

Planting Density Does Not Affect Root Shape Traits Associated with Market Class in Carrot

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Keywords. *Daucus carota* var. *sativus*, root phenotyping, seeding rate

Abstract. Carrot (*Daucus carota* var. *sativus*) cultivars with common root shape, appearance, and end-use are grouped and commercialized in market classes. The shape of the carrot storage root is the result of growth and development, which is highly influenced by genotype; however, the extent to which planting density affects root shape traits and its interaction with genotype remains unexplored. To observe the effects of market class and density on carrot root shape characteristics, five cultivars classified in five different market classes, including Imperator, Nantes, Danvers, Chantenay, and Ball, were each grown at five planting densities ranging from 0.5 million to 4.5 million plants/ha. A generalized complete block design with a two-way factorial treatment arrangement of the two factors, density and genotype, was used in three environments. Roots were phenotyped using a digital imaging pipeline and scored for root size (length, maximum width) and compound root shape traits including traits derived from the principal component analysis of root contour profiles like root fill and tip and shoulder curvature. The results suggest that planting density had minimal impact on the shape of carrot roots, and the expected shape for each market class was maintained regardless of planting density; however, the analysis was constrained by the presence of interactions among genotype, density, and environment, which influence the contribution of main effects to shape. For the Nantes, Danvers, Chantenay, and Imperator market classes, planting density influenced the size of the carrot root, with size decreasing by up to 50% in length and width at high planting densities. We found high estimates of broad-sense heritability for traits that determine the shape of the carrot root, such as root fill and length-to-width ratio, which capture size-independent variation of the storage root. Although environmental signals play a role, our results suggested that the shape of the carrot root is primarily determined by genotype, and that planting density generally does not have a significant effect on its shape.

The concept of market classes in carrot (*Daucus carota* var. *sativus*) breeding and economics establishes a standardized classification system to group cultivars based on root shape. The categorization of carrot cultivars based on their root shape dates back to at least the 17th century (Banga 1957). However, by the 1940s, the practice of forming market classes and cataloging cultivars through the description of a standard type to facilitate trade

was well-established in the United States (Magruder 1940).

In North America, specific market classes have been associated with the fresh and processing carrot markets (Goldman 2018). For instance, the Imperator and Nantes types are used in the fresh market, whereas Danvers and Chantenay types are used in the processing market for freezing, canning, juice extraction, and other processing operations (Goldman 2018; Lucier and Lin 2007). Market classes such as the Ball (Parisienne), are used in specialty markets because of their distinctive shape. In Europe, the most common carrot market classes for the fresh market include two additional types, Berlicum and Amsterdam. Carrot cultivars destined for the processing market also include Flakkee and Kuroda, commonly used in European and Asian carrot markets, respectively (Rubatzky et al. 1999).

The Vegetable Cultivar Description Lists for North America published by *HortScience*, along with recent studies on phenotypic and genotypic diversity of carrot cultivars, help understand the progress and history of carrot market classes (Luby et al. 2016; Mou 2022). According to the lists, carrot cultivars released between the 1930s and 2022 were

categorized into at least 10 market classes, with the number of cultivars increasing until the 1990s (Fig. 1). The notable surge in the release of new carrot cultivars during the 1980s and 1990s coincided with the development of fresh-cut technology and the increasing popularity of baby-cut carrots [US Department of Agriculture (USDA), Economic Research Service 2022]. The lists also described a rise in cultivar releases attributed to the adoption of hybrid technology starting in the 1960s and the growing number of cultivars introduced in the specialty market class from the 1990s onward (Fig. 1). Specialty market cultivars are characterized by appealing shapes, colors, and improved flavor. In addition, according to the lists, the two market classes with the most released cultivars are Imperator followed by Nantes (Fig. 1), making them of high commercial value in North American and European markets.

The market classes system groups carrot cultivars based primarily on root shapes tailored to a specific use, but because of variation in carrot root shapes, not all cultivars clearly fit within a single market class (Brainard et al. 2021). This observed variation in root shape (root fill, length-to-width ratio, curvature of the shoulders and tips) and size (length, maximum width) is influenced by selection and cultivar genetic differences (Brainard et al. 2022; Macko-Podgórní et al. 2017).

Recommended planting density for carrot cultivars also varies depending on market class. Fresh market cultivars are planted at densities as high as 3.0 million plants/ha, and processing market classes, such as Chantenay, are planted between 0.5 million and 1.5 million plants/ha (Goldman 2018). In addition to the influence of genotype, planting density can further influence root shape and overall plant morphology. For example, density affects the stability of sex expression and biomass partitioning in cucumber (*Cucumis sativus*; Lower et al. 1983; Nienhuis et al. 1984; Serquen et al. 1997; Widders and Price 1989). Density influenced shape traits, including root length and

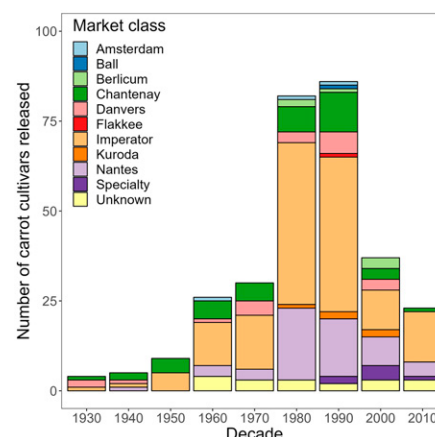


Fig. 1. Number of carrot cultivars released by market class in the years 1937 through 2022 according to the Vegetable Cultivar Description Lists for North America 1–28 published by *HortScience* (Mou 2022) and the study of Luby et al. (2016).

Received for publication 1 May 2023. Accepted for publication 5 Jun 2023.

Published online 11 Aug 2023.

We express our gratitude to the following individuals and institutions for their valuable contributions to this research: Michael Liou from the University of Wisconsin-Madison Statistical Consulting Lab for helping with experimental design, statistical modeling, and data analysis; the Crescio family for their generous support during the trials conducted at Randolph, WI; and the staff at Hancock Agricultural Research Station for their valuable assistance in conducting the field trials at that location.

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width in table beet (*Beta vulgaris*; Goldman 1995), and differences in planting density contributed to the expression of genetic variation in seed mass of radish (*Raphanus sativus*; Mazzer and Wolfe 1992).

Plant breeding programs consider the role of planting density in modifying plant morphology. In addition, density management could complement breeding to improve yield both in vegetables and row crops, but it is often at the expense of high seed requirements (Cao et al. 2022; Lauer et al. 2012; Osei et al. 2014; Zahara 1970). In carrot, studies show that high population density tends to increase carrot root yield up to a threshold, but the mass of each individual root tends to be reduced (Bradley et al. 1967; Lazcano et al. 1998; Robinson 1969; Stanhill 1977). Density has also been manipulated to increase total seed yield in carrot seed production as density modifies crop canopy architecture, seed yield, and disease pressure (Noland et al. 1988). However, only one recent study has investigated the role of density on specific root shape characteristics (Rohwer 2021). This study suggested that the cylindricity of carrot roots is primarily determined by genotype and bed shape, rather than density.

Researchers have used digital imaging to accurately phenotype carrot root traits (Brainard et al. 2021, 2022; Turner et al. 2018), providing an opportunity to characterize novel carrot root shape traits associated with market class. We carried out field experiments across three environments (defined as combination of location and year) using five genotypes with contrasting shape, each planted at densities ranging from 0.5 to 4.5 million plants/ha with the objective of observing the effect of genotype and planting density on carrot root shape traits.

Materials and Methods

Plant material. Each market class was represented by a single genotype (Table 1). The market classes studied included Imperator, Ball, Nantes, Danvers, and Chantenay. Imperator types are characterized by their elongated and cylindrical shape, and medium to large length. They also have tapering roots and small shoulders, and are used in the fresh market for baby-cut carrots. The Ball market class consists of compact and spherical carrots that are relatively

small in size, often preferred for home gardens. Nantes types exhibit straight, cylindrical roots with uniform width and diameter, ending in blunt tips. They are suitable for both fresh consumption and processing markets. Danvers cultivars, on the other hand, are primarily used for processing because of their broad shoulders that gradually taper to a stumped end. Chantenay types are cone-shaped carrots intended for processing. They are usually wedge-shaped with wide shoulders, featuring a blunt, rounded end and a tapered tip. Genotype and market class terms can be used interchangeably in this paper, as only one genotype per market class was used. However, market class is suggestive of a carrot root shape ideotype, which is a more meaningful term in cultivar improvement contexts compared with the name of the cultivar.

Locations, trial establishment, and maintenance. Field experiments were conducted at the University of Wisconsin Hancock Agricultural Research Station in Hancock, WI, in 2021 and 2022, and at Jack's Pride Farms, Randolph, WI, in 2022. The soil at Hancock Agricultural Research Station is a Plainfield loamy sand (Typic Udipsamment), consisting of deep and very well drained mesic, mixed, and sandy plains known as the Wisconsin Central Sands. The granular structure is medium and very friable. The soil in Jack's Pride Farm is a Houghton Muck (Typic Haplosaprists), which consists of a deep muck soil with weak and medium granular structure with ~20% organic matter (Colquhoun et al. 2019; USDA, National Cooperative Soil Survey 2021). Both types of soil are used for commercial carrot cultivation in Wisconsin.

Carrot seed was hand planted in raised beds 1.8 m wide (center to center) and 0.40 m high at custom spacing (Table 2). Effective bed spacing was 1.5 m. Rows were marked with a Bed Preparation Rake and Row Markers (Johnny's Selected Seeds, Winslow, ME). Plots were 1 m long and 0.75 m wide with a custom spacing between rows and plants (Table 2). The five expected densities corresponded to 0.5 million, 1.0 million, 1.5 million, 3.0 million, and 4.5 million plants/ha in all three environments. Trials were planted on 17 May 2021 and 17 May 2022 at Hancock Agricultural Research Station and on 16 May 2022, at Jack's Pride Farms in Randolph, WI. Plots were overseeded and thinned to their appropriate

density 30 d after planting. A stand count was performed 70 d after planting to estimate the actual (observed) planting density for each plot. Carrots were established with a barley (*Hordeum vulgare* L.) nurse crop seeded at a rate of 22 kg·ha⁻¹. Barley was seeded (broadcast) 1 week before carrots were planted at the time the soil was prepared and raised beds were constructed. Barley was killed 22 d and 15 d after planting in 2021 and 2022, respectively, using Select Max® (12.6% Clethodim; Valent, Libertyville, IL, USA) at a rate of 0.10 kg a.i./ha. Preemergent herbicide [Prowl® H2O (BASF Agricultural Solutions, Durham, NC, USA) or Nortron® SC (Bayer Crop Science, St Louis, MO, USA)] was applied within 2 d after planting for weed control according to the manufacturer's indication. One or two applications of either Caparol 4L (Syngenta Crop Protection, Greensboro, NC, USA) or Select 2 EC (Valent Agricultural, San Ramon, CA, USA) were applied between 30 and 50 d after planting for weed control. Standard carrot crop fertilization was maintained per Hancock Agricultural Research Station and Jack's Pride Farms practices as recommended by the University of Wisconsin-Madison Division of Extension (Bradford et al. 2023). Harvest was carried out 106 d after planting at Hancock, WI (31 Aug 2021 and 31 Aug 2022), and 100 d after planting at Randolph, WI (24 Aug 2022).

Experimental design. The experiment was planted in a generalized complete block design with a two-way factorial treatment arrangement with two blocks within each environment and two experimental unit replicates within each block. For each experiment, experimental units were randomized within blocks. Two replications of the experimental unit within each block were used to increase statistical power. Each factor (density and genotype) had five levels (Tables 1 and 2). A subsample of 10, or all if less than 10 carrot roots were available, were harvested from the center rows of each plot and stored at 6°C until phenotypic evaluation.

Root image analysis. Roots were cleaned from excess soil using water and a nail brush. Excess secondary roots were removed using a damp cloth. Forked or split roots and plants with at least one inflorescence during harvest were discarded. Using scaled images, the digital imaging platform developed by Brainard

Table 1. Cultivar name, market class, vendor, and root characteristics of the five cultivars of *Daucus carota* var. *sativus* used in field-based experiments.

Cultivar name	Market class	Vendor ⁱ	Maturity (days) ⁱ	Root			
				Length (cm) ⁱ	Diam (cm) ⁱ	Shoulder width (cm)	Color ⁱⁱ
Fresh market							
Sugarsnax 54 F1	Imperator	Johnny's Seed	68	23–25	2–2.5	2.5	DO
Atlas (OP) ⁱⁱⁱ	Ball	Johnny's Seed	70	5–7	4–5	–	O
Naval F1	Nantes	Johnny's Seed	70	18–23	2–3	4	O
Processing							
Danvers 126 (OP) ⁱⁱⁱ	Danvers	Stokes Seeds	70–80	18–21	4	5–6	O
Hercules F1	Chanteney	Johnny's Seed	65	16–23	4	5–9	O

ⁱ Maturity is defined as the days from seed planting to horticultural maturity of the roots. Maturity, root length, diameter, and shoulder width obtained from Stokes Seed Company (2021), Johnny's Selected Seeds (2021), and Luby et al. (2016).

ⁱⁱ O, DO = orange and dark orange, respectively.

ⁱⁱⁱ Open pollinated.

Table 2. Experimental row number, distance between rows and plants and approximate expected planting density for each of the levels of the factor density.

Number of experimental 1-m rows per plot	Distance between rows (cm)	Distance between plants (cm)	Total number of plants per 1-m row	Expected planting density (plants/ha)
3	22.0	9.1	11	500,000
4	18.4	5.3	19	1,000,000
4	14.7	4.5	22	1,500,000
6	11.0	3.0	33	3,000,000
7	8.0	2.8	36	4,500,000

et al. (2021) was used to phenotype carrot roots. Briefly, roots along with a machine-readable quick response (QR) code with genotype, unique identification, and other relevant information were placed in digital imaging templates. A high-resolution picture was acquired using a Nikon 5600 digital single-lens reflex camera (Nikon USA, Melville, NY, USA) connected to a computer running Smart Shooter (version 3.0; Kuvacode Oy; Kerava, Finland). Custom Python scripts were used to store a color image renamed with the information provided by the QR code. In the pre-processing step, the raw color image was converted into a binary mask by discriminating the background from the carrot pixels using custom MATLAB scripts. The binary mask was further standardized by removing residual root tips, and curving. This process generated a straight mask of the carrot root. Straight masks were used as inputs to extract phenotypes using custom Python scripts as described by Brainard et al. (2021). A total of 2332 root straight masks were analyzed.

Root phenotyping. The digital imaging pipeline outputs traits that have been traditionally measured by hand (i.e., length, maximum width) and traits based on principal component analysis of root contours like root fill, shoulder curvature and tip curvature. All root traits were phenotyped using digital images. Root length (mm) was estimated as the distance between the center top of the root crown to the root tip. Maximum width (mm) was estimated as the distance at the widest portion of the root. Length-to-width ratio was the ratio of length (mm) to maximum width (mm). Digital biomass (simply, biomass throughout the paper) was the area of the entire straight mask (mm²). The variables derived from principal component analysis of root contours included the following: 1) root fill, which quantified the degree to which the width of the carrot is maintained along the total length of the root, 2) root shoulder curvature, and 3) root tip curvature. The curvature values were computed at each point along the root profile to generate a vector of curvature values that were added and decomposed using principal component analysis (Brainard et al. 2021). These traits quantified

size-independent variation along the entire root contour profile (root fill), root shoulders (first 50 contour points/pixels of the root), and root tip (last 50 contour points/pixels of the root). For traits derived from principal component analysis, images were length and width normalized to an equal size to estimate size-independent variation. An illustration of the traits derived from principal component analysis and length-to-width ratio is presented in Fig. 2.

Statistical analysis. R statistical software (version 4.2.2; R Foundation for Statistical Computing, Vienna, Austria) was used for data visualization, correlations, and inferential statistics. Analysis of variance (ANOVA) (Table 3) was calculated using an all-fixed effect model fitted using the nlme::gls function (Pinheiro and Bates 2022) according to the following linear model:

$$y_{ijklmn} = \mu + G_i + D_j + E_k + (GD)_{ij} + (GE)_{ik} + (DE)_{jk} + (GDE)_{ijk} + \beta_{l(k)} + r_{m(lk)} + \varepsilon_{ijklm} + \delta_{ijklmn},$$

where y_{ijklm} is the response variable (all measured root traits), μ is the overall mean, G_i is

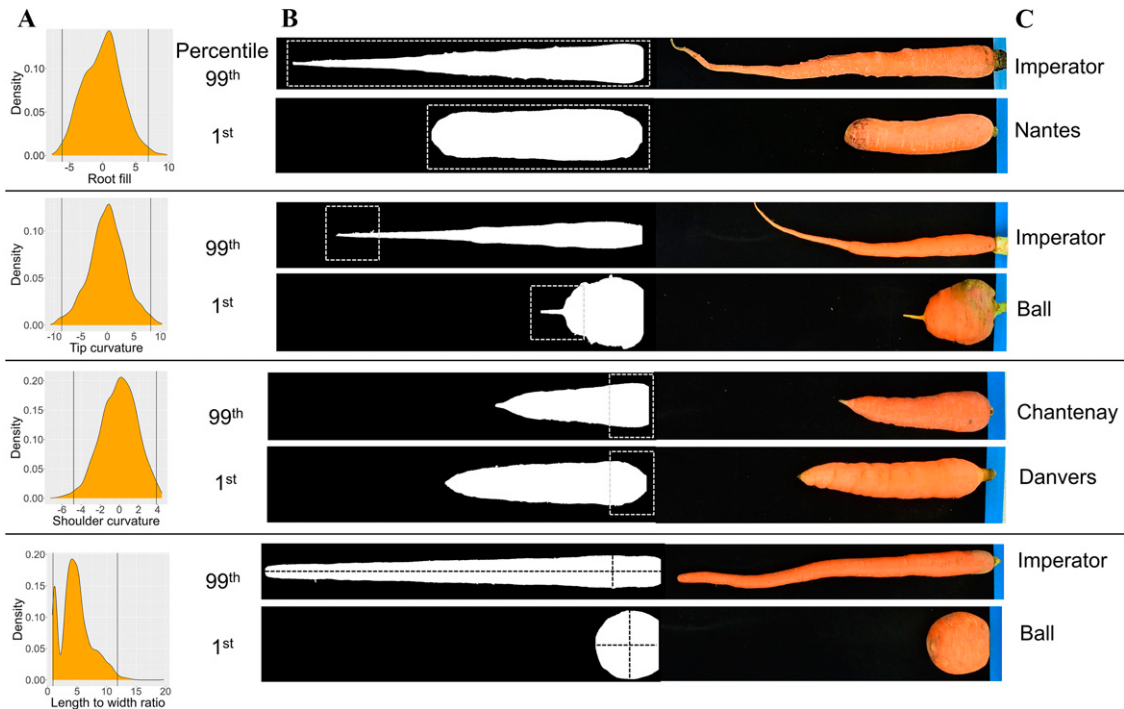


Fig. 2. Illustration of the variables root fill, tip curvature, shoulder curvature, and length-to-width ratio. Root fill, tip curvature, and shoulder curvature were derived from principal component analysis of curvature values estimated from length and width normalized root contours. (A) Density histogram for each variable and the percentile from which representative root images were drawn. The vertical lines in the density histogram mark the first and 99th percentiles. (B) Representative roots sampled from the extremes of each distribution (99th and first percentiles). Black and white images are straightened binary masks of the raw carrot image immediately to the right. The dashed rectangles or lines show the region of the root that the variable quantifies and contrast differences between the two roots. (C) Reported market class of the roots represented in B.

Table 3. F values from type I analysis of variance, variance components, and broad-sense heritability (H^2) for carrot root shape traits. Field trials were carried out in three Wisconsin environments (Hancock 2021, Hancock 2022, and Randolph 2022). Variance components estimates are in units squared.

Source of variance	df	F-value						
		Length (mm)	Max width (mm)	Length-to-width ratio	Root fill	Shoulder curvature	Tip curvature	Biomass (cm ²)
Environment (E)	2	3.10 ^{NS}	223.80***	50.42***	77.53***	73.85***	50.02***	219.55***
Block/E	3	0.75 ^{NS}	7.72***	1.05 ^{NS}	0.06 ^{NS}	3.25**	1.08 ^{NS}	0.31 ^{NS}
Genotype (G)	4	238.97***	522.38***	5289.12***	455.26***	141.92***	249.73***	981.73***
Density (D)	4	1.18 ^{NS}	189.05***	0.87 ^{NS}	2.32 ^{NS}	38.29***	1.30 ^{NS}	193.45***
G × D	16	3.41***	3.46***	1.98 ^{NS}	0.72 ^{NS}	2.07**	1.35 ^{NS}	19.37***
D × E	8	1.79 ^{NS}	1.92***	1.8 ^{NS}	2.43*	6.95***	1.59 ^{NS}	2.33*
G × E	8	9.54***	5.24 ^{NS}	7.26***	12.20***	11.71***	5.50***	27.83***
G × D × E	32	3.96***	1.91***	1.40 ^{NS}	1.68**	1.60*	0.83 ^{NS}	2.27***
Variance components		Estimate						
σ_G^2		4542.60	47.77	6.75	3.22	0.41	4.17	16,691
σ_{GD}^2		486.55	25.40	0.02	0	0.15	0.02	15,293
σ_{GE}^2		692.90	31.70	0.04	0.21	0.28	0.74	20,231
σ_{GDE}^2		75.46	0	0	0	0.08	0	225
σ_e^2		3439.41	200.30	3.10	8.70	3.82	9.78	78,310
PEV ⁱⁱ		390.63	24.50	0.12	0.21	0.20	0.41	111,222
		Broad-sense heritability (H^2) ⁱⁱⁱ						
		0.92	0.66	0.96	0.90	0.68	0.91	0.60

ⁱ NS, *, **, *** = nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

ⁱⁱ Prediction error variance (PEV) is given by the expression $PEV = \frac{\sigma_{GD}^2}{d} + \frac{\sigma_{GE}^2}{e} + \frac{\sigma_{GDE}^2}{de} + \frac{\sigma_e^2}{rebd}$, where σ_{GD}^2 , σ_{GE}^2 , σ_{GDE}^2 , and σ_e^2 are variance components associated with genotype × density, genotype × environment, genotype × density × environment, and the residuals, respectively, and d , e , b , and r are the number of planting densities, environments, blocks, and replications, respectively.

ⁱⁱⁱ Broad-sense heritability is given by the expression $H^2 = \frac{\sigma_G^2}{\sigma_G^2 + PEV}$, where σ_G^2 is the variance associated with genotypes and PEV is the prediction error variance.

the effect of the i^{th} level of factor genotype ($i=5$), D_j is the effect of the j^{th} level of the factor density ($j=5$), E_k is the effect of the k^{th} environment ($k=3$), $(GD)_{ij}$ is the genotype × density interaction, $(GE)_{ik}$ is the genotype × environment interaction, $(DE)_{jk}$ is the density × environment interaction, $(GDE)_{ijk}$ is the genotype × density × environment interaction, $\beta_{1(k)}$ is the block effect nested within environment ($l=2$), $r_{m(lk)}$ is the experimental unit replication nested within block and environment ($m=2$), $\varepsilon_{ijklm} \sim N(0, \sigma_e^2)$ is the random residual error among samples (plots), and $\delta_{ijklm} \sim N(0, \sigma_\delta^2)$ is the subsampling random error (roots). For mean comparisons, the same model above was fitted but including the term δ_{ijklm} as a random effect and weighted by the $(GE)_{ik}$ interaction to control for within-group heteroscedasticity using the function nlme::lme (Pinheiro and Bates 2022). Mean separation procedures were estimated using the mixed effect model described previously and the emmeans function. Alpha level was corrected for multiple comparisons using Šidák.

Broad-sense heritability estimation and correlations. Broad-sense heritability (H^2) was estimated according to Holland et al. (2002) and Hanson and Goldman (2019). All terms of the following model were fit as random for variance component estimation using the lme4::lmer function.

$$y_{ijklm} = \mu + G_i + D_j + E_k + (GD)_{ij} + (GE)_{ik} + (DE)_{jk} + (GDE)_{ijk} + \beta_{1(k)} + \varepsilon_{ijklm}$$

The model used for heritability estimation differs from the model for mean comparisons in the previous section by excluding the term that accounts for the subsampling structure of the experimental design. In the heritability model, the response variable is the average root phenotype per plot, whereas in the mean

comparisons model, the response variable is each individual root observation. Furthermore, the mean comparisons model is an all-fixed effects model, and the heritability estimation model is an all-random effects model.

Broad-sense heritability was estimated using Eq. [1]:

$$H^2 = \frac{\sigma_G^2}{\sigma_G^2 + PEV}, \quad [1]$$

where σ_G^2 is the variance associated with genotypes and PEV is the prediction error variance. PEV is given by Eq. [2]:

$$PEV = \frac{\sigma_{GD}^2}{d} + \frac{\sigma_{GE}^2}{e} + \frac{\sigma_{GDE}^2}{de} + \frac{\sigma_e^2}{rebd}, \quad [2]$$

where σ_{GD}^2 , σ_{GE}^2 , σ_{GDE}^2 , and σ_e^2 are variance components associated with genotype × density, genotype × environment, genotype × density × environment interaction terms, and the residual error, respectively. The terms d , e , b , and r in the denominator (Eq. [2]) are the number of densities (five), environments (three), blocks (two), and replications (two), respectively. Correlations among pairs of environments and root shape variables were estimated using the function stats::cor.test (R Core Team 2022).

Results and Discussion

The objective of this investigation was to evaluate the effect of density on carrot root shape. The findings indicate that density did not have a major effect on carrot root shape. Expectations of shape for each market class were generally preserved regardless of planting density; however, the interpretation of our results is limited by interactions among genotype, environment, and density, which modulate the effects of each factor on root shape.

Genotype was the main source of variance, but interactions also contributed significantly to root shape variation. The ANOVA identified either genotype × environment or genotype × density × environment interactions as significant sources of variance for all the measured root shape traits (Table 3). The interactions observed in the measured root traits were attributed to unequal variance among different genotypes. In addition, variations in magnitude across environments and minor shifts in rankings between cultivars in the phenotypically similar Danvers and Nantes market classes also contributed to these interactions. Genotype was the most significant source of variance for all measured variables with highly significant differences among genotypes in length, maximum width, length-to-width ratio, and root fill. However, either significant genotype × density × environment or genotype × environment interactions were detected for all the measured root shape traits, limiting the interpretation of main genotype and density effects.

Despite the involvement of two- and three-way interactions, genotype constituted a primary source of variation. This claim was supported by the high estimates of broad-sense heritability (H^2 , Table 3). High values of H^2 highlight larger variance components associated with genotype relative to variance components associated with density, environment, or experimental error (Table 3). Estimates of H^2 ranged from 0.60 for biomass to 0.96 for length-to-width ratio. The high heritability values observed can be attributed to multiple levels of replication within and across environments, low error in phenotypes obtained through the digital imaging pipeline, and the use of a subsample of 10 roots per plot. This reduced the variance associated with environment and contributed to high H^2 estimates and agrees with similar studies that

Table 4. Spearman rank correlation between pairs of environments for all measured carrot root shape traits.

Environment pair	Spearman rank correlation coefficient						
	Length (mm)	Max width (mm)	Length-to-width ratio	Root fill	Shoulder curvature	Tip curvature	Biomass (cm ²)
Hancock 2021-Hancock 2022	0.70*** ¹	0.47***	0.76***	0.42***	0.17**	0.28***	0.56***
Hancock 2021-Randolph 2022	0.67***	0.47***	0.75***	0.28***	0.20***	0.27***	0.50***
Hancock 2022-Randolph 2022	0.68***	0.54***	0.80***	0.37***	0.26***	0.29***	0.53***

¹ **, *** = significant correlation at $P \leq 0.01$ or 0.001 , respectively.

used digital imaging systems to estimate low error phenotypes (Lee et al. 2018; Sunvittayakul et al. 2022). The traits length, maximum width, length-to-width ratio, and root fill have been found to be under genetic control, which may also help explain large estimates of H^2 in those traits (Brainard et al. 2022). Similarly, McCollum (1971) found length-to-width ratio to have the highest narrow-sense heritability among a group of root shape traits including length and diameter.

Density was not a significant source of variance in length, length-to-width ratio, root fill, and tip curvature (Table 3); however, density did significantly contribute to the variance of maximum width, shoulder curvature, and biomass. Genotype $\times$ density interactions were involved, which limit the interpretation of density main effects. The factor genotype had a greater influence than density on traits related to the shape of the carrot root, such as length-to-width ratio and root fill (Table 3). The high H^2 estimates, and significant F values associated with genotype compared with genotype $\times$ environment or genotype $\times$ density $\times$ environment, indicate that genotype explains a large amount variance in carrot root shape. Density effects were not statistically significant for traits related to root shape, such as length-to-width ratio, and root fill; however, interactions and environmental effects significantly contributed to trait variation.

Correlations among environments were consistent across all measured root shape traits. Spearman rank correlation analysis between pairs of environments for all the measured carrot root shape traits revealed significant correlations among the environments (Table 4). The correlations for length, maximum width, length-to-width ratio, and biomass were found to be strong to moderate, whereas correlations for root fill, shoulder curvature, and tip curvature were moderate to weak. Despite variations in strength, all correlations for each trait across different environments remained consistent and statistically significant (Table 4). The correlation analysis indicates that genotype and density trends remained consistent across environments, even in the presence of statistically significant genotype $\times$ environment or genotype $\times$ density $\times$ environment interactions. In addition, correlation analysis showed that length ($r = 0.80$, $P < 0.05$) and maximum width ($r = 0.53$, $P < 0.05$) were correlated with biomass, highlighting the association of these variables with carrot root size. Moreover, length-to-width ratio and root fill are traits associated with carrot storage root shape (Brainard et al. 2021, 2022). Taken together, the correlation analysis indicated

consistency across environments and revealed associations of length and maximum width to root size. Despite the involvement of length and maximum width with root size, they are also used to estimate descriptors of shape, including length-to-width ratio. Therefore, the association of length and maximum width with root size does not exclude their involvement in shape modulation.

Observed density correlates with expected density. Strong, positive, and statistically significant correlations were detected between observed and expected densities across all environments (Fig. 3). However, the observed density measured in the field 70 d after trial establishment was consistently lower than the expected density. Regardless of the environment, we found a consistent increase in the median of the observed density as the expected density increased, resulting in distinct planting density levels across all environments (Fig. 3). Previous investigations of seeding rate effects on carrot shape or yield have not reported the observed density in the field (Rajasekaran et al. 2006); however, the trend of achieving densities lower than targeted has been previously reported (Da Silva et al. 2008; Rohwer 2021; Salter et al. 1979). Rohwer (2021), for example, reported an average of close to 1.0 million plants/ha at harvest,

including unmarketable roots for cultivars in the Nantes market class while the average seeding rate was close to 1.5 million plants/ha. Rohwer (2021) also reported ~ 0.40 million plants/ha at harvest with an average seeding rate of 0.70 million plants/ha for a cultivar within the Chantenay market class. Differences in the number of plants per unit area have been attributed to many factors, including differences in seedling emergence caused by differential planting depths (Salter et al. 1979). In addition, Salter et al. (1980) reported a gradual decrease in observed density compared with the target density at establishment, which the authors attributed to self-thinning effects observed at higher densities. Self-thinning is a density-biomass relationship in which plants undergo density-dependent mortality over time (Weiner and Freckleton 2010). Although the hypothesis of self-thinning was not tested in the current experiment, it provides an explanation for the consistently lower than targeted density. Carrots, known for their characteristic staggered germination, have been used in pioneering single-species plant competition studies that examine the relationship between density and biomass (Bleasdale 1967). This phenomenon of asynchronous emergence often leads to smaller, nonproductive seedlings competing for resources, reducing the vigor of

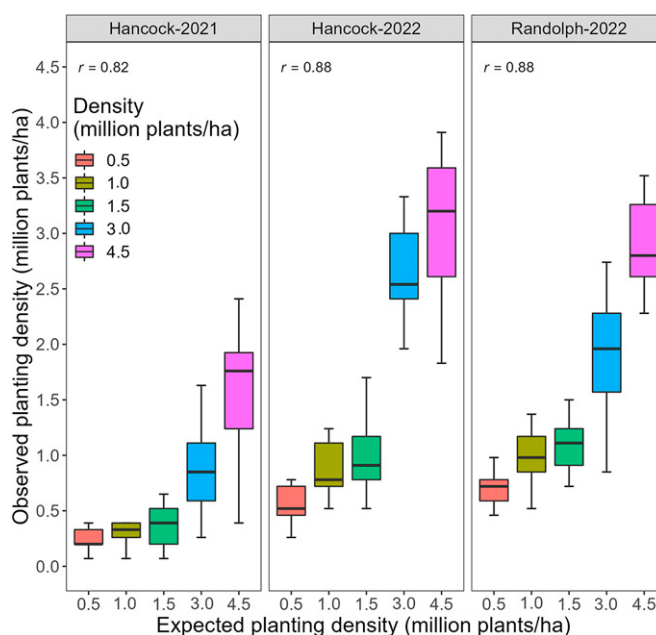


Fig. 3. Observed vs. expected planting density (million plants/ha) and coefficient of Spearman correlation (r) between the expected and the observed planting densities for each environment. All three coefficients of correlation are statistically significant at $P \leq 0.001$. Boxplots (in the style of Tukey) show the 25th and 75th percentiles on the lower and upper hinges, respectively. Data extending beyond the end of either whisker were not plotted individually.

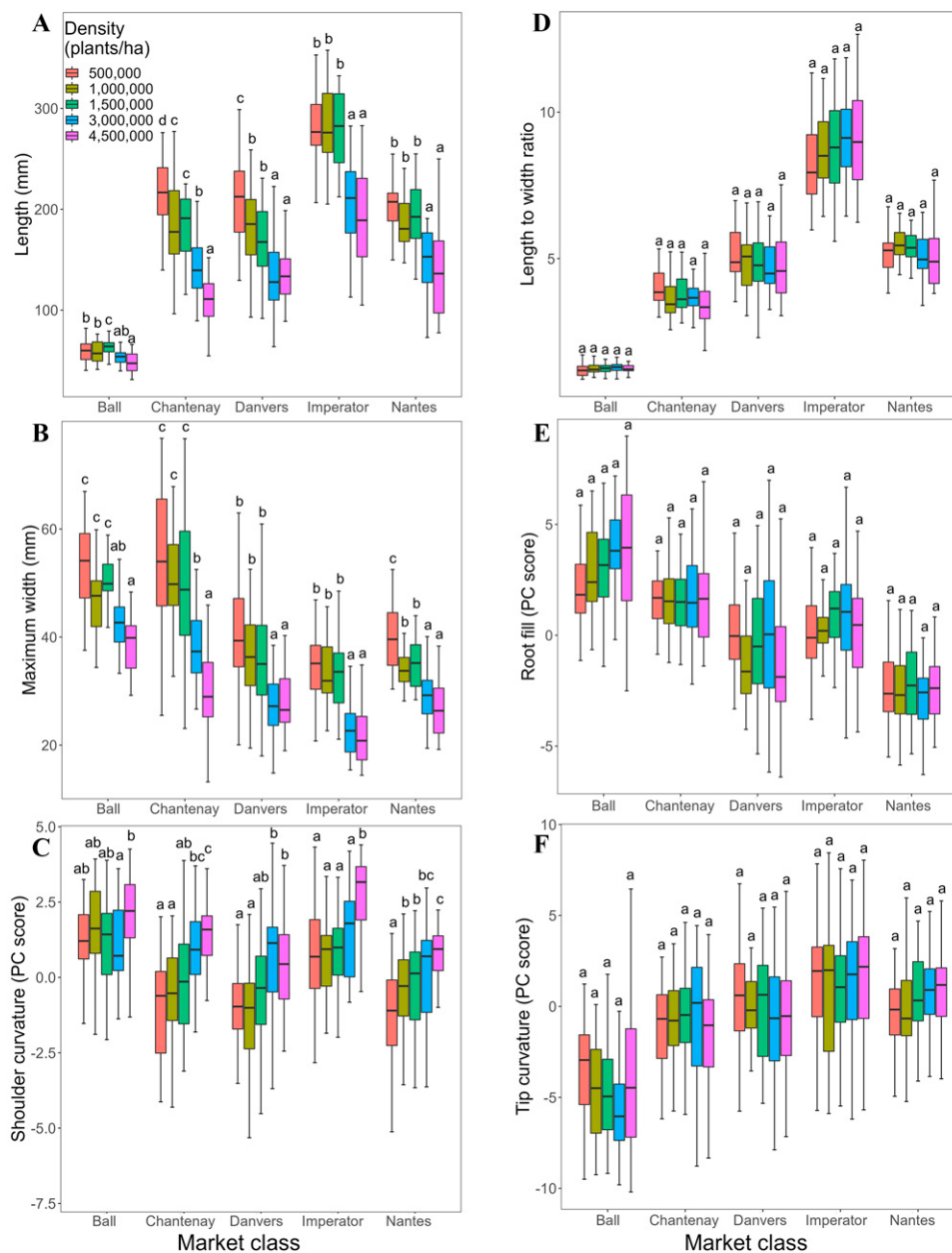


Fig. 4. Effects of planting density on carrot root shape traits by market class. Because of the presence of genotype $\times$ environment and genotype $\times$ density $\times$ environment interactions, the boxplots show data for a single representative environment, Hancock 2022: (A) length (mm), (B) maximum width (mm), (C) shoulder curvature, (D) length-to-width ratio, (E) root fill (the degree to which maximum width is maintained across the total length of the root), and (F) tip curvature. Data for C–F are either ratios or principal component scores. See Fig. 2. for an illustration of those variables on carrot roots. Boxplots (in the style of Tukey) show the 25th and 75th percentiles on the lower and upper hinges, respectively. Data extending beyond the end of either whisker were not plotted individually. Boxplots not sharing a letter within each market class are significantly different at $P \leq 0.05$. Alpha level was corrected for multiple comparisons using Sidák.

earlier emerged seedlings (Rubatzky et al. 1999). In sum, results suggest that observed density was consistently smaller than the targeted density, but strong, positive, and statistically significant correlations were observed between the observed and expected density. In all environments, five contrasting levels of density were successfully obtained (Fig. 3).

Genotype $\times$ density interactions. To simplify the visualization of trends while still considering interactions, a single representative environment (Hancock 2022) was selected to study genotype $\times$ density trends (Fig. 4). This decision was supported by the statistically significant correlations observed

between environments (Table 4). Although the discussion of results in this section focuses on Hancock 2022, the other two environments showed similar trends.

Regardless of genotype (market class), planting density significantly reduced root length (Fig. 4A) and root width (Fig. 4B) and increased root shoulder curvature (Fig. 4C). The trend of reduced length and width was attributed to a response to dynamics of resource competition that led to a smaller rate of growth and development in plants grown at a high density. For instance, in the Chantenay market class, the difference in mean root length between the lowest density (0.5 million plants/

ha) and highest density (4.5 million plants/ha) was 110 mm, and the difference in mean maximum width was 25 mm. This indicates $\sim 50\%$ decrease in both length and width. Similarly, for genotypes in the Danvers, Imperator, and Nantes market classes, the reduction in mean length and width ranged from 32% to 50% and 38% to 48%, respectively. These results suggest a change in magnitude interaction on the overall size (length and maximum width) for the market classes (Fig. 4A and B), but the trend of decreasing length and width as density increased was conserved, regardless of market class. Previous reports suggest that the competition for soil area and volume, mimicked by

high densities, accounted for as much as 72% of the variation of root size in carrot roots (Reid and English 2000). In onion, increases in plant density were reported to result in reductions in plant size, mean bulb weight, and dry weights but did not affect the bulb length-to-width ratio (McGeary 1985).

High planting density led to the development of concave shoulders (located close to the crown of the root), irrespective of the market class. Low planting densities resulted in convex shoulders (located away from the crown of the root, Figs. 2B and 4C). This observation suggests high density may inhibit or delay lateral growth of the crown, which is a result of cambial layer expansion. In contrast, lower density allows or potentiates cambial layer expansion, resulting in the shoulders being farther away from the central core of the root, resembling a physiologically mature carrot (Goldman 2020). Previous studies have demonstrated that the variation in root shoulder shapes is influenced by cultivar, density, and environmental conditions, as well as phenology (Rubatzky et al. 1999).

The reduction in length (19%) and maximum width (25%) due to increased density was less pronounced for the Ball market class, probably because the genotype tends to be ball-like in shape. However, regardless of market class, no significant effect of density was observed on the length-to-width ratio (Fig. 4D), root fill (Fig. 4E), or root tip curvature (Fig. 4F). These results agree with the ANOVA where the density and genotype $\times$ density interactions were not found to be significant sources of variation for shape traits, including length-to-width ratio, root fill, and root tip curvature, averaging across environments (Table 3). Both length-to-width ratio and root fill are traits associated with the shape of the carrot storage root, which suggests that density has a primary effect on traits that contribute to size (length, maximum width, and biomass) but no significant effect on traits that contribute to the shape of the root (length-to-width ratio, root fill, curvature of tips and shoulders). Furthermore, regardless of market class, differences between densities for tip curvature (Fig. 4F) were not statistically significant, likely explained by the large variation observed for this trait among density levels. The tapered, unenlarged part of the tip usually breaks during harvest, transportation, or handling, leading to reduced accuracy of tip curvature phenotypes; however, tip curvature is a novel trait that describes carrot root tip and is likely under genetic control and associated with visual root tip phenotypes used by breeders to characterize cultivars (i.e., Nantes tip, blunt, intermediate, tapered, etc.).

Root shape is less altered by density than root size. To explore the effect of density on root size, length-to-width ratio, a main descriptor of root shape, and biomass, a main descriptor of size, were plotted against observed density (Fig. 5). Data are shown for each of the environments and market classes separately. In all market classes, root biomass showed a significant decrease under high

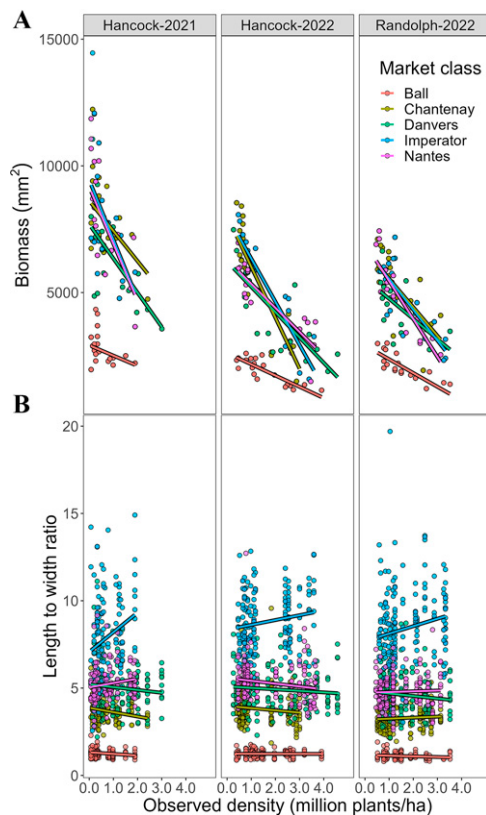


Fig. 5. Scatter plot of (A) root biomass and (B) length-to-width ratio vs. observed density. Data are shown for each of the environments separately due to the involvement of genotype $\times$ environment and genotype $\times$ density $\times$ environment interactions. The trend lines are the smoothed conditional means to aid visualization when overplotting and were calculated using the “glm” method and ggplot2 (Wickham 2016) for each market class.

density, regardless of environment (Fig. 5A); however, the length-to-width ratio did not respond to the increased density in genotypes from the Nantes, Danvers, Ball, and Chantenay market classes. In contrast, the genotype from the Imperator market class exhibited a slight increase in the length-to-width ratio as density increased (Fig. 5B), suggesting a potential interaction between genotype and density. This finding aligns with the conclusion by Salter et al. (1979) that plant density is one of the key factors influencing mean carrot root size, as high density was found to shorten the length of the storage root in carrots (Fig. 4A). Length-to-width ratio is characterized as a key shape trait in plant organs (Wang et al. 2012). In contrast, digital biomass is a trait associated with the overall size of plant organs and is usually found to correlate with fresh weight (Neumann et al. 2015). High-density planting mimics a low state of physiological maturity in which less biomass is accumulated. In contrast, low densities tend to produce plants that have reached a more advanced physiological maturity if harvested at the same time (Weiner and Freckleton 2010). Taken together, the data suggest that density significantly affects the size of carrot storage root, but generally does not alter the shape. An exception is the Imperator market class, whose shape was marginally affected by density.

Root shape is a crucial trait in root crop breeding because of its direct association with consumer purchasing decisions and processing efficiency (Iwata et al. 1998). Although environmental cues may play a role (Rubatzky et al. 1999), we found that the shape of the carrot root is primarily determined by genotype, and planting density generally does not have a significant effect on its shape. This finding was supported by high estimates of broad-sense heritability for traits that determine the shape of the carrot root, including length-to-width ratio, and root fill. Planting density significantly influenced the size of the carrot root, with size decreasing by $\sim 50\%$ in both length and width as density increased to 4.5 million plants/ha. In addition, novel traits derived from principal component analysis of root contours were included, which captured variation along the whole root, root shoulder, and root tip (Fig. 2). Our results are limited to the five cultivars used here and likely other cultivars phenotypically similar within the same market classes. One strength of using principal component-derived traits is that they are based on normalized root profiles, standardizing all root images in length and maximum width. This normalization step allowed for the quantification of subtle shape variations in carrot roots, regardless of size.

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