



Phenotypic segregation of seedling UCB-1 hybrid pistachio rootstock

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Abstract

Key message The growth of UCB-1 pistachio rootstock seedlings in the earliest years is a poor predictor of subsequent growth. Therefore, rogueing during the 1st years of growth is not effective.

Abstract The UCB-1 hybrid, produced from a controlled cross between *Pistacia atlantica* (female) and *P. integerrima* (male), is the main pistachio rootstock used in the USA. Variation has been observed in orchards planted with seedling UCB-1 rootstocks for over 20 years. Reduced vigor and stunting of some trees are of particular concern to growers due to decreased nut yield. This study was conducted to better understand the growth of non-grafted UCB-1, as well as between UCB-1 rootstock and *Pistacia vera* scions in commercial orchards. Phenotypic traits were evaluated in the non-grafted orchard. Grafted tree data were collected for both *P. vera* female scions and their UCB-1 seedling rootstocks in commercial orchards. The uniformity of tree height, trunk caliper, and canopy volume decreased annually during the first 5 years of growth. Individual tree growth was not linear and was poorly synchronized among siblings, causing the population to become increasingly less uniform as it aged. Consequently, growth in the earliest years is a poor predictor of subsequent growth. The strongest correlation was between growth parameters during the later years. There was a significant correlation between rootstock and scion caliper of the grafted trees in commercial orchards, with the least vigorous rootstocks producing the least vigorous scions. These data confirm the need to reliably rogue out seedlings that later will not be vigorous; however, our data show that rogueing based on the 1st years of growth is ineffective. This study suggests the need to develop predictive molecular markers for rootstock vigor.

Keywords Grafting · *Pistacia atlantica* · *Pistacia integerrima* · *Pistacia vera* · Propagation

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Introduction

The genus *Pistacia* (Anacardiaceae) consists of at least 11 species of trees and shrubs, of which, *P. vera* L. ($2n = 2x = 30$) is the most important due to its edible nuts (Zohary 1952, 1972). Pistachios are one of the top nut crops in California, which produces approximately 98% of the pistachios in the USA (USDA NASS 2017). All *Pistacia* species are dioecious, wind pollinated, and obligate outcrossers (Crane and Iwakiri 1981); consequently, they are highly heterozygous.

Most pistachio trees in the USA are produced by grafting clonal scions of *P. vera* onto interspecific hybrid rootstocks of *P. atlantica* Desf. \times *P. integerrima* J. L. Stewart ex Brandis. (UCB-1) or *P. integerrima* \times *P. atlantica* (PGII). The UCB-1 rootstock was developed by Dr. Lee Ashworth at the University of California, Berkeley (Morgan et al. 1992) and was selected for commercial use in the 1980s because of its moderate resistance to Verticillium wilt and frost tolerance

(Epstein et al. 2004). Beginning in the 1980s, UCB-1 seeds have been produced from a single female *P. atlantica* tree pollinated by a single male *P. integerrima*. Both were located at the University of California Kearney Agricultural Research Center in Parlier, CA. In 1996, production and distribution shifted to the Foundation Plant Services (FPS) at UC Davis after ten clonal copies of the female *P. atlantica* and four clonal copies of the male *P. integerrima* parents were propagated. In 2002, FPS began distributing the UCB-1 seed produced at Davis to nurseries who germinated, grew, and sold the rootstock.

Because UCB-1 seedlings are the products of an interspecific cross between two outbreeding, highly heterozygous species, they segregate for vegetative vigor. Commercial cultivars grafted onto UCB-1 seedlings grow unevenly, with nut yield varying greatly from tree to tree. Clonal UCB-1 rootstocks are available, but some of these suffered from deleterious somaclonal variation, making them less desirable than seedling rootstocks. However, some seedling rootstocks lack vigor and when grafted, the trees have low yields with reduced nut quality (Beede 2017). The frequency of low vigor trees has been reported to be between 1 and 30%; however, it is unclear how much of this is from environmental factors versus genetic causes. Currently, growers and nurseries rogue rootstocks or grafted trees at a young age based on visual cues, such as a grayer and smaller leaves, and/or smaller plants. Roguing is not satisfactory because stunted trees still appear in orchards. Therefore, variation within seedling UCB-1 tree populations needs to be better understood.

This study was conducted to analyze the growth of UCB-1 seedlings over 5 years and how they segregated for multiple phenotypic traits. The objectives of this research were to determine the relationships between early and later years of growth of non-grafted UCB-1 seedlings and for grafted trees in commercial orchards, to determine the relationship between growth of UCB-1-seedling rootstocks and their *P. vera* scions.

Materials and methods

Plant material

Growth of non-grafted trees

In July 2013, 960 UCB-1 seedlings, germinated from FPS seeds, were planted in an experimental orchard located at UC Davis Russell Ranch (38°33'00.4" N lat. 121°51'26.9" W long.) located west of Davis, Calif. Prior to planting, a micro-emitter Netafim (Fresno, Calif., USA) irrigation system (1.905 cm drip tube with 7.57 L emitter) was installed in the field to apply groundwater from a local

well approximately every 10 days during each growing season. The trees were planted 3 m apart within rows, with rows spaced 4.25 m apart. All trees were staked at the time of planting. After the 1st year, stakes were removed from most trees, with stakes remaining only for some of the weaker-stemmed trees (9.4% of the population) during the 2nd year of growth to protect from wind damage and to prevent trees from leaning. Stakes were removed once the trees became more established.

In 2013, all trees survived; one and three trees died in 2014 and 2015, respectively. After 2 years of growth, some trees had developed basal suckers, and after counting and measuring, they were pruned off in Jan. of both 2015 and 2016. In addition, after the 2nd year, some trees developed branches growing into the aisles; after counting and measuring, they were also pruned off to allow tractor access. By the end of the 3rd year, the trees had grown to the point that they were going to physically interfere with each other unless the orchard was thinned. Therefore, during the summer of 2015 every alternate tree was removed, leaving a total of 480 trees. No trees died in 2016 and 2017.

Data were recorded on 960, 959, and 956 trees for the first, second, and 3rd years of growth, respectively, and on 480 trees for the fourth and 5th years of growth. Measurements on 1st-year growth were conducted in Jan. 2014 on tree height, trunk caliper (30 cm above ground level), and branching (number of primary branches > 2 cm long and caliper of each branch 10 cm from the primary branch, height from the ground to base of each branch). 2nd-year growth measurements were made in Jan. 2015 on tree height, trunk caliper, presence of a central leader, branching at whorls (number of branches per whorl and height from the ground to each branch whorl), canopy height, canopy diameter at the widest point, branch crotch angle of the lowest branch. 3rd-year growth measurements were made in Jan. 2016 on tree height, trunk caliper, presence of central leader, number of whorls per tree, canopy height, and canopy diameter at the widest point. Fourth and 5th year growth measurements were made in Jan. 2017 and Jan. 2018, respectively, on height, trunk caliper, canopy height, canopy diameter at the widest point, and canopy diameter in a direction perpendicular to the first measurement of the widest point of the canopy.

Growth of grafted trees

Pistacia vera cultivars in commercial orchards in California grafted onto UCB-1 seedling rootstocks were also phenotyped. Trees along the orchard edge were not measured and data were collected only on interior female trees. Trees with male scions were not measured. Data were collected on rootstock trunk caliper (30 cm above ground level) and scion caliper (10 cm above grafting point). Trees were

measured in seven commercial orchards in the central valley of Calif.: Chowchilla (164 trees, *P. vera* ‘Golden Hills’), Corcoran (291 trees, *P. vera* ‘Golden Hills’), Merced (287 trees, *P. vera* ‘Kerman’), Coalinga A (290 trees, *P. vera* ‘Golden Hills’), Coalinga B (198 trees, *P. vera* ‘Kerman’), Coalinga C (199 trees, *P. vera* ‘Kerman’), and Buttonwillow (196 trees, *P. vera* ‘Golden Hills’) (Table 1). The distance between trees in all of these orchards was 5.2 m and between rows was 6.1 m.

Statistical analysis

All statistics were calculated using base R 3.5.1 (R core team 2013). The coefficient of determination (r^2) and associated *p* values were calculated by fitting a linear model to the data using the lm function. The coefficient of determination is such that $0 \leq r^2 \leq 1$ and denotes the proportion of variation in the dependent variable (‘y’) explained by the independent variable (‘x’), or the goodness of fit of the linear model to the data. To test for normality, the W-statistic and associated *p* values were calculated using the Shapiro–Wilk test, implemented in the function shapiro.test. Theoretical normal distributions were calculated using the function rnorm and the mean and standard deviation of each data set. All plots were generated using the R package ggplot2 (Wickham 2016), with kernel density estimates computed using the function geom_density.

To calculate canopy volume after the third, fourth, and 5th years of growth, the formula for an oblate spheroid was

used together with linear measures of canopy shape for each year, such that $\text{volume} = 4/3\pi a^2 b$, where *a* is canopy diameter and *b* is canopy height. Canopy height was measured from the base of the lowest branch to the top of the tree, and canopy diameter is the average of the diameter measured in two perpendicular directions with the widest diameter measured first, thus it represents the average equatorial diameter of that canopy.

Results and discussion

Growth of non-grafted trees

Height

The mean height after the 1st year of growth was 108.2 cm (Table 2). In the 2nd year of growth (2014), tree height increased rapidly, by approximately 160 cm (Fig. 1, Table 2). The trees grew approximately 41 cm taller during the 3rd year. The trees then grew 83 cm on average during the 4th year, and gained another 105 cm of height during the 5th year. Therefore, in the 2nd year, tree height was increasing exponentially, but during subsequent years, the trees were in a linear phase of growth (Fig. 1, Myhrvold 2013).

During the first growing season, the trees grew relatively uniformly, as evidenced by the narrow density distribution (SD = 22.8) with the trees ranging from 15 to 174 cm tall (Fig. 2). At the end of the 2nd year of growth (2014), the tree

Table 1 Phenotyped grafted trees in the Central Valley of California

Location	Coordinates	Age of trees (years)	Number of trees	Scion
Chowchilla	37.128744, -120.575375	7	164	<i>P. vera</i> ‘Golden Hills’
Corcoran	36.097520, -119.598992	8	291	<i>P. vera</i> ‘Golden Hills’
Merced	37.156753, -120.556466	8	287	<i>P. vera</i> ‘Kerman’
Coalinga A	36.1015374, --120.0066809	8	290	<i>P. vera</i> ‘Golden Hills’
Coalinga B	36.185559, -120.283635	11	198	<i>P. vera</i> ‘Kerman’
Coalinga C	36.117082, -120.270868	14	199	<i>P. vera</i> ‘Kerman’
Buttonwillow	35.688358, -119.43306	10	196	<i>P. vera</i> ‘Golden Hills’

Table 2 Mean and standard deviation for non-grafted UCB-1 tree heights, trunk calipers, and canopy volumes during each year from 2013 to 2017

Year	Tree Height (cm)					Trunk Caliper (cm)					Canopy Volume (m ³)			
	2013	2014	2015	2016	2017	2013	2014	2015	2016	2017	2014	2015	2016	2017
Mean	108.2	272.2	313.5	396.2	501.6	1.15	3.2	7.0	9.5	13.7	3.3	11.6	20.3	38.5
SD	22.8	31.1	50.2	43.7	56.9	0.19	6.8	1.2	1.5	2.3	1.7	4.1	7.0	13.8

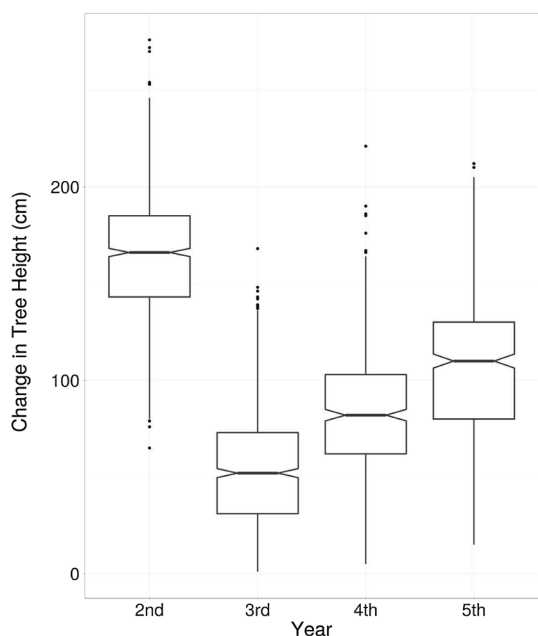


Fig. 1 Growth rate of non-grafted UCB-1 tree heights from 2013 to 2017

heights ranged between 150 and 400 cm tall ($SD = 31.1$); by the 3rd year of growth (2015), the tree heights were between 155 and 443 cm tall ($SD = 50.2$); by the 4th year (2016), tree heights were between 180 cm and 530 cm ($SD = 43.7$). The height ranged between 220 cm and 627 cm at the end of the 5th year of growth (2017, $SD = 56.9$). The range of tree heights in the population increased annually as the distribution curves became broader and the standard deviations became larger. This increasing range of height distribution reflects the fact that the trees did not grow synchronously. Each individual grew at different rates each year. The individual trees grew rapidly for a year or more then slowed down for 1–2 years, then grew more rapidly again. The result of the different growth rates was an increasingly phenotypically diverse population as the trees aged, as well as a population, where early growth was a poor predictor of later tree size.

Tree height at the end of the first growing season is a very poor predictor of subsequent height of the trees (Fig. 3), with r^2 values ranging from 0.061 to 0.11. Year 2 growth was better correlated with growth during later years with r^2 values ranging from 0.21 to 0.29; however, this still predicted less

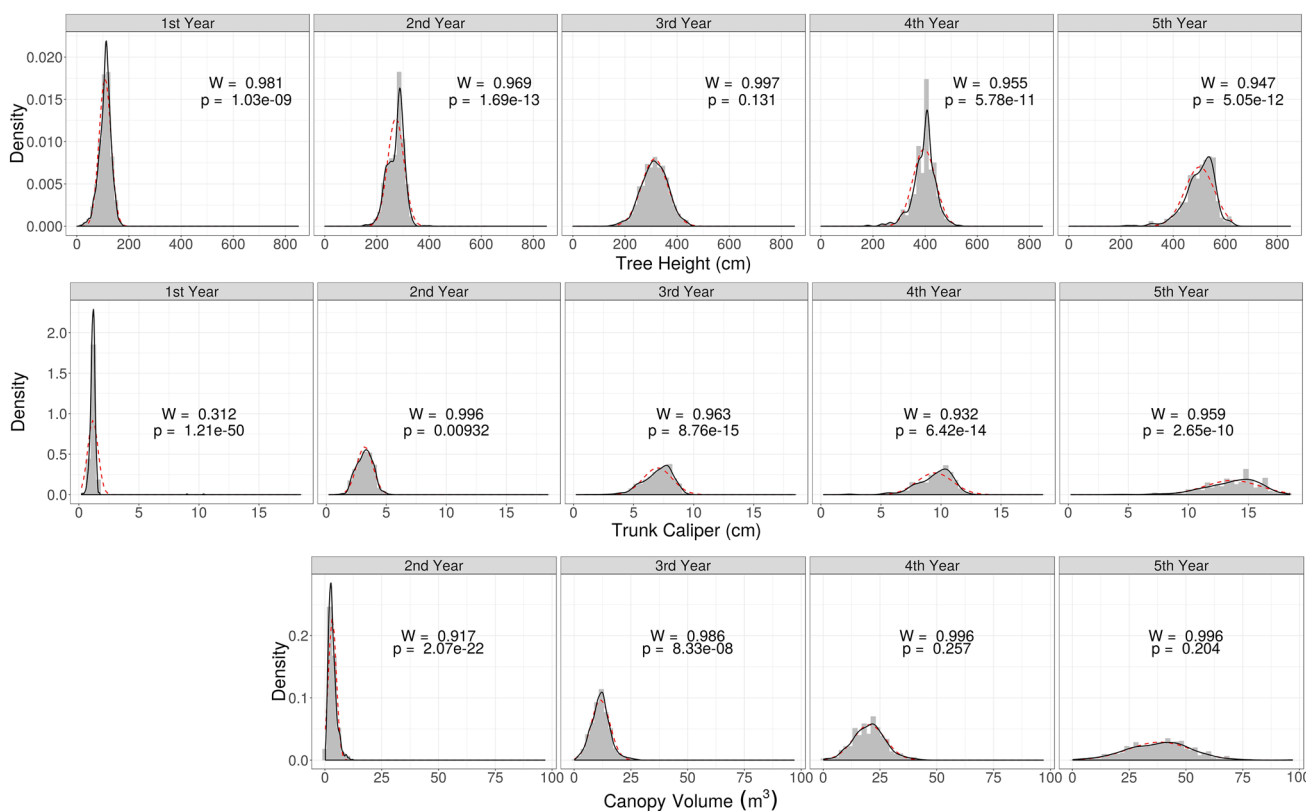


Fig. 2 Yearly frequency density distributions for non-grafted UCB-1 tree heights, trunk calipers, and canopy volumes from 2013 (i.e., 1st year) to 2017 (i.e., 5th year). Lines show the kernel density estimate (solid gray), as well as a theoretical normal distribution with the same

mean and standard deviation (red dashed line). Both the test statistic (W) and associated p value from a Shapiro–Wilk normality test are shown. The null hypothesis that the data are normally distributed is rejected if the p value is less than 0.05

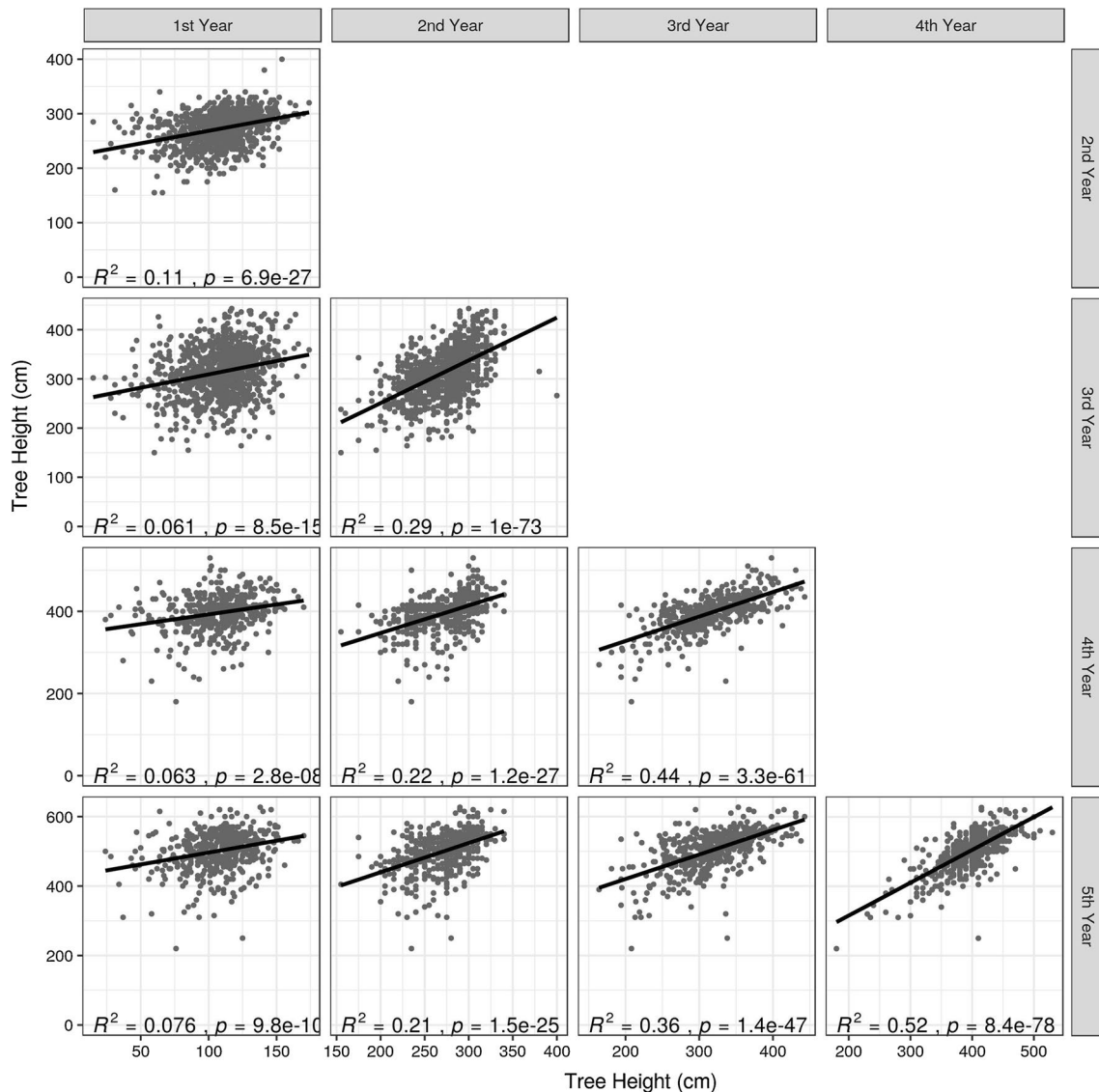


Fig. 3 Regression analysis of non-grafted UCB-1 tree height from 2013 to 2017. R^2 and the associated p value are shown at the bottom of each panel

than one-third of the variation in subsequent years. Year 3 growth was better correlated to year 4 and 5 growth with r^2 values of 0.44 and 0.36. The best correlation was where year 4 height growth predicted 54% ($r^2 = 0.54$) of year 5 height growth; however, this was still only a moderate correlation. These low r^2 values were due to uneven growth rates of individual trees.

Trunk caliper

Trunk caliper 30 cm above the soil line was a better measurement of overall vigor than tree height because both vigorous trees with large calipers and weak trees with narrow calipers often had similar heights. Trees with greater trunk

calipers were stronger and much sturdier, which is desirable for withstanding the shaking required for harvesting. Similar to tree height, trunk calipers were much more uniform during the 1st year (2013) and showed greater variation during the 2nd year (Fig. 4). The trees increased in caliper at a somewhat steady rate (Table 2), growing more slowly during the 2nd and 4th years and more rapidly during the third and 5th years, indicating that the trees were in a linear phase of growth (Fig. 4). This alternation in growth rate was not seen with the height measurements. Individual trees did not seem to follow a pattern of caliper growth, in that some grew rapidly for two to three years, and then slowed down for one or two years. The trees in the population were not synchronous for either caliper or height increases.

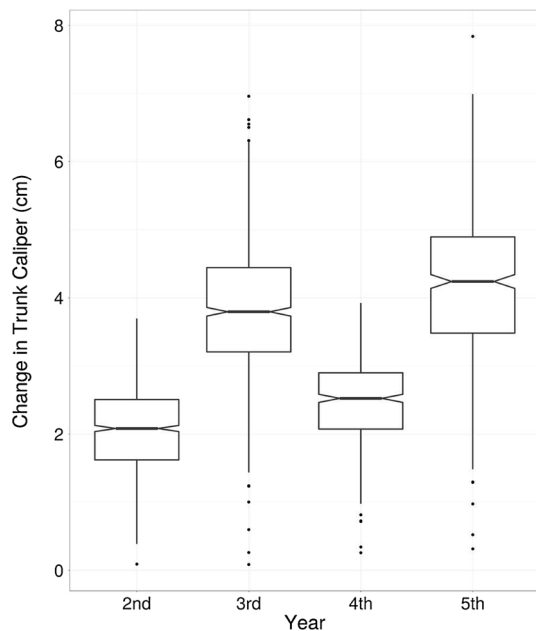


Fig. 4 Growth rate of non-grafted UCB-1 tree trunk calipers from 2013 to 2017

The trunk caliper during the 1st year was also a poor predictor of subsequent trunk caliper, similar to tree height (Fig. 5), with r^2 values ranging from 0.18 to 0.25. Year 2 caliper data were somewhat more correlated to subsequent years than year 1 data with r^2 values ranging from 0.25 to 0.35. Trunk caliper measured at the end of year 3 correlated well to years 4 and 5 with r^2 values of 0.79 and 0.8, respectively. There was again a strong correlation between caliper measurements from years 4 and 5 with $r^2=0.88$. Therefore, not only is trunk caliper a better measure of tree vigor than tree height, but once the trees have completed their third growing season, they remain consistent in their phenotype with the largest and smallest trees retaining their extreme sizes. This is consistent with grower observations that the less vigorous trees retain their low vigor and do not grow out of it.

Vargas and Romero (1998) reported that for 1626 seedlings of *P. vera* from 30 controlled crosses, trunk caliper was well correlated ($r^2=0.69$) between 2- and 3-year-old seedlings as well as between 3- and 4-year-old seedlings ($r^2=0.86$). The weakest correlation ($r^2=0.56$) was found between 2- and 4-year-old trees (Vargas and Romero 1996). Although UCB-1 seedlings grow differently than *P. vera* seedlings, variation in trunk caliper has predictive value for both *P. vera* and the interspecific hybrid UCB-1.

Canopy volume

Branching was minimal during the 1st year when the trees grew mainly as whips and, therefore, had no measurable

canopies. The trees had branched by the end of the 2nd year, allowing canopy diameter to be measured for the calculation of canopy volume. Similar to the first measurements of tree heights and stem caliper, canopy volume had low variance during the 1st year that it was measured (2014) and showed more variation in subsequent years (Fig. 1). Mean canopy volume expanded rapidly from 3.3 to 38.5 m³ from years 2 to 5 (Table 2). Canopy branching occurred mainly as whorls as the growth alternated between rapid elongation with strong apical dominance and temporarily slowing of the apical bud growth, compression of internodes, and branching from this point when the strong dominant growth resumed. As the trees and canopies grew, the number of whorls increased and the branches that formed at the whorls elongated and added to the canopy density and volume. Canopy volume more than tripled during year 3 and nearly doubled during each of the subsequent years, indicating that the trees were also in the linear phase of growth for this trait (Myhrvold 2013).

Early canopy growth was not a good predictor of subsequent canopy growth. For example, just 34% of the variation in canopy volume during the 3rd year is predicted by the variation during the 2nd year (Fig. 6). Slightly more variation ($r^2=0.38$) in canopy volume during the 4th year was explained by the variation during the 3rd year; however, 52% of the variation in canopy volume during the 5th year was predicted by the variation during the 4th year, indicating that as with other measurements, later year correlations are the most meaningful and early growth measurements poorly predict subsequent growth.

Basal suckering

Suckering is undesirable on a rootstock because it requires labor each year to remove these shoots. During the 2nd year of growth, 32% of trees did not sucker. Suckers were removed annually; after the third and final year, suckers were present on approximately 80% of trees. Suckering is one of the main factors that is crucial in rootstock selection. If low or no-suckering rootstocks could be selected and cloned, production costs could be reduced (Beede et al. 2015). The fact that UCB-1 seedlings segregated to produce no or only a few suckers after 5 years is encouraging that this may be a selectable trait.

Presence of a central leader

Pistachio trees tolerate moderate winters with sustained temperatures above 4 °C and no hard freezes but are sensitive to lower temperatures (Ferguson and Kallsen 2016). Between the 1st and 2nd years of growth, on 6 Dec. 2013, the lowest temperature (−4 °C) was recorded for the winter of 2013–2014 (<https://www.wunderground.com>). This killed the central leaders of 36% of the trees, possibly because

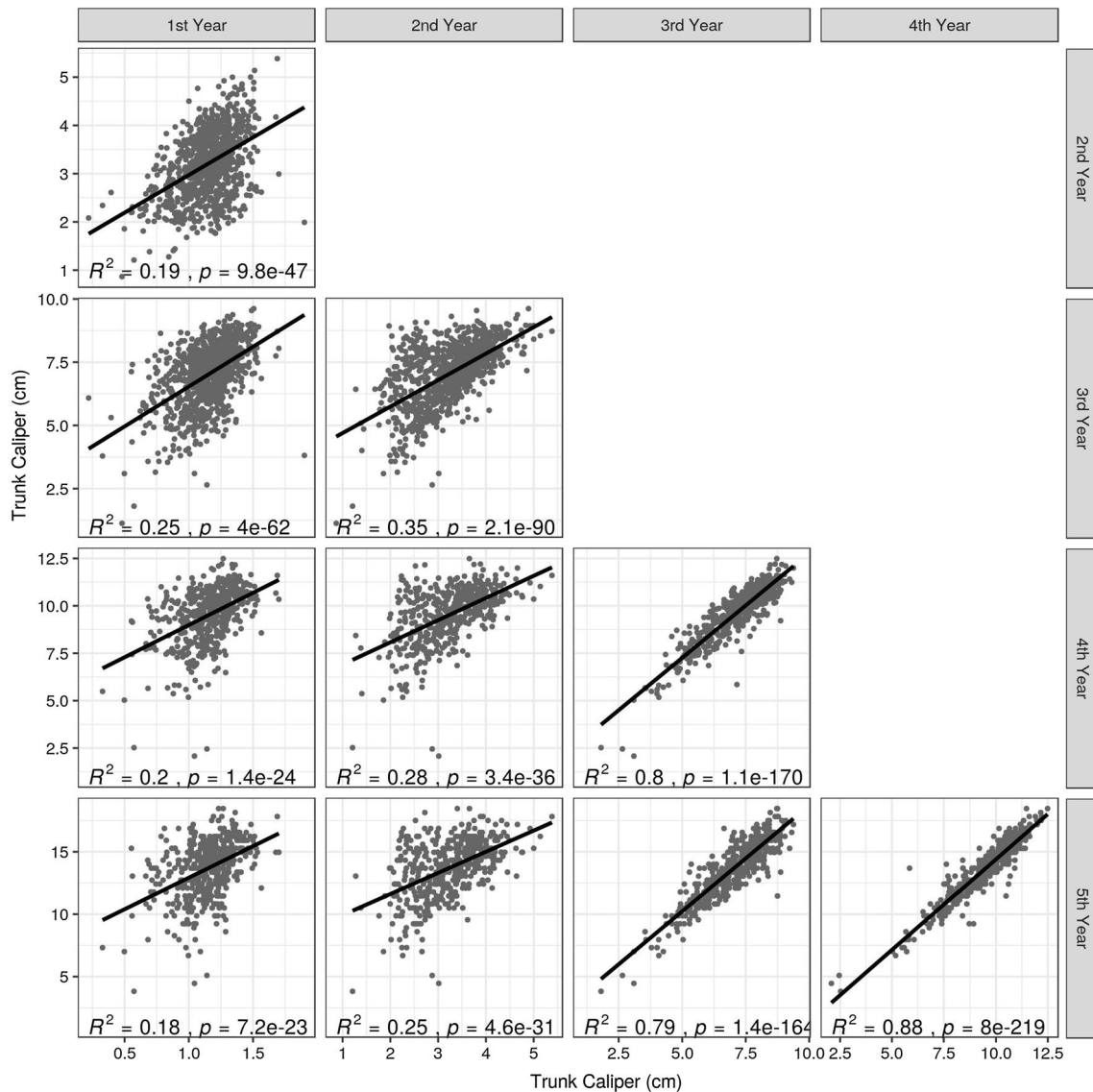


Fig. 5 Regression analysis of non-grafted UCB-1 trunk calipers from 2013 to 2017. R^2 and the associated p value are shown at the bottom of each panel

these trees had not cold-hardened as much as those not affected by this freeze event. After the winter of 2013–2014, 64% of the trees had live central leaders. The 36% of trees negatively affected by this low temperature may have had less cold hardiness and, therefore, might be poor selections for cloning as rootstocks.

Relationships among growth phenotypes

Tree height and trunk caliper

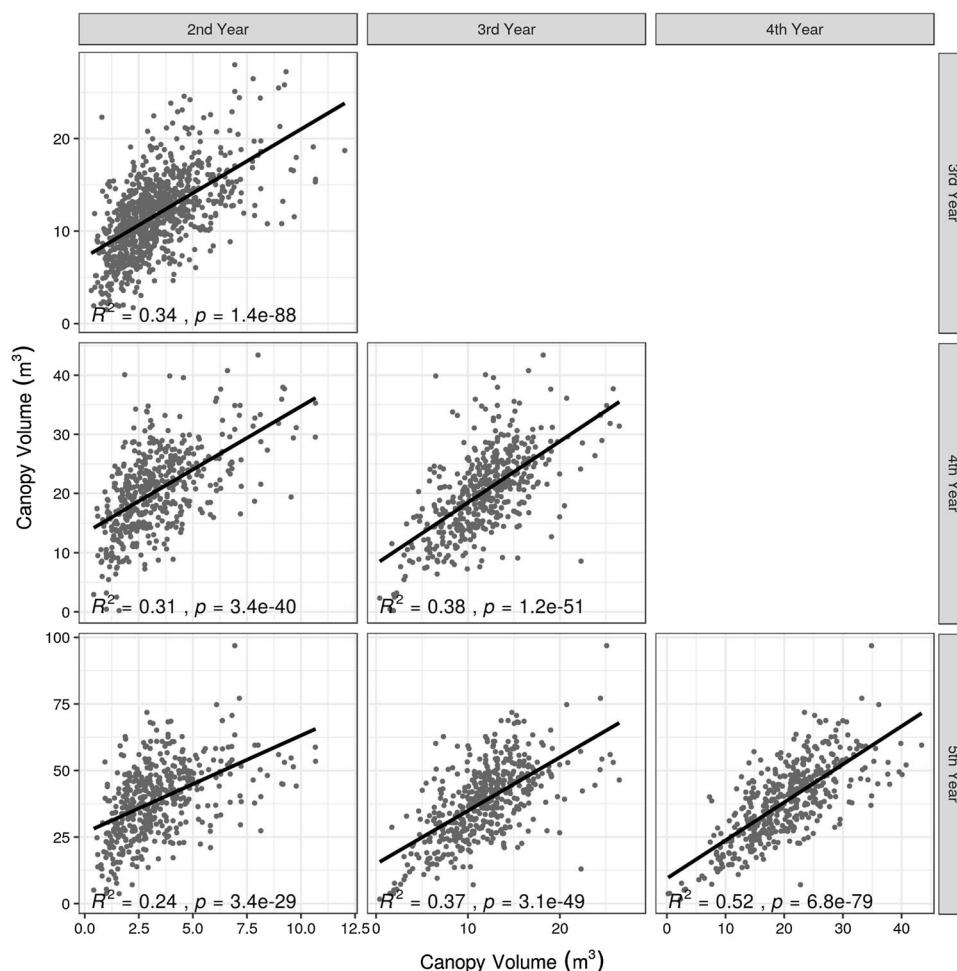
Trunk caliper and tree height were not good predictors of each other, with the highest correlation coefficient ($r^2=0.46$) observed in the 5th year of growth, 2017 (Fig. 7). This is

consistent with the observation that tall trees could have stems with large or small calipers. The tall trees with small calipers did not support themselves well during the second and 3rd years and required staking that was not necessary on those trees with larger calipers. The largest trees were those that were tall with large stem calipers. On young trees, stem caliper appears to be a better measure of tree vigor and robustness than height because weaker trees could be tall, they just did not have large stem calipers.

Canopy volume and tree height

During the first 2 years, when canopy volume could be calculated (second and 3rd years of growth), there were

Fig. 6 Regression analysis of non-grafted UCB-1 canopy volumes from 2014 to 2017. R^2 and the associated p value are at the bottom of each panel



weak relationships between tree height and canopy volume (Fig. 8). However, as the trees became larger during their fourth and 5th years of growth, there was a stronger correlation between height and volume with r^2 values of 0.65 and 0.71, respectively. Tree height is somewhat related to the measurement of canopy volume because it is calculated from the bottom branch (unchanging) to the top of the tree. Therefore, as a tree grows taller, its height becomes a greater contributor to canopy volume than when the trees were younger and shorter.

Canopy volume and trunk caliper

Canopy volume is the most important trait that growers monitor for vigor, because grafted pistachios with larger canopy volumes have greater yields than those with smaller volumes (personal communication with growers). Trunk caliper was not a good predictor of canopy volume during the second through 4th years of growth (Fig. 9). However, by the 5th year, the trees with the largest calipers also tended to have the largest canopies ($r^2 = 0.63$). Arpaci et al. (2014) compared the growth of different pistachio rootstocks (*Pistacia*

atlantica, *P. khinjuk*, *P. terebinthus*, and *P. vera*) between 1994 and 2012. Their study showed that the most stimulatory rootstock was *P. atlantica*, which stimulated the canopy growth of the scion ‘Siirt’ to a volume of 31.8 m³ and growth of the trunk to a caliper of 13.47 cm after 15 years of growth.

Growth of grafted trees

Caliper

Although the scion cultivar varied between orchards, all of the trees analyzed were grafted onto seedling UCB-1 rootstocks. There was a significant correlation between rootstock and scion caliper in the commercial orchards with 56.9%, 63.9%, 80.4%, 70.1%, 52.4%, 79.2%, and 85.4% of the variation in scion caliper being predicted by the variation in rootstock caliper in Buttonwillow, Chowchilla, Coalinga A, Coalinga B, Coalinga C, Corcoran, and Merced, respectively (Fig. 10). Kallsen and Parfitt (2011) reported an even stronger correlation between scion and rootstock circumference for ‘Kerman’ or other female cultivars grafted onto UCB-1 ($r^2 = 0.98$ and $r^2 = 0.97$, respectively) than in the

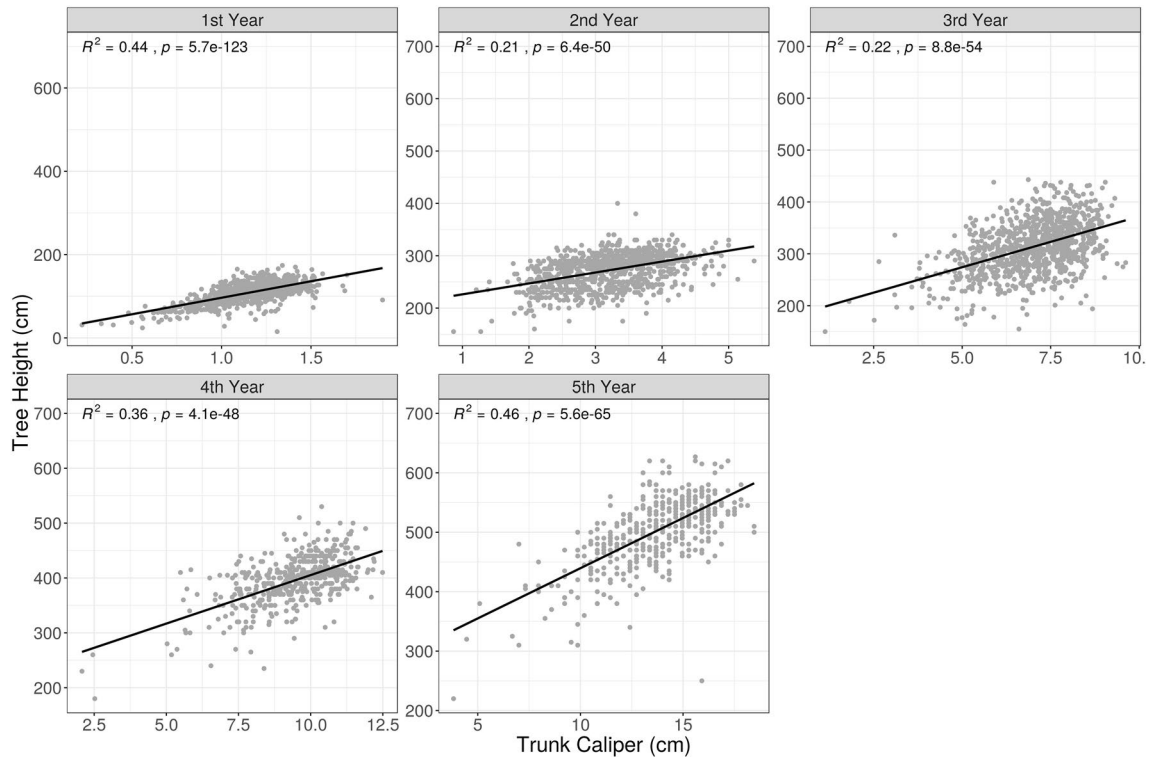


Fig. 7 Regression analysis of non-grafted UCB-1 trunk calipers and tree heights among years from 2013 to 2017. R^2 and the associated p value are shown at the top of each panel

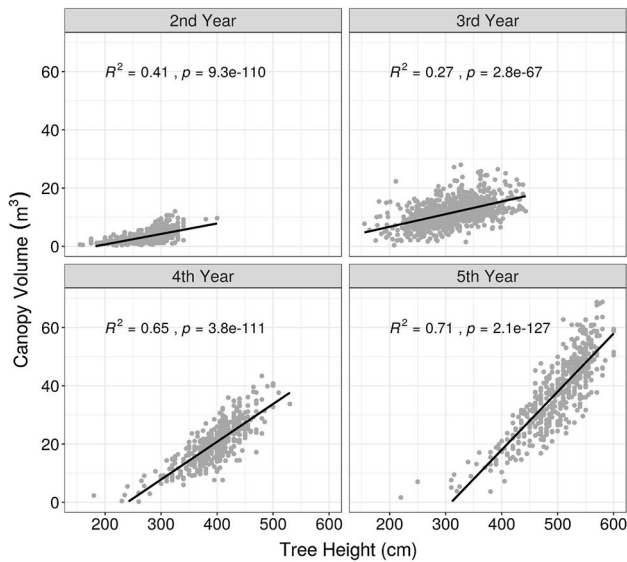


Fig. 8 Regression analysis for non-grafted UCB-1 tree heights and canopy volumes from 2014 to 2017. R^2 and the associated p value are shown at the top of each panel

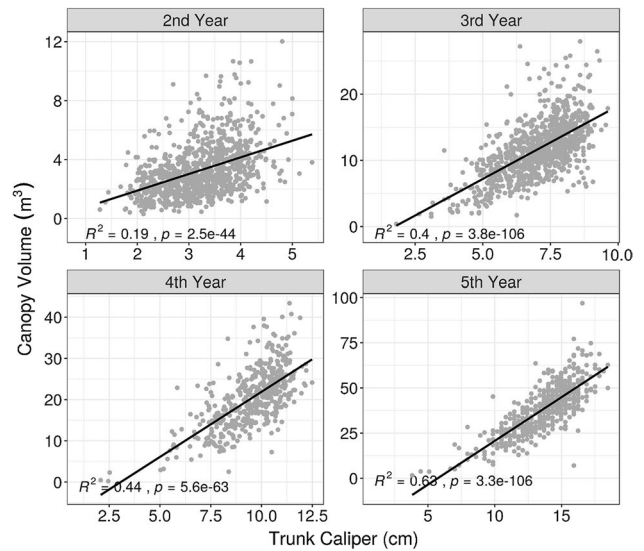


Fig. 9 Regression analysis of non-grafted UCB-1 trunk calipers and canopy volumes from 2014 to 2017. R^2 and the associated p value are shown at the bottom of each panel

orchards measured in our study. Therefore, the vigor of the rootstock greatly influences the growth of the grafted cultivar. This supports grower observations and their desire to have nurseries rogue out less vigorous UCB-1 seedlings.

Twelve out of the 14 distributions for rootstock and scion caliper differed significantly from normal (Fig. 11), with the exception of rootstock caliper at Buttonwillow and scion caliper at Corcoran (Shapiro–Wilk test, $p < 0.05$). When not

Fig. 10 Regression analysis for grafted UCB-1 rootstock and scion calipers. R^2 and the associated p value are shown at the top of each panel

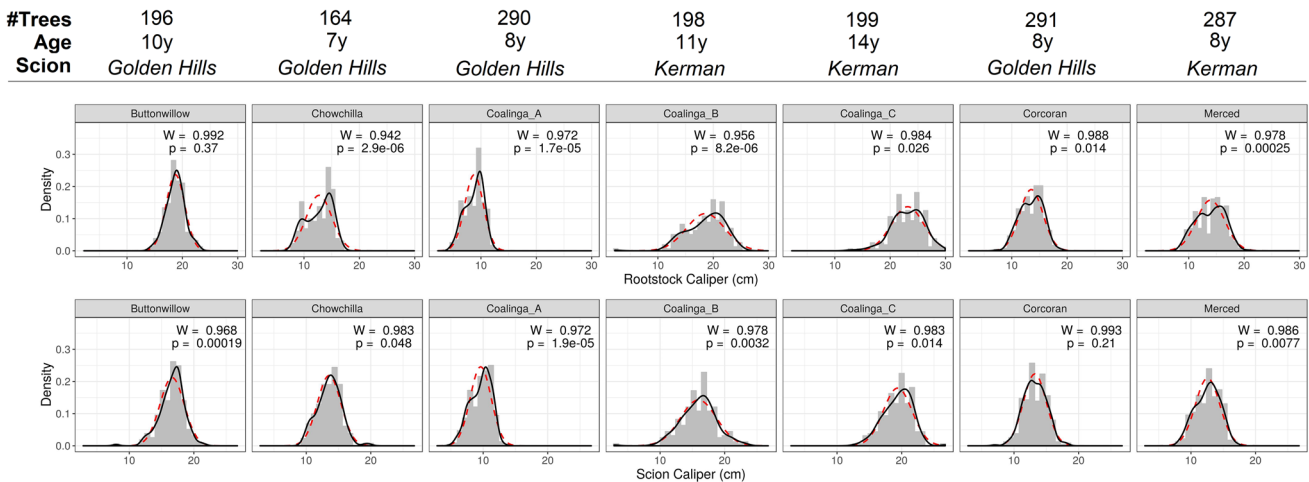
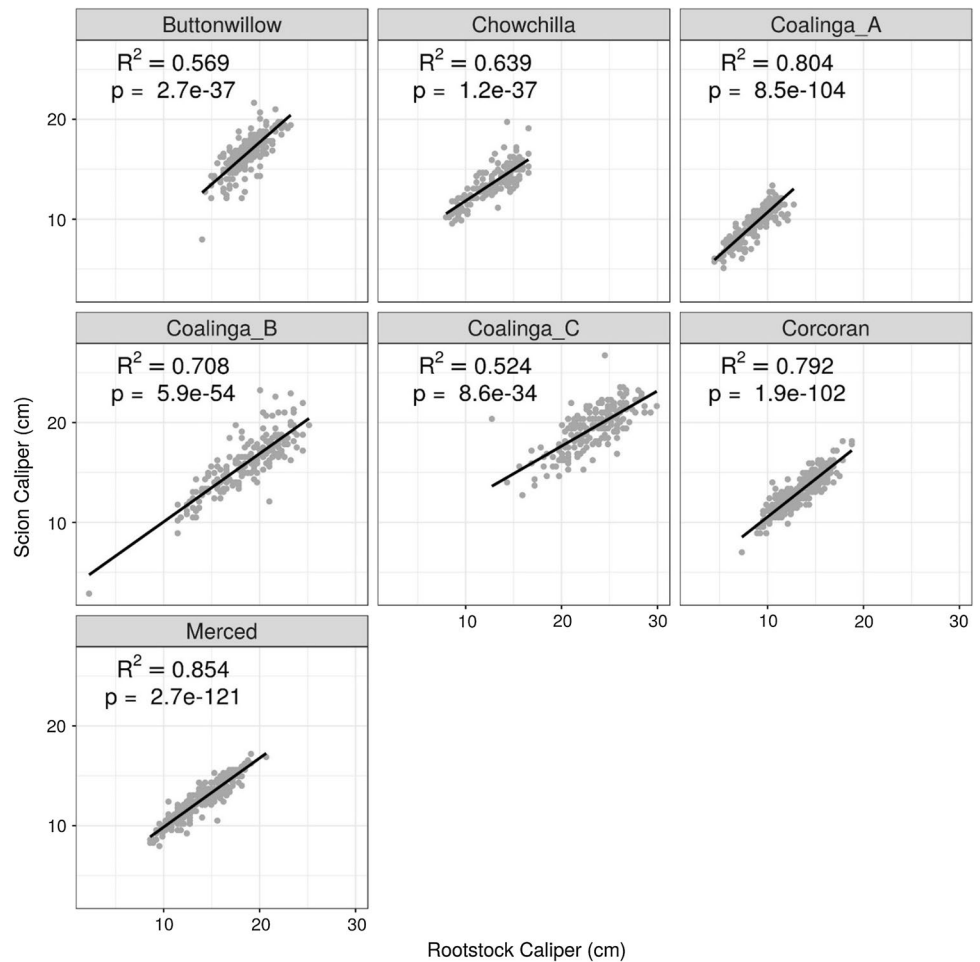


Fig. 11 Frequency distributions for grafted UCB-1 trunk (rootstock) and scion calipers. Lines show the kernel density estimate (black solid line), as well as a theoretical normal distribution with the same mean and standard deviation as the data (red dashed line). Both the

test statistic (W) and associated p value from a Shapiro–Wilk normality test are shown. The null hypothesis that the data are normally distributed is rejected if the p value is less than 0.05

normally distributed, rootstock calipers appeared to exhibit a bimodal distribution, with two distinct peaks. These were particularly pronounced for rootstocks at Chowchilla, Coalinga A, Coalinga B, Coalinga C, and Merced. While also differing significantly from normal, the rootstock caliper distribution at Corcoran was better described as skewed-normal, with no clearly discernable second peak. Similarly, the scion caliper distributions at Chowchilla, Coalinga B, Coalinga C, and Merced differed significantly from normal (Shapiro–Wilk test, $p < 0.05$), but did not exhibit two clear peaks.

This study elucidated the variation in growth of non-grafted UCB-1 seedling trees as well as variation in grafted trees in commercial orchards. The phenotypic data collected over multiple years provided detailed understanding of how UCB-1 seedlings grow and the variation that is inherent in a UCB-1 population. The strong correlation between trunk caliper of the grafted seedling UCB-1 rootstocks and the scions showed that vigor of the scion and rootstock are closely related and that they likely influence each other's growth. The poor relationship between early UCB-1 seedling vigor and subsequent tree size question the value of early roguing of seedlings. However, growers cannot wait until rootstocks are established 5-year-old trees, when growth parameters are better correlated, before selecting and grafting because the rootstocks would be too large and old. Therefore, during the 1st year of growth in the nursery, nursery staff currently rogue out UCB-1 seedlings that are small and they anticipate will not grow vigorously and produce robust bearing trees. They also rogue out trees with grayish-green leaf color and small leaves, neither of which have been correlated with slow growth. Because tree growth in the 1st year is a poor predictor of later growth, rouging has not eliminated trees that impart low vigor to the scion in commercial orchards and growers remain unsatisfied.

Molecular markers for vigor would be of great benefit to the industry, replacing ineffectual roguing based upon phenotypes that are poorly correlated with growth. The availability of molecular markers that accurately predict the ultimate size and vigor of UCB-1 seedlings would allow nurseries to supply growers with vigorous rootstocks. They would be able to select for large, vigorous trees with high yields on each tree. In addition, identification of rootstocks that will result in smaller trees would allow such trees to be planted more densely, maintaining a high yield per acre. The understanding of how rootstock seedlings grow and having rich phenotypic segregation data are the foundation for the development of such molecular markers.

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Author contribution statement EJ, JEP, DG, and RM conceptualized the experiments. EJ collected the data. EJ, WJP, JEP, and RM analyzed the data and WJP generated the figures. EJ and JEP wrote the manuscript. All authors read, edited and approved the final manuscript.

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