.2E-16
	Error	1,726	1,443,219.00	836.20		
Inhibition index	Replication	5	18,079.00	3,615.90	2.80	1.59E-02
	Region	13	201,691.00	15,514.70	12.01	<2.2E-16
	Error	1,726	2,228,985.00	1,291.40		
Relative salt tolerance	Replication	5	1.84	0.37	2.85	1.43E-02
	Region	13	19.93	1.53	11.89	<2.2E-16
	Error	1,726	222.58	0.13		
Salt tolerance index	Replication	5	1.57	0.31	1.86	9.75E-02
	Region	13	19.21	1.48	8.99	<2.2E-16
	Error	1,726	290.95	0.17		

DF = degrees of freedom.

Table 4. Mean separation of four salt tolerance measurements across 14 geographic regions of origin for all 294 accessions (63 wild PIs, 210 cultivated PIs, 16 inbred lines, and 5 hybrids).

Region of origin	Relative salt tolerance index		Salt tolerance index		Absolute decrease (%)		Inhibition index (%)	
Southern Asia	0.60	A[z]	0.56	AB	30.35	D	39.78	D
Eastern Asia	0.60	A	0.60	A	33.16	D	39.04	D
Northern Africa	0.56	AB	0.50	AB	37.88	CD	44.24	CD
Southern Asia	0.52	ABC	0.57	AB	41.97	CD	48.17	CD
North America	0.48	BC	0.61	A	43.97	C	52.19	C
Central Asia	0.46	BC	0.49	B	42.10	C	54.14	C
Eastern Europe	0.42	CD	0.43	B	49.86	BC	58.00	BC
Western Europe	0.37	CDE	0.38	BC	51.93	BC	63.50	ABC
Western Asia	0.36	CDE	0.39	BC	51.64	BC	63.80	ABC
Northern Europe	0.33	DE	0.31	C	55.04	ABC	66.91	ABC
Eastern Africa	0.29	DE	0.33	BC	57.50	ABC	71.20	ABC
Southern Europe	0.29	E	0.27	C	57.91	AB	71.40	AB
South America	0.15	E	0.19	C	77.45	A	84.61	AB
Oceania	0.10	E	0.12	C	68.22	AB	89.72	A

[z]Means with the same letter are not significantly different using Fisher's least significant difference test at alpha = 0.05.

Table 5. Mean separation for four salt tolerance measurements based on region of origin among 210 cultivated carrot accessions.

Region of origin	Relative salt tolerance index		Salt tolerance index		Absolute decrease (%)		Inhibition index (%)	
Northern Africa	0.78	A[z]	0.70	BC	19.80	EF	22.16	E
Western Asia	0.76	A	0.82	B	18.89	F	23.70	E
North America	0.70	A	0.94	A	28.71	DE	30.02	DE
Southern Asia	0.66	AB	0.63	C	25.99	E	34.02	CD
Eastern Asia	0.61	B	0.60	C	33.40	CD	39.20	C
South Africa	0.52	BC	0.57	CD	41.97	BC	48.17	BC
Central Asia	0.50	C	0.54	CD	39.08	BCD	49.72	BC
Southern Europe	0.48	CD	0.43	DE	41.67	BCD	51.78	BC
Eastern Europe	0.43	CD	0.45	D	48.92	AB	56.80	B
Western Europe	0.38	CD	0.39	DE	51.23	AB	62.47	B
Northern Europe	0.33	DE	0.31	E	55.04	AB	66.91	AB
Eastern Africa	0.29	DE	0.33	DE	57.50	AB	71.20	AB
Oceania	0.10	E	0.12	E	68.22	A	89.72	A

[z]Means with the same letter are not significantly different using Fisher's least significant difference test at alpha = 0.05.

II and AD values ranging from 67.76% to 91.76%, along with RST and STI values of 0.2 or less (Table 6).

Salt tolerance according to domestication status and root color. No significant difference was observed between cultivated PIs, wild PIs, and inbred lines regarding the average percent of germination under nonstress conditions (Table 7). In contrast, cultivated PIs demonstrated significantly greater average salt tolerance during the germination stage than the wild PIs and inbred lines, with a mean percent of germination of 45.4% (range, 0.8% to 95.0%) under salt stress, an AD of 36.7% (range, –4.1% to 93.0%), II of 44.5% (range, –8.0% to 98.8%), RST of 0.55 (range, 0.1 to 1.1), and STI of 0.58 (range, 0.01 to 1.38). Most wild PIs and inbred lines demonstrated a higher level of sensitivity to salt stress than cultivated PIs, with no significant difference between the mean of these two groups. Both groups had a mean percent of germination under stress less than 17%, but with a range from 0.0% to 71.1%, mean AD and II values ranging from 59.9% to 82.0%, and RST and STI values of 0.22 or less (Table 7). Although both domestication status groups were not equally represented in this study, these results suggested that cultivated PIs are an especially promising source of salt tolerance during the germination stage for carrot breeding programs.

Analyzing the mean of each salinity response trait according to the primary root color of cultivated carrot demonstrated that all five color categories had relatively similar average percent of germination values under nonstress conditions. Although there were significant differences between some colors for the various parameters measured, all traits of the red and purple roots were similar and demonstrated the highest average level of salt tolerance, with germination more than 48.0% under salt stress, AD values less than 26.0%, II values less than 34.0%, RST values of 0.70, and STI values of 0.66 (Table 7). Given the relatively few samples of white and red accessions in this study, trends reported here should be confirmed with larger sample sizes.

Evaluations using varying concentrations of NaCl. ANOVA for the percent of seed germination of three tolerant and three sensitive accessions displayed significant treatment (F = 123.5; P < 0.0001) and accession (F = 15.68; P < 0.0001) effects on the percent of seed germination (Table 8), which was not unexpected given the previous findings of this evaluation. The most significant difference between accessions was observed with the 150 mM treatment (F = 90.27; P < 0.0001), confirming that 150 mM was the optimum concentration for screening carrot germplasm for salt tolerance. Treatments using 0 and 50 mM differed only slightly among accessions (P = 0.03 and P = 0.02, respectively) (Table 9). With increased salt concentrations, there was a decrease in the percent of germination for both tolerant and sensitive accessions, and this trend was more noticeable in sensitive accessions (Fig. 3). The pool of sensitive accessions demonstrated a 37.5% reduction in germination when the concentration of salt was increased from 50 to 100 mM. Increasing the NaCl concentration to 150 mM resulted in a further reduction of 42.9%, thus supporting results from the larger accession evaluation, with no germination at 200 and 250 mM NaCl. Tolerant accessions had a minimal reduction (4.6%) in germination when the NaCl concentration was increased from 0 to 100 mM; however, they had a large reduction (64.6%) when it was increased from 150 to 200 mM. No accession had any germination with the 250 mM treatment (Fig. 3), indicating that a concentration between 200 and 250 mM NaCl is the threshold at which germination is completely suppressed. The results of this experiment indicated that future germplasm screening for salt tolerance in diverse carrot accessions should be performed with a concentration of 150 mM NaCl. The identification of carrot germplasm capable of germinating at 200 mM NaCl would be an outstanding discovery.

Broad-sense heritability. High broad-sense heritability (H^2) was identified for all germination-related measurements. Seed germination under nonstress conditions had an H^2 of 0.88, which increased to 0.92 under salt stress. H^2 values were 0.87, 0.88, 0.88, and 0.93 for AD, II, RST, and STI, respectively. The heritability of traits estimated for the carrot accessions evaluated in this analysis was higher than that displayed by cowpea (0.84) (Ravelombola et al., 2017) and by tomato (0.76) (Foolad and Jones, 1992), indicating a significant genetic basis for these traits. These genetic factors warrant further investigation, as has been performed for cowpea (Ravelombola et al., 2018), which was found to have a significant quantitative trait locus (QTL) associated with salt tolerance during the germination stage in mapping populations.

Correlation among salt tolerance parameters and seed weight. Pearson correlation coefficients calculated for each of the salt tolerance measurements and for the hundred seed weight (HSW) of each accession (Table 10) demonstrated that germination under nonstress conditions had a moderate positive linear correlation with STI (r = 0.54) and germination under stress conditions (r = 0.4). This is not surprising because the percent of germination under nonstress conditions sets the upper limit for germination under stress conditions. There was no strong correlation between the nonstress percent of germination and the other four measurements (r range, –0.17 to 0.15), indicating that there was no relationship between the percent of germination under nonstress conditions and salt tolerance. The HSW had a weak positive linear correlation with the percent of germination under salt

Table 6. Mean separation for four salt tolerance measurements based on region of origin among 63 wild carrot accessions.

Region of origin	Relative salt tolerance index		Salt tolerance index		Absolute decrease (%)		Inhibition index (%)	
Eastern Asia	0.66	A[z]	0.51	A	24.74	D	33.49	C
North Africa	0.33	B	0.28	B	56.73	BC	67.27	B
Southern Asia	0.31	B	0.25	B	52.41	C	68.91	B
Western Europe	0.24	BC	0.26	B	63.08	ABC	75.85	AB
Eastern Europe	0.19	BC	0.18	BC	67.50	ABC	80.66	AB
Southern Europe	0.18	C	0.19	BC	66.03	ABC	81.22	AB
South America	0.15	C	0.20	BC	77.46	A	84.61	AB
Western Asia	0.13	C	0.14	C	70.52	A	86.91	A
Central Asia	0.08	C	0.07	C	67.76	AB	91.72	A

[z]Means with the same letter are not significantly different using Fisher's least significant difference test at alpha = 0.05.

Table 7. Mean (± SE) for the percent of germination without salt stress (Nonstress), percent of germination with 150 mM salt stress (Stress), absolute decrease (AD), inhibition index (II), relative salt tolerance (RST), and salt tolerance index (STI) separated by domestication status (DS) and primary root color (excluding wild PIs) with the number of accessions found in each category.

Factor	Category	Accessions	Nonstress (%)		Stress (%)		AD (%)		II (%)		RST		STI	
DS	Cultivated PI	210	82.1 ± 0.9	A[z]	45.4 ± 1.7	A	36.7 ± 1.5	B	45.5 ± 1.8	B	0.55 ± 0.02	A	0.58 ± 0.02	A
	Wild PI	63	80.3 ± 1.2	A	14.2 ± 1.8	B	66.1 ± 2.1	A	82.0 ± 2.5	A	0.18 ± 0.03	B	0.17 ± 0.02	B
	Inbred	16	76.8 ± 3.7	A	16.9 ± 5.0	B	59.9 ± 5.1	A	78.3 ± 6.5	A	0.22 ± 0.06	B	0.21 ± 0.07	B
Color	White	5	84.5 ± 6.7	A	43.2 ± 13.4	A	41.2 ± 12.0	AB	47.8 ± 13.4	AB	0.52 ± 0.14	B	0.57 ± 0.21	A
	Orange	157	82.8 ± 1.1	A	40.9 ± 2.0	A	41.9 ± 1.7	A	51.0 ± 2.2	A	0.49 ± 0.02	AB	0.54 ± 0.03	A
	Yellow	38	82.2 ± 1.8	A	45.8 ± 3.8	A	36.5 ± 3.4	AB	44.3 ± 4.3	AB	0.56 ± 0.04	AB	0.58 ± 0.05	A
	Red	9	76.7 ± 5.0	AB	51.3 ± 6.0	A	25.5 ± 5.9	B	30.1 ± 8.1	B	0.70 ± 0.08	A	0.61 ± 0.09	A
	Purple	19	73.9 ± 3.1	AB	48.1 ± 4.7	A	25.8 ± 4.7	B	33.6 ± 6.0	B	0.66 ± 0.06	A	0.55 ± 0.06	A

[z]Means with the same letter are not significantly different using Fisher's least significant difference test at alpha = 0.05.

Table 8. ANOVA for the percent of seed germination among six carrot accessions using six salt concentrations of NaCl.

Source	DF	Sum of squares	Mean square	F ratio	*P* > F
Replication	3	126.00	42	0.12	0.9457
Treatment	5	208,339.00	41,668	123.5	2.20E-16
Accession	5	26,458.00	5,292	15.68	4.60E-12
Error	130	43,860.00	337		

DF = degrees of freedom.

Table 9. ANOVA for seed germination among six carrot accessions under six concentrations of NaCl.

Salt concn	Source	DF	Sum of squares	Mean square	F ratio	*P* > F
0 mM	Rep	3	25.00	8.33	1.25	0.3268
	Accession	5	108.33	21.67	3.25	0.0347
	Error	15	100.00	6.67		
50 mM	Rep	3	353.13	117.71	4.00	0.0279
	Accession	5	530.21	106.04	3.61	0.0241
	Error	15	440.63	29.38		
100 mM	Rep	3	458.30	152.8	0.51	0.6849
	Accession	5	17,633.30	3,526.7	11.65	9.87E-05
	Error	15	4,541.70	302.8		
150 mM	Rep	3	111.00	37.2	0.44	0.7285
	Accession	5	38,209.00	7,641.9	90.27	1.19E-10
	Error	15	1,270.00	84.7		
200 mM	Rep	3	945.80	315.28	3.40	0.0456
	Accession	5	4,325.00	865	9.32	3.39E-04
	Error	15	1,391.70	92.78		
250 mM	Rep	3	0.00	0		
	Accession	5	0.00	0		
	Error	15	0.00	0		

DF = degrees of freedom.

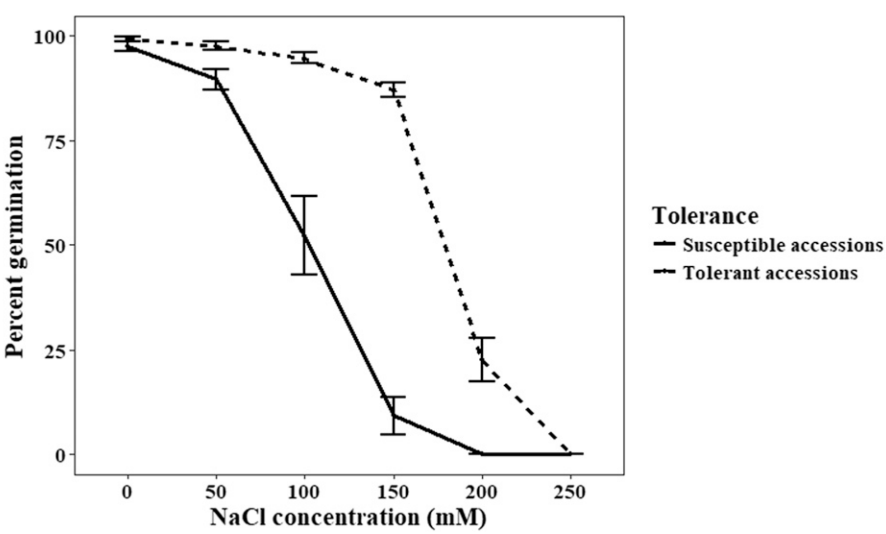

Fig. 3. Pooled percent of seed germination for three sensitive (solid line) and three tolerant (dotted line) carrot accessions using six NaCl concentrations (0, 50, 100, 150, 200, and 250 mM).

Table 10. Correlation among seven salt stress parameters: absolute decrease (AD), hundred seed weight (HSW), inhibition index (II), under nonstressed condition (Nonstress), relative salt tolerance (RST), salt tolerance index (STI), and under salt stress (Stress).

Parameter	Nonstress	Stress	RST	STI	AD	II	HSW
Nonstress	1						
Stress	0.40	1					
RST	0.15	0.95	1				
STI	0.54	0.98	0.87	1			
AD	0.10	–0.87	–0.95	–0.78	1		
II	–0.15	–0.95	–1.00	–0.87	0.95	1	
HSW	–0.17	0.25	0.33	–0.18	–0.36	–0.33	1

stress (r = 0.25) and a negligible negative correlation (r = –0.17) under nonstress conditions. These results suggest that seed weight had minimal effects on the ability of an accession to tolerate salt stress during germination.

Conclusions

This study identified a wide range of phenotypic variations for salt tolerance during the germination stage in a collection of diverse carrot accessions. Five cultivated carrot accessions, all from Turkey (PI 509433, PI 652374, PI 652402, PI 652403, and PI 652405), were identified as salt-tolerant accessions, whereas inbred lines B493B and Nb6526B and four wild accessions (PI 177381, PI 279764, PI 652344, and PI 652380) were identified as highly salt-sensitive accessions. These accessions could serve as potential parents for creating mapping populations to identify the QTL associated with salt tolerance during the germination stage of carrot. The discovery of tolerant cultivated accessions is promising for breeders because they may be used to develop salt-tolerant cultivars. The development of carrot cultivars with tolerance to salt stress will provide growers everywhere with additional tools for growing on salt-affected soil. This evaluation of salt tolerance of diverse carrot germplasm provides valuable information for future studies of salt tolerance of carrots.

Literature Cited

Abel, G.H. and A.J. MacKenzie. 1964. Salt tolerance of soybean varieties (*Glycine max* L. Merrill) during germination and later growth. Crop Sci. 4:157–161.

Bates, D., M. Maechler, B. Bolker, S. Walker, R.H.B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, and P. Green. 2018. Linear mixed-effects models using 'Eigen' and S4. R. package, version 17, p. 42–44.

Baxter, I., J.N. Brazelton, D. Yu, Y.S. Huang, B. Lahner, E. Yakubova, Y. Li, J. Bergelson, J.O. Borevitz, M. Nordborg, O. Vitek, and D.E. Salt. 2010. A coastal cline in sodium accumulation in *Arabidopsis thaliana* is driven by natural variation of the sodium transporter AtHKT1;1. PLoS Genet. 6(11):e1001193.

Bernstein, L. and A. Ayers. 1953. Salt tolerance of five varieties of carrots. J. Amer. Soc. Hort. Sci. 61:360–366.

Chinnusamy, V., A. Jagendorf, and J.K. Zhu. 2005. Understanding and improving salt tolerance in plants. Crop Sci. 45(2):437–448.

Cuartero, J. and R. Fernández-Muñoz. 1998. Tomato and salinity. Scientia Hort. 78(1-4):83–125.

Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Pearson, Essex, England.

De Mendiburu, F. 2014. Agricolae: Statistical procedures for agricultural research. R. package, version 1, p. 1–6.

FAO. 2017. FAOSTAT production crops. 29 Nov. 2017. <http://www.fao.org/faostat/en/#data/QC>.

Flowers, T.J., H.K. Galal, and L. Bromham. 2010. Evolution of halophytes: Multiple origins of salt tolerance in land plants. Funct. Plant Biol. 37(7):604–612.

Flowers, T.J. and A.R. Yeo. 1995. Breeding for salinity resistance in crop plants: Where next? Austral. J. Plant Physiol. 22:875–884.

Foolad, M.R. and R.A. Jones. 1992. Parent off-spring regression estimates of heritability for salt tolerance during germination in tomato. Crop Sci. 32(2):439–442.

Foolad, M.R. and G.Y. Lin. 1997. Genetic potential for salt tolerance during germination in lycopersicon species. HortScience 32:296–300.

Francois, L.E., T. Donovan, and E.V. Maas. 1984. Salinity effects on seed yield, growth, and germination of grain sorghum. Agron. J. 76(5):741–744.

Iorizzo, M., D.A. Senalik, S.L. Ellison, D. Grzebelus, P.F. Cavagnaro, C. Allender, J. Brunet, D.M. Spooner, A.V. Deynze, and P.W. Simon. 2013. Genetic structure and domestication of carrot (*Daucus carota* subsp. *sativus*) (Apiaceae). Amer. J. Bot. 100(5):930–938.

Jamil, M., D.B. Lee, K.Y. Jung, M. Ashraf, S.C. Lee, and E.S. Rha. 2006. Effect of salt (NaCl) stress on germination and early seedling growth of four vegetable species. J. Cent. Eur. Agr. 7:273–281.

Kahouli, B., Z. Borgi, and C. Hannachi. 2014. Effect of sodium chloride on the germination of the seeds of a collection of carrot accessions (*Daucus carota* L.) cultivated in the region of Sidi Bouzid. J. Stress Physiol. Biochem. 10(3):28–36.

Khoury, C.K., N.P. Castañeda-Alvarez, H.A. Achicanoy, C.C. Sosa, V. Bernau, M.T. Kassa, S.L. Norton, L.J.G. van der Maesen, H.D. Upadhyaya, J. Ramírez-Villegas, A. Jarvis, and P.C. Struik. 2015. Crop wild relatives of pigeonpea [*Cajanus cajan* (L.) Millsp.]: Distributions, ex situ conservation status, and potential genetic resources for abiotic stress tolerance. Biol. Conserv. 184:259–270.

Maas, E.V. and G.J. Hoffman. 1977. Crop salt tolerance - current assessment. J. Irrig. Drain. Div. 103:115–134.

Maas, E.V., G.J. Hoffman, G.D. Chaba, J.A. Poss, and M.C. Shannon. 1983. Salt sensitivity of corn at various growth stages. Irrig. Sci. 4(1):45–57.

Munns, R. 2005. Genes and salt tolerance: Bringing them together. New Phytol. 167(3):645–663.

Qadir, M., A. Tubeileh, J. Akhtar, A. Larbi, P.S. Minhas, and M.A. Khan. 2008. Productivity enhancement of salt-affected environments through crop diversification. Land Degrad. Dev. 19:429–453.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ravelombola, W., A. Shi, Y. Weng, B. Mou, D. Motes, J. Clark, P. Chen, V. Srivastava, J. Qin, L. Dong, W. Yang, G. Bhattarai, and Y. Sugihara. 2018. Association analysis of salt tolerance in cowpea (*Vigna unguiculata* (L.) Walp) at germination and seedling stages. Theor. Appl. Genet. 131(1):79–91.

Ravelombola, W.S., A. Shi, Y. Weng, J. Clark, D. Motes, P. Chen, and V. Srivastava. 2017. Evaluation of salt tolerance at germination stage in cowpea [*Vigna unguiculata* (L.) Walp]. HortScience 52:1168–1176.

Rode, A., T. Nothnagel, and E. Kampe. 2012. Developing methods to evaluate salt stress tolerance in carrot cultivars. Acta Hort. 960:393–400.

Rozema, J. and T. Flowers. 2008. Crops for a salinized world. Science 322:1478–1480.

Saad, F.F., A.A.A. El-Mohsen, M.A.A. El-Shafi, and I.H. Al-Soudan. 2013. Effective selection criteria for evaluating some barley crosses for water stress tolerance. Egypt. J. Plant Breed. 17(5):79–98.

Schmidhalter, U. and J.J. Oertli. 1991. Germination and seedling growth of carrots under salinity and moisture stress. Plant Soil 132:243–251.

Simon, P.W., L.M. Pollak, B.A. Clevidence, J.M. Holden, and D.B. Haytowitz. 2009. Plant breeding for human nutritional quality. Plant Breed. Rev. 31:325–392.

Xu, C. and B. Mou. 2015. Evaluation of lettuce genotypes for salinity tolerance. HortScience 50:1441–1446.

Supplemental Table 1. Carrot accession, root color, country of origin, domestication status (DS), mean percent germination without salt stress (Nonstress) ± standard error, mean percent germination with 150 mM salt stress (Stress) ± standard error, mean absolute decrease (AD), mean inhibition index (II), relative salt tolerance (RST), mean salt tolerance index (STI), hundred seed weight (HSW), and rank based on STI.

Accession	Root Color	Origin	DS	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI	HSW	Rank
Ames 25040	Red/Purple	India	Cultivated PI	74.2 ± 2.4	14.4 ± 4.9	59.7	80.9	0.19	0.16	0.18	219
Ames 25732	White	Syria	Wild PI	71.9 ± 7.4	22.1 ± 8.1	49.8	67.2	0.32	0.23	0.11	193
Ames 25773	White	Syria	Wild PI	85.8 ± 3.3	36.7 ± 4.8	49.2	56.7	0.43	0.47	0.09	127
Ames 26382	White	Portugal	Wild PI	63.3 ± 7.7	7.3 ± 3.9	56.0	88.2	0.12	0.07	0.13	253
Ames 26383	White	Portugal	Wild PI	90.8 ± 2.4	3.3 ± 1.7	87.5	96.3	0.04	0.05	0.15	261
Ames 26384	White	Portugal	Wild PI	88.3 ± 4.8	29.8 ± 9.8	58.4	65.0	0.35	0.39	0.15	153
Ames 27396	White	Uzbekistan	Wild PI	75.2 ± 7.3	4.2 ± 2.7	71.0	93.8	0.06	0.04	0.08	266
Ames 27397	White	Uzbekistan	Wild PI	72.8 ± 5.1	8.3 ± 4.0	64.5	89.7	0.10	0.10	0.08	241
Ames 27398	Orange	Uzbekistan	Cultivated PI	62.5 ± 4.0	40.8 ± 4.5	21.7	34.0	0.66	0.39	0.12	153
Ames 27399	Yellow	Uzbekistan	Cultivated PI	89.2 ± 3.0	63.3 ± 6.5	25.8	28.1	0.72	0.84	0.11	57
Ames 27400	Yellow	Uzbekistan	Cultivated PI	85.8 ± 3.3	80.0 ± 8.5	5.8	5.4	0.95	1.02	0.15	28
Ames 29084	Orange	Tunisia	Cultivated PI	77.5 ± 5.6	65.0 ± 8.0	12.5	12.1	0.88	0.74	0.25	71
Ames 29087	White	Tunisia	Wild PI	89.3 ± 3.9	0.8 ± 0.8	88.5	98.9	0.01	0.01	0.14	286
Ames 30198	White	Tunisia	Wild PI	64.7 ± 5.0	49.4 ± 8.2	15.3	23.6	0.77	0.49	0.20	125
Ames 30259	White	Tunisia	Wild PI	90.8 ± 2.4	43.0 ± 9.1	47.9	52.0	0.48	0.58	0.08	103
Ames 30276	Orange	Tunisia	Cultivated PI	84.2 ± 3.8	66.7 ± 5.4	17.5	19.7	0.80	0.84	0.20	57
Ames 31193	White	France	Wild PI	78.3 ± 4.4	21.7 ± 4.4	56.7	72.6	0.27	0.26	0.09	183
PI 163234	Yellow	India	Cultivated PI	58.0 ± 9.6	25.0 ± 1.3	33.0	52.1	0.47	0.22	0.21	197
PI 163235	Yellow	Pakistan	Cultivated PI	82.5 ± 5.0	70.8 ± 6.5	11.7	12.0	0.88	0.88	0.25	48
PI 163238	Orange/Yellow	India	Cultivated PI	80.8 ± 3.5	73.3 ± 4.0	7.5	7.5	0.93	0.88	0.14	48
PI 163239	Yellow	India	Cultivated PI	84.9 ± 3.9	30.0 ± 8.5	54.9	65.7	0.35	0.40	0.34	148
PI 163240	Yellow/Orange	India	Cultivated PI	83.3 ± 3.8	57.5 ± 12.5	25.8	28.6	0.71	0.70	0.19	76
PI 163241	Yellow/Orange	India	Cultivated PI	71.8 ± 4.5	54.4 ± 6.8	17.4	25.0	0.74	0.60	0.26	98
PI 164943	Yellow	Turkey	Cultivated PI	75.0 ± 5.9	45.8 ± 12.5	29.2	37.1	0.63	0.52	0.18	114
PI 165522	Orange	India	Cultivated PI	75.0 ± 6.1	43.3 ± 10.0	31.7	42.6	0.57	0.50	0.12	120
PI 167143	Purple/Yellow	Turkey	Cultivated PI	60.0 ± 5.6	50.0 ± 8.5	10.0	15.1	0.85	0.46	0.20	130
PI 167211	Purple	Turkey	Cultivated PI	60.0 ± 4.1	35.8 ± 10.8	24.2	44.5	0.56	0.35	0.21	164
PI 176563	Purple	Turkey	Cultivated PI	67.5 ± 5.0	43.3 ± 6.1	24.2	32.5	0.67	0.43	0.24	138
PI 177381	White	Turkey	Wild PI	63.0 ± 4.6	0.0 ± 0.0	63.0	100.0	0.00	0.00	0.11	289
PI 181052	Orange/Yellow	Pakistan	Cultivated PI	56.7 ± 5.4	23.3 ± 5.3	33.3	57.5	0.42	0.20	0.13	204
PI 181880	Orange/Yellow	Syria	Cultivated PI	76.3 ± 5.0	50.8 ± 6.8	25.5	32.8	0.68	0.59	0.17	101
PI 187235	Orange	Belgium	Cultivated PI	69.2 ± 3.0	17.5 ± 4.8	51.7	74.9	0.25	0.18	0.10	211
PI 187236	Orange	Belgium	Cultivated PI	63.3 ± 5.6	15.8 ± 5.1	47.5	75.3	0.25	0.15	0.09	223
PI 193504	Orange	Ethiopia	Cultivated PI	82.5 ± 5.3	25.0 ± 10.2	57.5	71.2	0.29	0.33	0.16	170
PI 205997	Orange	Sweden	Cultivated PI	79.8 ± 5.3	10.0 ± 4.3	69.8	86.7	0.13	0.11	0.10	234
PI 211024	Yellow	Afghanistan	Cultivated PI	93.3 ± 4.0	75.8 ± 9.5	17.5	17.5	0.83	1.06	0.26	23
PI 211590	Yellow	Afghanistan	Cultivated PI	73.3 ± 1.7	9.3 ± 3.8	64.1	87.2	0.13	0.10	0.12	241
PI 218076	Orange	Pakistan	Cultivated PI	96.7 ± 2.5	84.3 ± 3.0	12.4	12.3	0.88	1.22	0.27	10
PI 222250	Orange/White	Iran	Cultivated PI	85.7 ± 1.5	35.0 ± 11.3	50.8	59.3	0.41	0.45	0.15	132
PI 223504	Yellow/White	Afghanistan	Cultivated PI	76.2 ± 3.8	55.5 ± 5.3	20.7	27.4	0.74	0.65	0.21	89
PI 225867	Orange	Denmark	Cultivated PI	87.5 ± 4.2	5.8 ± 4.2	81.7	94.1	0.06	0.09	0.08	248
PI 225868	Orange	Denmark	Cultivated PI	95.8 ± 2.0	41.0 ± 7.5	54.9	56.5	0.43	0.58	0.11	103
PI 225869	Orange	Denmark	Cultivated PI	90.6 ± 5.4	7.5 ± 5.1	83.1	92.2	0.08	0.11	0.13	234
PI 225870	Orange	Denmark	Cultivated PI	71.7 ± 5.6	9.2 ± 2.4	62.5	85.7	0.14	0.09	0.12	248
PI 225871	Orange	Denmark	Cultivated PI	75.8 ± 4.7	22.5 ± 6.5	53.3	70.0	0.30	0.26	0.10	183
PI 226043	Orange	Japan	Cultivated PI	83.3 ± 3.8	29.2 ± 11.9	54.2	66.2	0.34	0.38	0.14	157
PI 226309	Orange	Mexico	Cultivated PI	62.5 ± 5.9	43.9 ± 7.3	18.6	25.8	0.73	0.41	0.19	145
PI 226310	Orange	Mexico	Cultivated PI	96.7 ± 2.1	78.3 ± 5.4	18.3	18.7	0.81	1.14	0.20	16
PI 226464	Orange	Iran	Cultivated PI	74.4 ± 5.4	24.6 ± 8.3	49.8	64.5	0.36	0.27	0.18	180
PI 234620	Orange	South Africa	Cultivated PI	82.5 ± 2.5	60.8 ± 4.0	21.7	26.1	0.74	0.76	0.15	69
PI 234621	Orange	South Africa	Cultivated PI	94.2 ± 1.5	46.7 ± 13.8	47.6	51.3	0.49	0.67	0.16	86
PI 249535	Orange	Spain	Cultivated PI	87.5 ± 1.1	52.5 ± 8.8	35.0	40.1	0.60	0.69	0.15	78
PI 251228	Purple	Afghanistan	Cultivated PI	64.2 ± 4.7	50.8 ± 5.4	13.3	19.9	0.80	0.50	0.34	120
PI 256065	Orange/Yellow	Afghanistan	Cultivated PI	54.5 ± 3.6	2.5 ± 1.7	52.0	95.3	0.05	0.02	0.13	278
PI 256066	Purple	Afghanistan	Cultivated PI	74.2 ± 4.2	78.3 ± 3.1	-4.2	-8.0	1.08	0.87	0.23	53
PI 261648	Orange	Netherlands	Cultivated PI	89.2 ± 4.0	30.8 ± 10.3	58.4	64.3	0.36	0.40	0.14	148
PI 261650	Orange	Netherlands	Cultivated PI	96.7 ± 1.1	14.0 ± 5.5	82.7	85.3	0.15	0.20	0.13	204
PI 261781	Orange	France	Cultivated PI	82.5 ± 3.4	9.2 ± 5.8	73.3	88.5	0.11	0.11	0.20	234
PI 261782	Orange	France	Cultivated PI	86.0 ± 6.0	54.2 ± 4.7	31.8	32.5	0.74	0.68	0.11	83
PI 261783	Orange	France	Cultivated PI	56.7 ± 6.0	40.0 ± 7.0	16.7	17.2	0.83	0.32	0.27	171
PI 263023	Orange	UK	Cultivated PI	90.0 ± 4.7	20.8 ± 10.7	69.2	76.3	0.24	0.28	0.13	176
PI 264232	Orange	France	Cultivated PI	62.5 ± 4.4	10.0 ± 5.0	52.5	83.3	0.17	0.09	0.10	248
PI 264234	Orange	France	Cultivated PI	97.5 ± 1.7	51.7 ± 11.2	45.8	46.4	0.54	0.75	0.13	70
PI 264235	Orange	France	Cultivated PI	90.0 ± 3.9	32.7 ± 11.2	57.3	62.6	0.38	0.43	0.12	138
PI 264238	Orange	France	Cultivated PI	99.2 ± 0.8	71.5 ± 10.7	27.7	27.8	0.71	1.06	0.13	23
PI 264543	Red/Orange	Japan	Cultivated PI	76.7 ± 4.8	59.2 ± 5.7	17.5	20.8	0.79	0.68	0.21	83
PI 264669	Orange	Germany	Cultivated PI	73.3 ± 3.3	24.6 ± 7.7	48.7	64.8	0.34	0.26	0.12	183
PI 267090	Orange	Tajikistan	Cultivated PI	78.3 ± 4.6	60.8 ± 7.2	17.4	18.4	0.79	0.69	0.13	78
PI 267091	Yellow	Soviet Union	Cultivated PI	94.2 ± 2.0	73.3 ± 7.9	20.9	22.5	0.77	1.04	0.17	27
PI 268382	Orange	Afghanistan	Cultivated PI	80.0 ± 2.6	66.7 ± 3.3	13.3	16.5	0.84	0.80	0.11	61
PI 269316	Orange	Sweden	Cultivated PI	81.7 ± 7.7	20.5 ± 13.6	61.2	60.9	0.41	0.18	0.14	211
PI 269319	Orange	Sweden	Cultivated PI	75.0 ± 5.3	52.5 ± 11.3	22.5	23.8	0.76	0.57	0.11	106

(*Continued on next page*)

Supplemental Table 1. (*Continued*) Carrot accession, root color, country of origin, domestication status (DS), mean percent germination without salt stress (Nonstress) ± standard error, mean percent germination with 150 mM salt stress (Stress) ± standard error, mean absolute decrease (AD), mean inhibition index (II), relative salt tolerance (RST), mean salt tolerance index (STI), hundred seed weight (HSW), and rank based on STI.

Accession	Root Color	Origin	DS	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI	HSW	Rank
PI 269322	Orange	Sweden	Cultivated PI	82.0 ± 6.0	11.0 ± 6.0	71.0	87.6	0.12	0.15	0.08	223
PI 269485	White	Pakistan	Wild PI	87.4 ± 3.8	5.0 ± 3.4	82.4	94.6	0.05	0.07	0.10	253
PI 269486	Yellow	Pakistan	Cultivated PI	69.4 ± 6.0	43.9 ± 9.8	25.5	33.0	0.67	0.44	0.25	137
PI 269487	White	Pakistan	Wild PI	88.3 ± 3.6	8.3 ± 4.9	80.0	89.7	0.10	0.10	0.11	241
PI 269488	Orange	Pakistan	Cultivated PI	95.0 ± 3.2	84.0 ± 6.3	11.0	10.6	0.89	1.19	0.12	12
PI 271044	Purple/Orange	India	Cultivated PI	52.5 ± 4.8	34.2 ± 5.7	18.3	34.1	0.66	0.28	0.28	176
PI 271470	White	India	Cultivated PI	69.8 ± 2.5	52.0 ± 6.5	17.8	24.3	0.77	0.54	0.29	112
PI 271471	NA	India	Cultivated PI	81.7 ± 3.8	69.2 ± 6.9	12.5	13.4	0.87	0.84	0.29	57
PI 274297	White	Pakistan	Wild PI	62.5 ± 6.9	2.5 ± 1.1	60.0	95.3	0.05	0.02	0.12	278
PI 274298	White	Pakistan	Wild PI	76.6 ± 5.8	8.5 ± 2.4	68.2	88.9	0.11	0.10	0.13	241
PI 277285	Orange	India	Cultivated PI	71.7 ± 5.4	32.5 ± 5.6	39.2	53.3	0.47	0.35	0.11	164
PI 277668	Orange	Netherlands	Cultivated PI	96.7 ± 2.1	75.8 ± 8.9	20.8	21.8	0.78	1.11	0.09	21
PI 279764	White	Libya	Wild PI	79.0 ± 4.3	0.0 ± 0.0	79.0	100.0	0.00	0.00	0.20	289
PI 279776	Purple	Egypt	Cultivated PI	75.0 ± 7.2	58.3 ± 3.3	16.7	17.3	0.83	0.65	0.30	89
PI 279777	Yellow	Egypt	Cultivated PI	80.0 ± 4.7	47.5 ± 6.2	32.5	39.6	0.60	0.57	0.22	106
PI 280706	White	Chile	Wild PI	91.6 ± 2.1	14.2 ± 3.5	77.5	84.6	0.15	0.20	0.13	207
PI 285613	Orange	Poland	Cultivated PI	74.4 ± 4.4	32.5 ± 7.7	41.9	54.3	0.45	0.35	0.09	164
PI 294079	Orange	Japan	Cultivated PI	80.8 ± 3.0	40.8 ± 11.4	40.0	49.3	0.51	0.50	0.14	120
PI 294080	Orange	Japan	Cultivated PI	72.5 ± 5.9	55.0 ± 9.3	17.5	21.2	0.79	0.61	0.13	95
PI 294082	Orange	Japan	Cultivated PI	95.0 ± 2.6	78.3 ± 6.7	16.6	17.4	0.83	1.12	0.20	20
PI 294084	Orange	Japan	Cultivated PI	78.3 ± 10.5	37.5 ± 13.8	40.8	22.8	0.77	0.37	0.13	159
PI 294090	Orange	Japan	Cultivated PI	84.9 ± 3.1	33.8 ± 8.2	51.1	60.5	0.38	0.43	0.12	138
PI 295862	White	Spain	Cultivated PI	67.5 ± 8.5	19.2 ± 6.0	48.3	63.4	0.37	0.16	0.09	219
PI 306810	Orange	New Zealand	Cultivated PI	77.4 ± 4.4	9.2 ± 7.4	68.2	89.7	0.10	0.12	0.11	230
PI 319860	Red	Japan	Cultivated PI	78.3 ± 6.1	52.5 ± 6.2	25.8	27.7	0.72	0.60	0.17	98
PI 321688	Red	Japan	Cultivated PI	57.0 ± 4.6	41.0 ± 7.8	16.0	26.8	0.73	0.35	0.17	164
PI 325993	Orange	Russia	Cultivated PI	97.5 ± 1.7	61.7 ± 4.4	35.8	36.5	0.64	0.90	0.11	46
PI 326009	Orange	Uzbekistan	Cultivated PI	91.6 ± 2.8	14.2 ± 5.1	77.5	85.0	0.15	0.20	0.12	204
PI 326010	Orange	Tajikistan	Cultivated PI	80.8 ± 5.5	28.6 ± 5.9	52.2	63.4	0.36	0.35	0.16	164
PI 341204	Orange	France	Cultivated PI	74.2 ± 2.4	10.0 ± 5.9	64.2	85.8	0.14	0.11	0.15	234
PI 341207	Orange	France	Cultivated PI	56.9 ± 4.9	0.8 ± 0.8	56.1	98.8	0.01	0.01	0.19	287
PI 341208	Orange	France	Cultivated PI	67.5 ± 2.8	33.3 ± 8.7	34.2	51.2	0.49	0.34	0.17	169
PI 344447	White	Iran	Wild PI	60.0 ± 1.8	41.7 ± 10.6	18.3	29.6	0.70	0.37	0.20	159
PI 419109	Yellow	China	Cultivated PI	70.3 ± 4.5	53.3 ± 4.9	17.0	24.3	0.75	0.58	0.16	103
PI 419110	Orange/Red	China	Cultivated PI	80.8 ± 3.3	50.0 ± 8.2	30.8	38.3	0.62	0.61	0.15	95
PI 419184	Orange	China	Cultivated PI	95.0 ± 3.2	60.8 ± 14.1	34.1	36.6	0.64	0.88	0.14	48
PI 430524	Yellow	Azerbaijan	Cultivated PI	59.6 ± 5.8	33.3 ± 4.0	26.3	39.9	0.60	0.29	0.15	174
PI 430527	Orange	Uzbekistan	Cultivated PI	94.2 ± 2.4	31.5 ± 11.9	62.7	66.7	0.33	0.45	0.13	132
PI 430528	Yellow	Uzbekistan	Cultivated PI	87.5 ± 2.8	54.2 ± 9.3	33.3	37.3	0.63	0.71	0.13	74
PI 430529	Yellow	Uzbekistan	Cultivated PI	87.5 ± 4.8	62.5 ± 6.4	25.0	26.3	0.74	0.81	0.16	60
PI 430530	Orange	Tajikistan	Cultivated PI	83.2 ± 4.0	37.5 ± 10.1	45.7	54.6	0.46	0.47	0.13	127
PI 430531	Purple	Azerbaijan	Cultivated PI	85.0 ± 4.1	54.2 ± 7.8	30.8	35.4	0.65	0.69	0.16	78
PI 430532	Purple/White	Russia	Cultivated PI	97.5 ± 1.1	38.3 ± 13.4	59.2	60.4	0.40	0.56	0.11	108
PI 430533	Orange	Iraq	Cultivated PI	94.2 ± 2.4	48.0 ± 6.6	46.2	49.4	0.51	0.69	0.10	78
PI 430534	Yellow	Afghanistan	Cultivated PI	94.3 ± 2.0	85.8 ± 4.4	8.5	8.6	0.87	1.21	0.11	11
PI 432898	Orange/Yellow	China	Cultivated PI	94.2 ± 5.8	77.5 ± 7.7	16.7	17.1	0.83	1.11	0.16	21
PI 432899	Purple/Yellow/Orange	China	Cultivated PI	70.0 ± 4.7	65.0 ± 4.5	5.0	6.2	0.94	0.69	0.16	78
PI 432900	Orange	China	Cultivated PI	56.9 ± 5.4	26.7 ± 7.4	30.2	49.8	0.48	0.23	0.14	193
PI 432901	Orange	China	Cultivated PI	90.0 ± 2.6	74.2 ± 5.1	15.8	17.9	0.82	1.01	0.15	31
PI 451752	Yellow/White	Netherlands	Cultivated PI	87.4 ± 4.3	19.2 ± 5.4	68.2	77.5	0.23	0.25	0.14	189
PI 451753	Yellow	Netherlands	Cultivated PI	68.3 ± 5.3	7.7 ± 3.8	60.6	89.3	0.10	0.09	0.20	248
PI 451754	Yellow	Netherlands	Cultivated PI	84.2 ± 3.5	20.8 ± 5.7	63.3	75.1	0.25	0.26	0.14	183
PI 451755	Yellow	Netherlands	Cultivated PI	85.8 ± 3.0	2.5 ± 2.5	83.3	97.2	0.03	0.03	0.09	274
PI 451756	Yellow/White	Netherlands	Cultivated PI	71.7 ± 2.1	9.2 ± 3.3	62.5	86.9	0.13	0.10	0.16	241
PI 451757	White	Netherlands	Cultivated PI	88.3 ± 2.5	14.2 ± 7.0	74.2	83.6	0.16	0.18	0.13	211
PI 451758	Yellow	Netherlands	Cultivated PI	88.3 ± 5.1	55.8 ± 9.3	32.5	33.8	0.66	0.72	0.11	72
PI 451759	Yellow/White	Netherlands	Cultivated PI	88.3 ± 3.3	33.3 ± 7.0	55.0	63.0	0.37	0.45	0.11	132
PI 451761	Yellow/White	Netherlands	Cultivated PI	94.2 ± 2.4	10.8 ± 4.2	83.3	88.6	0.11	0.16	0.14	219
PI 458857	Orange	Russia	Cultivated PI	83.3 ± 4.0	29.2 ± 10.0	54.2	65.1	0.35	0.37	0.13	159
PI 458858	Orange	Russia	Cultivated PI	96.7 ± 1.1	40.8 ± 14.1	55.8	58.3	0.42	0.60	0.11	98
PI 458859	Orange	Russia	Cultivated PI	58.9 ± 2.5	27.5 ± 5.6	31.4	52.9	0.48	0.24	0.15	191
PI 458860	Orange	Russia	Cultivated PI	95.8 ± 1.5	40.8 ± 12.1	55.0	57.5	0.43	0.59	0.10	101
PI 478369	White	China	Wild PI	71.0 ± 6.8	46.3 ± 9.8	24.7	33.5	0.66	0.51	0.13	117
PI 478370	Orange	China	Cultivated PI	62.7 ± 3.7	50.8 ± 9.7	11.9	21.6	0.78	0.50	0.23	120
PI 478883	White	France	Wild PI	83.4 ± 1.3	8.3 ± 5.3	75.1	89.9	0.10	0.10	0.16	241
PI 483348	Orange	Japan	Cultivated PI	79.8 ± 6.7	56.0 ± 7.0	23.8	28.1	0.72	0.68	0.18	83
PI 483352	Orange	Japan	Cultivated PI	88.3 ± 3.3	64.2 ± 5.4	24.2	26.8	0.73	0.85	0.17	56
PI 502239	Orange	South Africa	Cultivated PI	81.7 ± 5.4	25.0 ± 13.7	56.7	67.1	0.33	0.29	0.12	174
PI 502347	Orange	Uzbekistan	Cultivated PI	98.4 ± 1.0	65.8 ± 10.2	32.5	33.5	0.66	0.98	0.08	35
PI 502654	Yelllow/Purple	Pakistan	Cultivated PI	63.7 ± 5.1	21.7 ± 8.3	42.0	67.0	0.33	0.22	0.34	197
PI 502655	White	Pakistan	Wild PI	82.5 ± 5.3	60.0 ± 10.3	22.5	30.1	0.70	0.78	0.18	65
PI 502656	Yellow/White	Pakistan	Cultivated PI	86.7 ± 3.3	60.0 ± 10.6	26.7	30.2	0.70	0.78	0.30	65

(*Continued on next page*)

Supplemental Table 1. (*Continued*) Carrot accession, root color, country of origin, domestication status (DS), mean percent germination without salt stress (Nonstress) ± standard error, mean percent germination with 150 mM salt stress (Stress) ± standard error, mean absolute decrease (AD), mean inhibition index (II), relative salt tolerance (RST), mean salt tolerance index (STI), hundred seed weight (HSW), and rank based on STI.

Accession	Root Color	Origin	DS	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI	HSW	Rank
PI 502914	Orange	Germany	Cultivated PI	51.1 ± 6.2	31.7 ± 9.2	19.4	38.5	0.61	0.26	0.12	183
PI 502915	Orange/White	Germany	Cultivated PI	80.8 ± 4.0	14.2 ± 5.7	66.7	82.2	0.18	0.17	0.12	217
PI 502919	Orange	Germany	Cultivated PI	95.8 ± 2.4	31.7 ± 5.3	64.2	66.3	0.34	0.45	0.15	132
PI 503344	Orange	Lithuania	Cultivated PI	80.8 ± 3.5	35.8 ± 6.8	45.0	54.1	0.46	0.42	0.14	144
PI 503345	Orange	Lithuania	Cultivated PI	93.3 ± 2.5	80.8 ± 5.1	12.5	13.0	0.87	1.13	0.09	18
PI 506444	Orange	Kazakhstan	Cultivated PI	97.5 ± 2.5	77.5 ± 5.4	20.0	20.2	0.80	1.13	0.12	18
PI 506445	Orange	Kazakhstan	Cultivated PI	59.7 ± 4.9	5.0 ± 2.6	54.7	92.6	0.08	0.05	0.15	261
PI 508473	Orange	South Korea	Cultivated PI	52.1 ± 2.9	36.7 ± 6.7	15.5	31.0	0.69	0.30	0.13	173
PI 509433	Purple/Yellow	Turkey	Cultivated PI	96.7 ± 1.7	90.0 ± 1.3	6.7	6.8	0.93	1.31	0.16	6
PI 509434	Red/White	Turkey	Cultivated PI	95.0 ± 2.2	74.2 ± 9.3	20.8	21.3	0.79	1.05	0.18	26
PI 515990	Orange	Hungary	Cultivated PI	99.0 ± 1.0	6.0 ± 3.7	93.0	94.0	0.06	0.09	0.11	248
PI 515992	Orange	Hungary	Cultivated PI	96.7 ± 1.7	35.0 ± 10.5	61.7	64.1	0.36	0.51	0.10	117
PI 531326	Orange	Hungary	Cultivated PI	70.8 ± 8.2	2.5 ± 2.5	68.3	95.8	0.04	0.02	0.09	278
PI 535887	Orange	Poland	Cultivated PI	97.5 ± 1.1	15.0 ± 8.2	82.5	84.6	0.16	0.22	0.11	197
PI 537093	Orange	South Korea	Cultivated PI	90.8 ± 3.7	52.5 ± 9.6	38.3	40.6	0.59	0.70	0.20	76
PI 540419	Yellow	Uzbekistan	Cultivated PI	78.3 ± 8.6	43.8 ± 7.5	34.5	39.3	0.61	0.52	0.12	114
PI 540422	Yellow	Uzbekistan	Cultivated PI	71.4 ± 1.7	21.0 ± 7.9	50.4	69.7	0.31	0.22	0.10	197
PI 632381	Yellow	USA	Cultivated PI	99.2 ± 0.8	63.3 ± 5.9	35.8	36.1	0.64	0.94	0.14	40
PI 632382	Orange	USA	Cultivated PI	95.8 ± 2.4	66.7 ± 7.0	29.2	30.5	0.69	0.96	0.11	37
PI 632383	Orange	USA	Cultivated PI	90.0 ± 9.0	76.7 ± 5.3	13.3	5.4	0.95	1.02	0.14	28
PI 632384	Orange	USA	Cultivated PI	96.7 ± 1.7	85.0 ± 6.1	11.7	11.7	0.87	1.23	0.12	8
PI 632385	Orange	USA	Cultivated PI	99.2 ± 0.8	76.4 ± 9.1	22.7	22.9	0.77	1.14	0.15	16
PI 632386	Orange	USA	Cultivated PI	94.1 ± 2.4	55.0 ± 10.2	39.1	42.7	0.58	0.79	0.12	63
PI 632389	Orange	Netherlands	Cultivated PI	98.3 ± 1.7	62.3 ± 10.0	36.0	36.1	0.63	0.91	0.13	45
PI 632391	Orange	USA	Cultivated PI	100.0 ± 0.0	88.3 ± 4.8	11.7	11.7	0.88	1.33	0.12	4
PI 632393	Orange	USA	Cultivated PI	95.0 ± 2.2	82.2 ± 3.3	12.8	13.2	0.85	1.17	0.12	13
PI 634651	Orange	USA	Cultivated PI	99.2 ± 0.8	65.8 ± 11.4	33.3	33.4	0.67	0.98	0.12	35
PI 634652	Yellow	USA	Cultivated PI	96.7 ± 2.1	53.2 ± 9.1	43.5	45.2	0.54	0.78	0.09	65
PI 634653	Orange	USA	Cultivated PI	97.5 ± 1.1	63.2 ± 11.6	34.3	34.7	0.65	0.92	0.12	43
PI 634654	Orange	USA	Cultivated PI	96.7 ± 1.7	55.0 ± 7.9	41.7	42.9	0.57	0.80	0.08	61
PI 634655	Orange	USA	Cultivated PI	96.7 ± 2.1	72.5 ± 8.3	24.2	25.7	0.74	1.06	0.13	23
PI 634657	Orange	Netherlands	Cultivated PI	95.0 ± 1.8	49.2 ± 11.1	45.8	49.0	0.52	0.71	0.14	74
PI 642755	Orange	USA	Cultivated PI	97.5 ± 1.1	59.2 ± 10.4	38.3	39.0	0.61	0.86	0.13	55
PI 642756	Orange	Netherlands	Cultivated PI	100.0 ± 0.0	68.0 ± 10.8	32.0	32.0	0.68	1.02	0.11	28
PI 642761	Orange	USA	Cultivated PI	96.7 ± 1.7	64.8 ± 12.1	31.8	32.6	0.67	0.94	0.14	40
PI 643114	White	USA	Cultivated PI	99.2 ± 0.8	89.2 ± 4.2	10.0	10.0	0.90	1.33	0.13	4
PI 643118	White	USA	Cultivated PI	97.5 ± 1.7	41.7 ± 14.2	55.8	57.7	0.42	0.62	0.09	94
PI 643119	Orange	France	Cultivated PI	100.0 ± 0.0	61.7 ± 5.6	38.3	38.3	0.62	0.93	0.09	42
PI 652121	Orange	Japan	Cultivated PI	94.2 ± 2.4	71.7 ± 7.4	22.5	23.2	0.76	1.01	0.14	31
PI 652136	Orange	Japan	Cultivated PI	85.8 ± 2.7	49.2 ± 10.9	36.7	41.8	0.58	0.63	0.14	92
PI 652137	Orange	Japan	Cultivated PI	85.8 ± 6.0	27.5 ± 10.7	58.3	69.5	0.31	0.38	0.12	157
PI 652138	Orange	Japan	Cultivated PI	90.7 ± 2.7	46.7 ± 6.0	44.0	48.6	0.52	0.64	0.15	91
PI 652152	Orange	UK	Cultivated PI	59.2 ± 8.0	10.0 ± 5.9	49.2	83.7	0.16	0.10	0.11	241
PI 652153	Orange	Netherlands	Cultivated PI	90.0 ± 3.4	20.0 ± 6.5	70.0	77.7	0.22	0.27	0.12	180
PI 652154	Orange	Netherlands	Cultivated PI	51.2 ± 6.9	31.0 ± 6.9	20.1	34.6	0.65	0.24	0.10	191
PI 652155	Orange	Hungary	Cultivated PI	69.2 ± 3.7	24.2 ± 8.3	45.0	65.4	0.35	0.25	0.10	189
PI 652156	Orange	Czech Republic	Cultivated PI	77.8 ± 2.6	4.2 ± 2.7	73.6	94.2	0.06	0.05	0.10	261
PI 652157	Orange	Soviet Union	Cultivated PI	75.8 ± 5.8	47.9 ± 3.9	28.0	35.8	0.64	0.55	0.11	109
PI 652158	Orange	Georgia	Cultivated PI	74.2 ± 3.5	39.2 ± 5.8	35.0	46.2	0.54	0.43	0.11	138
PI 652163	Orange	Netherlands	Cultivated PI	74.2 ± 3.0	17.6 ± 4.6	56.5	75.6	0.24	0.19	0.10	209
PI 652171	Orange	Netherlands	Cultivated PI	78.3 ± 2.1	20.0 ± 4.5	58.3	74.1	0.26	0.23	0.14	193
PI 652173	Orange	UK	Cultivated PI	65.0 ± 4.3	27.5 ± 5.4	37.5	55.6	0.44	0.26	0.11	183
PI 652179	Orange/Yellow	USA	Cultivated PI	80.2 ± 4.3	32.1 ± 8.6	48.1	60.5	0.39	0.40	0.16	148
PI 652188	Purple	China	Cultivated PI	69.2 ± 5.1	3.3 ± 3.3	65.8	95.6	0.04	0.04	0.10	266
PI 652206	Orange	Bulgaria	Cultivated PI	90.8 ± 3.0	20.8 ± 9.4	70.0	76.2	0.24	0.28	0.16	176
PI 652207	Orange	China	Cultivated PI	90.8 ± 4.9	34.2 ± 12.1	56.7	61.5	0.39	0.46	0.08	130
PI 652208	Orange/Yellow/Red	China	Cultivated PI	99.2 ± 0.8	29.2 ± 15.5	70.0	70.4	0.30	0.43	0.15	138
PI 652209	Yellow	China	Cultivated PI	89.2 ± 3.0	34.7 ± 11.7	54.5	61.8	0.38	0.47	0.18	127
PI 652242	Yellow/White	India	Cultivated PI	83.3 ± 3.1	70.8 ± 4.7	12.5	13.6	0.86	0.88	0.17	48
PI 652243	Yellow	Turkey	Cultivated PI	78.1 ± 4.1	60.8 ± 5.2	17.2	21.7	0.79	0.72	0.28	72
PI 652245	White	India	Wild PI	75.0 ± 6.6	48.3 ± 7.5	26.7	28.3	0.72	0.52	0.23	114
PI 652246	Orange	Russia	Cultivated PI	66.7 ± 7.0	47.5 ± 4.0	19.2	23.7	0.76	0.48	0.24	126
PI 652247	Orange	Russia	Cultivated PI	65.0 ± 4.1	54.2 ± 11.6	10.8	11.1	0.89	0.50	0.18	120
PI 652248	Orange	Russia	Cultivated PI	95.0 ± 2.2	69.2 ± 9.4	25.8	27.7	0.73	1.00	0.21	33
PI 652249	Orange	Russia	Cultivated PI	90.0 ± 2.6	64.3 ± 7.2	25.7	28.0	0.73	0.87	0.15	53
PI 652252	Purple/Yellow	India	Cultivated PI	61.1 ± 6.0	40.6 ± 7.9	20.5	36.1	0.64	0.39	0.23	153
PI 652253	Red/Yellow	India	Cultivated PI	50.0 ± 3.7	49.6 ± 2.3	0.4	-1.4	1.00	0.37	0.25	159
PI 652254	Orange	India	Cultivated PI	69.2 ± 5.2	64.2 ± 6.2	5.0	5.8	0.94	0.67	0.12	86
PI 652255	Orange/Purple	India	Cultivated PI	97.0 ± 2.0	62.3 ± 9.3	34.7	35.2	0.64	0.90	0.20	46
PI 652256	Purple/Yellow	India	Cultivated PI	79.8 ± 5.2	53.0 ± 7.4	26.8	35.0	0.66	0.66	0.20	88
PI 652257	Red	India	Cultivated PI	90.8 ± 2.0	57.5 ± 4.6	33.3	36.5	0.64	0.78	0.18	65
PI 652258	Orange	India	Cultivated PI	78.7 ± 2.7	38.1 ± 8.6	40.6	51.1	0.47	0.45	0.20	132

(*Continued on next page*)

Supplemental Table 1. (*Continued*) Carrot accession, root color, country of origin, domestication status (DS), mean percent germination without salt stress (Nonstress) ± standard error, mean percent germination with 150 mM salt stress (Stress) ± standard error, mean absolute decrease (AD), mean inhibition index (II), relative salt tolerance (RST), mean salt tolerance index (STI), hundred seed weight (HSW), and rank based on STI.

Accession	Root Color	Origin	DS	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI	HSW	Rank
PI 652259	NA	India	Cultivated PI	95.0 ± 2.2	82.3 ± 5.0	12.7	13.1	0.85	1.17	0.41	13
PI 652260	Orange/Yellow	India	Cultivated PI	85.0 ± 2.6	68.3 ± 8.9	16.7	19.7	0.80	0.88	0.15	48
PI 652261	Red	India	Cultivated PI	85.0 ± 4.7	42.5 ± 10.1	42.5	50.5	0.49	0.55	0.27	109
PI 652276	Orange/Yellow	Tajikistan	Cultivated PI	65.8 ± 7.2	12.5 ± 6.6	53.3	83.9	0.16	0.15	0.22	223
PI 652277	Orange	Mongolia	Cultivated PI	91.6 ± 2.5	40.8 ± 8.7	50.8	54.2	0.46	0.55	0.11	109
PI 652288	Orange	Kazakhstan	Cultivated PI	60.0 ± 7.0	4.2 ± 4.2	55.8	90.7	0.09	0.03	0.11	274
PI 652290	White	Poland	Wild PI	82.5 ± 4.2	15.0 ± 10.5	67.5	80.7	0.19	0.18	0.12	211
PI 652291	White	Portugal	Wild PI	83.3 ± 3.1	21.1 ± 5.6	62.2	75.3	0.24	0.27	0.15	180
PI 652334	Purple	Syria	Cultivated PI	85.8 ± 2.4	76.7 ± 5.9	9.2	10.4	0.90	0.99	0.15	34
PI 652335	Purple	Syria	Cultivated PI	75.3 ± 4.5	35.0 ± 8.6	40.3	52.7	0.47	0.40	0.19	148
PI 652336	Purple	Syria	Cultivated PI	57.5 ± 5.1	46.7 ± 7.3	10.8	13.4	0.87	0.40	0.17	148
PI 652338	White	Syria	Wild PI	82.5 ± 4.6	18.3 ± 6.3	64.2	77.5	0.23	0.23	0.23	193
PI 652341	White	Syria	Wild PI	89.0 ± 2.9	9.0 ± 5.6	80.0	90.2	0.10	0.12	0.15	230
PI 652344	White	Syria	Wild PI	82.5 ± 3.2	0.0 ± 0.0	82.5	100.0	0.00	0.00	0.21	289
PI 652346	White	Syria	Wild PI	89.2 ± 3.5	1.7 ± 1.7	87.5	98.3	0.02	0.02	0.14	278
PI 652347	White	Syria	Wild PI	82.2 ± 3.9	4.2 ± 3.3	78.0	94.8	0.05	0.05	0.13	261
PI 652348	White	Turkey	Wild PI	58.3 ± 6.5	3.3 ± 1.7	55.0	94.2	0.06	0.03	0.18	274
PI 652349	White	Turkey	Wild PI	83.3 ± 7.5	4.2 ± 2.4	79.2	94.8	0.05	0.05	0.10	261
PI 652351	White	Turkey	Wild PI	85.8 ± 4.4	10.8 ± 4.7	75.0	86.9	0.13	0.14	0.14	228
PI 652352	White	Turkey	Wild PI	87.5 ± 3.4	21.7 ± 5.4	65.8	74.4	0.26	0.28	0.16	176
PI 652353	White	Turkey	Wild PI	88.3 ± 2.8	5.0 ± 3.4	83.3	94.4	0.06	0.07	0.11	235
PI 652354	White	Turkey	Wild PI	90.8 ± 4.4	12.5 ± 6.6	78.3	87.2	0.13	0.18	0.16	211
PI 652356	White	Turkey	Wild PI	90.8 ± 3.0	2.5 ± 1.7	88.3	97.3	0.03	0.04	0.15	266
PI 652358	White	Turkey	Wild PI	66.7 ± 5.1	14.3 ± 5.1	52.4	79.9	0.20	0.16	0.10	219
PI 652359	White	Turkey	Wild PI	91.7 ± 3.1	16.7 ± 9.9	75.0	80.3	0.20	0.21	0.11	202
PI 652362	White	Turkey	Wild PI	86.7 ± 2.8	14.2 ± 5.7	72.5	82.7	0.17	0.18	0.12	211
PI 652364	White	Turkey	Wild PI	83.3 ± 1.7	10.8 ± 8.0	72.5	87.2	0.13	0.14	0.14	228
PI 652368	White	Turkey	Wild PI	94.2 ± 4.0	45.1 ± 11.3	49.0	51.1	0.49	0.63	0.16	92
PI 652369	White	Turkey	Wild PI	94.7 ± 2.0	30.0 ± 5.0	64.7	68.6	0.31	0.43	0.08	138
PI 652370	White	Turkey	Wild PI	86.7 ± 5.4	9.2 ± 4.4	77.5	87.9	0.12	0.11	0.16	234
PI 652372	White	Turkey	Wild PI	75.8 ± 4.0	16.8 ± 11.2	59.0	79.3	0.20	0.21	0.09	202
PI 652373	White	Turkey	Wild PI	69.0 ± 8.1	2.1 ± 1.3	67.0	97.4	0.03	0.02	0.10	278
PI 652374	Yellow	Turkey	Cultivated PI	100.0 ± 0.0	91.7 ± 3.3	8.3	8.3	0.92	1.38	0.17	1
PI 652379	White	Turkey	Wild PI	89.2 ± 3.5	5.8 ± 4.2	83.3	92.6	0.07	0.07	0.06	253
PI 652380	White	Turkey	Wild PI	72.5 ± 4.2	0.0 ± 0.0	72.5	100.0	0.00	0.00	0.08	289
PI 652382	White	Turkey	Wild PI	82.4 ± 4.9	3.5 ± 2.6	79.0	95.0	0.05	0.04	0.16	266
PI 652384	White	Turkey	Wild PI	82.5 ± 4.2	3.4 ± 2.2	79.1	95.8	0.04	0.04	0.14	266
PI 652387	White	Turkey	Wild PI	62.8 ± 4.5	4.3 ± 2.0	58.5	93.6	0.06	0.04	0.12	266
PI 652388	White	Turkey	Wild PI	80.7 ± 6.3	2.5 ± 2.5	78.2	97.5	0.03	0.04	0.11	266
PI 652391	White	Turkey	Wild PI	82.5 ± 2.8	1.7 ± 1.7	80.8	97.8	0.02	0.02	0.18	278
PI 652392	White	Turkey	Wild PI	66.0 ± 5.8	3.0 ± 2.0	63.0	95.8	0.04	0.03	0.15	274
PI 652393	White	Turkey	Wild PI	77.4 ± 3.4	13.3 ± 6.8	64.1	83.8	0.16	0.17	0.17	217
PI 652394	White	Turkey	Wild PI	85.0 ± 3.4	16.8 ± 2.4	68.3	80.0	0.20	0.21	0.12	202
PI 652396	White	Turkey	Wild PI	71.4 ± 6.0	4.2 ± 2.7	67.3	93.6	0.06	0.04	0.20	266
PI 652398	White	Turkey	Wild PI	80.6 ± 4.4	8.3 ± 3.3	72.3	90.2	0.10	0.11	0.18	234
PI 652399	White	Turkey	Wild PI	70.7 ± 3.4	11.7 ± 5.3	59.0	83.4	0.17	0.12	0.10	230
PI 652400	Orange	Turkey	Cultivated PI	95.8 ± 2.4	85.7 ± 1.6	10.1	10.1	0.89	1.23	0.18	8
PI 652401	Orange	Turkey	Cultivated PI	90.0 ± 7.2	83.2 ± 8.0	6.8	8.3	0.90	1.17	0.15	13
PI 652402	Orange	Turkey	Cultivated PI	96.7 ± 2.1	95.0 ± 1.8	1.7	1.6	0.98	1.38	0.15	1
PI 652403	Orange	Turkey	Cultivated PI	94.2 ± 1.5	90.8 ± 3.0	3.3	3.3	0.97	1.28	0.22	7
PI 652404	Orange	Turkey	Cultivated PI	93.3 ± 1.1	67.5 ± 6.9	25.8	27.6	0.72	0.95	0.14	39
PI 652405	Orange	Turkey	Cultivated PI	97.5 ± 1.1	94.2 ± 2.4	3.3	3.4	0.97	1.38	0.15	1
PI 652406	White	Turkey	Wild PI	82.5 ± 2.5	11.7 ± 2.8	70.8	86.2	0.14	0.15	0.14	223
PI 652407	White	Turkey	Wild PI	77.5 ± 7.9	8.3 ± 3.8	69.2	90.5	0.09	0.11	0.09	234
PI 652409	White	Turkey	Wild PI	88.3 ± 2.1	5.0 ± 2.6	83.3	94.1	0.06	0.06	0.11	258
PI 652410	NA	India	Cultivated PI	95.8 ± 3.3	67.5 ± 7.7	28.3	28.4	0.72	0.96	0.26	37
PI 652411	White	France	Wild PI	88.3 ± 2.8	30.8 ± 9.3	57.5	65.1	0.35	0.41	0.09	145
B2327B	Orange	USA	Inbred	67.5 ± 8.2	10.8 ± 5.1	56.7	84.6	0.15	0.12	0.19	230
B2566B	Orange	USA	Inbred	90.0 ± 3.7	5.0 ± 5.0	85.0	93.3	0.07	0.06	0.13	258
B493B	Orange	USA	Inbred	56.0 ± 8.3	0.0 ± 0.0	56.0	100.0	0.00	0.00	0.15	289
B5208B	Orange	USA	Inbred	90.8 ± 3.3	29.2 ± 11.9	61.7	65.7	0.34	0.37	0.12	159
B5238B	Orange	USA	Inbred	69.2 ± 5.8	0.8 ± 0.8	68.3	98.2	0.02	0.01	0.20	287
B6279B	Orange	USA	Inbred	63.0 ± 8.6	8.6 ± 4.7	54.4	84.0	0.17	0.07	0.12	253
B7254B	Orange	USA	Inbred	58.3 ± 6.4	3.3 ± 3.3	55.0	90.5	0.10	0.02	0.18	278
B9253B	Orange	USA	Inbred	53.2 ± 7.0	2.5 ± 2.5	50.7	95.8	0.04	0.02	0.12	278
DH1[z]	Orange	Netherlands	Inbred	87.5 ± 2.8	4.2 ± 2.0	83.3	95.3	0.05	0.06	0.20	258
L1408B	Orange	USA	Inbred	65.0 ± 1.8	41.0 ± 6.5	24.0	37.6	0.60	0.41	0.18	145
Nb4001B	Orange	USA	Inbred	83.2 ± 2.2	10.8 ± 8.2	72.3	88.0	0.12	0.15	0.15	223
Nb4002B	Orange	USA	Inbred	88.3 ± 8.8	26.7 ± 8.5	61.7	72.7	0.27	0.39	0.15	153
Nb6526B	Orange	USA	Inbred	83.0 ± 6.2	0.0 ± 0.0	83.0	100.0	0.00	0.00	0.16	289
Ns5154	Orange	USA	Inbred	96.7 ± 1.7	13.3 ± 8.9	83.3	86.2	0.14	0.19	0.17	209
P1129B	Purple	USA	Inbred	93.0 ± 2.5	43.0 ± 5.8	50.0	54.1	0.46	0.61	0.18	95

(*Continued on next page*)

Supplemental Table 1. (*Continued*) Carrot accession, root color, country of origin, domestication status (DS), mean percent germination without salt stress (Nonstress) ± standard error, mean percent germination with 150 mM salt stress (Stress) ± standard error, mean absolute decrease (AD), mean inhibition index (II), relative salt tolerance (RST), mean salt tolerance index (STI), hundred seed weight (HSW), and rank based on STI.

Accession	Root Color	Origin	DS	Nonstress (%)	Stress (%)	AD (%)	II (%)	RST	STI	HSW	Rank
R6636	Red	USA	Inbred	84.2 ± 10.1	71.1 ± 6.0	13.1	7.5	0.93	0.92	0.20	43
Orange CC1	Orange	USA	Hybrid	98.3 ± 1.1	35.9 ± 11.5	62.5	63.8	0.37	0.53	0.12	113
Orange CC2	Orange	USA	Hybrid	93.3 ± 2.8	24.2 ± 11.2	69.2	72.8	0.27	0.32	0.24	171
Purple CC1	Purple	USA	Hybrid	80.0 ± 6.6	17.5 ± 6.3	62.5	78.0	0.22	0.22	0.19	197
Orange CC3	Orange	USA	Hybrid	89.0 ± 1.6	59.6 ± 6.3	29.5	32.8	0.67	0.79	0.20	63
Yellow CC1	Yellow	USA	Hybrid	94.2 ± 2.4	36.7 ± 9.1	57.5	60.3	0.40	0.51	0.10	117

[z]Developed and donated by Rijk Zwaan.