



VITICULTURE ORIGINAL RESEARCH ARTICLES

Grapevine adventitious root traits vary based on propagation method

Sam E. Dudley^{1,*}, Luis Diaz-Garcia¹, Isaac K. Uyehara¹, Andrew J. McElrone^{1,2}, Aviline Cannizzaro¹, Sadikshya Sharma¹, and Megan K. Bartlett¹

¹ University of California, Davis, Department of Viticulture and Enology, One Shields Ave Davis, CA, 95616

² USDA-ARS, Crops Pathology and Genetics Research Unit, Davis, 284 HUTCHISON HALL, UCD Davis, CA 95616

Article number: 9599



*correspondence:
sdudley@ucdavis.edu

Associate editor:
Nathalie Ollat



Received:
3 September 2025

Accepted:
11 February 2026

Published:
2 April 2026



This article is published under the **Creative Commons licence (CC BY 4.0)**.

Use of all or part of the content of this article must mention the authors, the year of publication, the title, the name of the journal, the volume, the pages and the DOI in compliance with the information given above.

ABSTRACT

Development of new rootstocks is an effective strategy to continue grape production despite increased abiotic stress in a changing climate. We measured an F1 population derived from a cross between a drought resistant (110R) and drought susceptible (101-14 MGT) rootstock to identify quantitative trait loci (QTL) for root system architecture traits. We also compared traits and QTL between two propagation methods: hardwood and herbaceous cuttings. Plants were grown for 35 days and measured by destructive harvest and imaging, which provided 17 traits related to root system architecture. We identified two significant QTL for root system architecture traits for root thickness and root angle. Generally, hardwood cuttings had significantly larger root systems, thicker roots, and a higher ratio of lateral roots to adventitious roots, however genotypes did not have consistent phenotypes across propagation methods. This finding indicates that the interpretation of experimental results should depend on the propagation method used. We also found complex, multigenic control of root system architecture traits, which supports the use of genomic selection models for breeding. We expect these results to guide future research using young grapevine root systems and provide insight into the genetic control of root architecture in grapevine.

KEYWORDS: grapevine, root, QTL, root system architecture, breeding, genetics, trait

INTRODUCTION

In 2016, grapes were estimated to be worth \$68 billion in the world market, making it the third most valuable horticultural crop in the world (Cantu & Walker, 2019). Mediterranean climate zones are renowned for their viticulture, however increased drought in these areas poses a threat to future production, with drought affecting both yield and grape quality (Del Pozo *et al.*, 2019; McLain & Castro, 2017; van Leeuwen & Darriet, 2016). While initially introduced for the purpose of controlling the pest grape phylloxera, grapevine rootstocks can also contribute to improved drought resistance (Ollat *et al.*, 2016), which may allow farmers to keep growing grapes despite periodic water shortages. Rootstocks have been utilized for their drought resistance since their widespread adoption in the 19th and 20th century, however breeding specifically for drought resistance has only started recently, creating an opportunity for continued progress (Chen *et al.*, 2024). Traditional breeding of grapevines takes roughly 25–30 years from cross to release (Eibach & Töpfer, 2015). Moreover, quantitative traits controlled by many genes combined with the difficulty of phenotyping root systems makes it difficult to select root traits. This study aims to assist breeding for grapevine root traits by providing information on their genetic basis and identifying molecular markers for these traits.

Drought resistant rootstocks are defined as those that produce adequate growth, yield, and fruit quality under water-limited conditions (Zhang *et al.*, 2016). Grape rootstocks generally achieve drought resistance through an avoidance rather than tolerance strategy, where avoidance is defined as the ability to prevent tissues from experiencing stress (*i.e.*, maintain high water potentials) and tolerance as the ability to function despite stress or damage from stress (Levitt, 1980). In typical viticultural systems, grapevines rarely reach critically low water potentials, and maintaining an adequate water supply to the canopy is more important to drought performance than the ability to tolerate low water potentials (Alsina *et al.*, 2011; Blum, 2005; Charrier *et al.*, 2018; Pouzoulet *et al.*, 2020). This tendency towards drought avoidance could also reflect the evolutionary history of wild *Vitis* species, which may have evolved deep and exploratory root systems to avoid direct competition with host trees for resources (Morano, 1995; Morano & Walker, 1995; Smart *et al.*, 2006).

Improving root system architecture (RSA), defined as the spatial distribution of roots throughout the soil, can improve resource acquisition in crops (Lynch, 2013; Osmont *et al.*, 2007; Uga *et al.*, 2013). Due to the complexity of the grape root system, there is not a single drought resistant ideotype, however numerous traits have been identified as important (Bernardo *et al.*, 2025). Extensive, deep roots that explore deeper soil layers, as well as the efficient utilisation of fine roots have been shown to be important traits for whole root system drought resistance (Atkinson *et al.*, 1999; Smart *et al.*, 2006; Swanepoel & Southey, 1989). The inability of roots to grow through

hard soil is also often a limiting factor in root system development, so root penetration ability, coupled to root thickness, plays a pivotal role in root system development and drought resistance (Clark *et al.*, 2002; Kolb *et al.*, 2017; Materechera *et al.*, 1992; Smart *et al.*, 2006). Root branching frequency and survivorship of roots over multiple years affects the woody structure of the root system (Puhe, 2003; Wells & Eissenstat, 2001), while lateral branching frequency, length, and growth rate affect the ability of fine roots to take up water and nutrients (Bauerle *et al.*, 2008; Song *et al.*, 2020; White & Kirkegaard, 2010). In general, drought resistant rootstocks have been observed to have deeper and more extensive root systems, thicker fine roots, steeper rooting angles, and more root growth throughout the year when compared to drought sensitive rootstocks (Bauerle *et al.*, 2008; Fort *et al.*, 2017; Reingwartz *et al.*, 2021; Smart *et al.*, 2006; Smart *et al.*, 2012).

So far, studies have shown that genetic control of RSA in grapevine is complex, with many small effect genes contributing to the overall phenotype (Alahakoon & Fennell, 2023). However, genes with agronomic significance have been identified in other crops, such as the *DRO1* gene, which controls rooting depth in rice, and the *TaMOR* (*MORE ROOT*) transcription factor in wheat, which produces more roots when overexpressed (Khalid *et al.*, 2024; Kulkarni *et al.*, 2017; Li *et al.*, 2016; Uga *et al.*, 2013). In grapevine, multiple studies have been published recently on the genetic determination of root system architecture (Alahakoon & Fennell, 2023; Bert *et al.*, 2013; Blois *et al.*, 2023; Mohtasebi, 2023; Smith *et al.*, 2013; Tandonnet *et al.*, 2018; Thapa, 2022). However, markers identified in these studies have yet to be integrated into breeding programs, so progress lags behind other crops. Previous studies in other plants have shown that RSA is heavily determined by hormone signaling pathways that regulate root growth and development (Jung & McCouch, 2013; Overvoorde *et al.*, 2010), so most candidate genes proposed in grapevine quantitative trait loci (QTL) studies have been those related to hormone signaling pathways (Alahakoon & Fennell, 2023; Tandonnet *et al.*, 2018). The clearest candidate genes in grapevine came from a genome-wide association study (GWAS) study for root traits in *V. berlandieri* from Blois *et al.* (2023), that found markers in genes regulating integral membrane components, metal ion binding proteins, a UMP kinase protein, nuclear organisation, and alkaloid pathways. Other transcriptomic studies into adventitious root formation in grapevine identified transcriptomic factors related to the effect of light on rooting and two novel genes coding for proline rich proteins (PRP) involved in rooting, however the exact function of the PRPs is unknown (Thomas *et al.*, 2003; Yuan *et al.*, 2024). Furthermore, root system development and persistence over multiple years can affect long term root system architecture (Lyford & Wilson, 1964; McCormack *et al.*, 2015; Wells & Eissenstat, 2001), and genes governing root function and lifespan have been discovered in other perennial species (Bagniewska-Zadworna *et al.*, 2014).

Grapevines can be propagated as hardwood cuttings from dormant lignified canes or softwood herbaceous cuttings from actively growing shoots. Research on grapevine root systems has used both hardwood and herbaceous propagation (Barrios-Masias *et al.*, 2015; Bartlett *et al.*, 2022; Cuneo *et al.*, 2021; Fichtl *et al.*, 2024; Gambetta *et al.*, 2013), but there is no published research directly comparing the two. Instead, previous research has focused on other factors such as different genotypes or propagation media (Farooq *et al.*, 2018), differences between cutting size (Larrey *et al.*, 2025), or grafted and non-grafted plants (Bert *et al.*, 2013), so direct comparisons between hardwood and herbaceous propagation may provide novel information on how to interpret results from different propagation methods. Hardwood cuttings are cheaper and easier to process at a large scale, robust to damage, and storable for months, so hardwood propagation is the primary technique used by commercial nurseries (Smart *et al.*, 2002; Waite *et al.*, 2015). Using hardwood cuttings in research could make the results easier to compare to commercial settings, but herbaceous propagation also has several advantages that make it a common approach in root biology research (Barrientos-Sanhueza *et al.*, 2024; Cuneo *et al.*, 2016; Gambetta *et al.*, 2013; Reingwartz *et al.*, 2021). Herbaceous cuttings can be taken from greenhouse-grown mother plants any time of the year, allowing experiments to be conducted year-round, and potted plants do not need induced dormancy cycles for propagation, unlike hardwood cuttings. Additionally, actively growing greenhouse populations may be easier to control environmental factors when compared to field populations used for hardwood cuttings.

The difficult nature of root phenotyping may dissuade selection for root traits in traditional breeding pipelines, however integration of genetic tools for root trait selection can work to close the gap and allow selection for root traits cheaply and easily without complicated root phenotyping systems. Genetic breeding tools such as marker assisted selection (MAS) and genomic selection (GS) have already been integrated into grapevine breeding pipelines to select for traits such as powdery and downy mildew resistance, cluster traits, and berry sugar content (Brault *et al.*, 2024; Viana *et al.*, 2016). MAS has been used to shorten breeding time and provides the possibility of introgression of loci into breeding gene pools (Eibach & Töpfer, 2015). GS models are a more recent advance in grapevine breeding and may perform better than MAS for selecting complex traits governed by many small effect genes (Bhat *et al.*, 2016; Viana *et al.*, 2016).

While research in the genetic determination of RSA in grapevine has increased in recent years, research is scarce compared to other agronomic crops. The goals of this study are to use a cross between a drought resistant (110R) and drought susceptible (101-14) rootstock to identify QTL for RSA traits and to determine how propagation methods influence trait values and QTL results. 110R and 101-14 also vary in root system architecture including angle, thickness, and growth rates, and thus we expect their progeny

to provide a wide diversity of root traits (Fort *et al.*, 2017; Reingwartz *et al.*, 2021). To our knowledge, this is the first study to directly compare the root architecture of grapevine using both hardwood and herbaceous propagation methods and the first QTL mapping study to include parentage from all three of the most used rootstocks for breeding (*Vitis riparia*, *Vitis berlandieri*, and *Vitis rupestris*). Our results will provide new molecular markers and information for rootstock breeding, as well as provide context to interpret studies from each propagation method.

MATERIALS AND METHODS

1. Plant material and growing conditions

This study examined root system architecture across a subset of an F1 population of 129 progeny derived from a cross between two commercial rootstocks with different root traits: drought sensitive 101-14 Millardet et de Grasset (101-14, *V. riparia* × *V. rupestris*) and drought resistant 110 Richter (110R, *V. rupestris* × *V. berlandieri*) (Dry & Coombe, 2005; Fort *et al.*, 2017; Keller, 2020; Rahemi *et al.*, 2022).

All experiments were conducted at the University of California, Davis between January and May 2024. We rooted herbaceous cuttings from mother vines that were actively growing in a greenhouse and hardwood cuttings from dormant field-grown vines, following standard procedures for grapevine propagation (Waite *et al.*, 2015). Field grown vines were 12 years old when cuttings were taken, growing in a Yolo silt loam soil (SoilWeb, n.d.) on a California sprawl trellis system. Average daily high temperatures range from 13.3 °C in December, to 34 °C in July, with 80 cm of rain throughout the year, mainly between November and March (National Weather Service, n.d.). Greenhouse mother vines were actively growing plants that had not gone through winter dormancy, between six months and one and a half years old. Three plants per genotype were planted in two-gallon pots with two to five actively growing shoots per plant. The shoots were trained up vertical wooden stakes to a height of approximately 1 meter and watered and fertilized with micro and macronutrients with drip irrigation. Supplemental lighting above the vines provided an artificial daylength of 16:8-hour light:dark cycle during the winter and spring.

In January 2024, we took 10 herbaceous cuttings from each genotype in the greenhouse and 20 cuttings from each parent. The cuttings were trimmed to a standard length (5–10 cm) and leaf area (~10 cm²), dipped in liquid rooting compound for 10 seconds (0.05 % indol-3-butyric acid, 0.025 % naphthalene acetic acid, Earth Science Products Corp., Wilsonville, OR), and planted in rooting bins (15 × 40 × 60 cm). In February 2024, we took 10 hardwood cuttings from a similar set of genotypes from dormant field-grown vines, and 20 cuttings for each parent. We pooled and weighed the 10 cuttings to get an average mass for each genotype, then put the cuttings into cold storage to meet chilling requirements. In March 2024, we removed

the cuttings from storage, rehydrated them in water for 24 hours, treated them with liquid rooting compound, and planted them in rooting bins. Including parental genotypes, 101 genotypes successfully rooted for the herbaceous cuttings and 101 for the hardwood cuttings, producing 93 shared genotypes.

Rooting bins were filled with fritted clay (Profile Products LLC, Buffalo Grove Ill). We selected clay for its porosity, to prevent excess water retainment, hypoxia, and mold growth around the root crowns, and higher mechanical resistance to root growth than typical growth media (*e.g.*, perlite), to simulate more realistic growing conditions. In total, we planted 10 replicates of each genotype and 20 replicates of each parent, split into 2 blocks. Within each block, five reps of each genotype were planted together in rooting bins, and their location in the block was randomized. All cuttings were grown in a humidified greenhouse under shade cloth, with natural day length and temperature between 10 and 27 °C. Benches provided bottom heat, and water was provided with sprayers that misted the plants every 10 minutes throughout the duration of the experiment. We removed any dead plant material weekly to prevent mold.

2. Destructive harvest and imaging

We destructively harvested all cuttings after 35 days of growth. We excavated and washed the root systems in water to remove soil, working carefully to avoid root breakage. Excavated plants were stored in humidified plastic bags with their roots in water until imaging later the same day. We imaged all plants using a backlit imaging setup adapted from Seethepalli *et al.* (2020). The imaging setup consisted of a box containing a backlight and a translucent background to provide a homogenous background for near binary silhouette images. We suspended root systems in front of the backlight at a consistent height and photographed the root systems at a consistent distance and angle with a Canon Rebel T3i DSLR camera. We included an object of known size in each image for scale. We imaged each cutting twice to average traits for two faces. The root system was first positioned so that the largest spread of roots was visible, then the cutting was rotated 90 degrees to obtain the second image. After imaging, the longest root was pulled straight and measured with a ruler. For hardwood cuttings, all roots and shoots for each genotype were cut off at the crown and bud and were dried at 70 °C for at least 48 hours to measure biomass.

3. Image analysis and trait extraction

All image analysis was carried out in Python 3.9.20. First, we cropped each image to a consistent stem length, excluding the plant label. Then, we segmented images with an automated script using Gaussian adaptive thresholding from the OpenCV module, to produce binary images of each root system (Figure 1). The binary image was then skeletonized on the midline of each root, and a graph of the root system was created with the NetworkX package. Each node in the graph corresponds to a pixel on the midline in

the binary image and has information on location, thickness, and connection to other nodes. During network creation, any roots with a total length shorter than approximately 1.2 mm were removed during the network creation to remove non-root artifacts such as bumps or curves on individual roots, and nodes with a diameter wider than 4.8 mm for hardwood cuttings and 4.2 mm for herbaceous cuttings were removed to eliminate the thick stem nodes from the root measurements.

We distinguished pixels of primary roots (adventitious roots originating from the cutting) from lateral root (daughters of the primary roots) based on user defined root thickness thresholds similar to other root image analysis software (WinRHIZO, RhizoVision Explorer) (Himmelbauer *et al.*, 2004; Seethepalli *et al.*, 2020). For 10 random individuals of different genotypes for each propagation method, we measured root thicknesses at 5 random points across multiple roots from each root order. The bottom quartile of the primary root thickness overlapped with the top quartile of the lateral root thickness for both hardwood and herbaceous cuttings, so we set a threshold width halfway between the minimum thickness for the primary roots and maximum thickness for the lateral roots (*i.e.*, 0.82 mm for herbaceous cuttings and 0.90 mm for hardwood cuttings). Using the data from the 10 random individuals, we calculated the ratio of nodes that would have been miscategorized from the threshold, which varied from 0.059 to 0.116 (Figure S2).

We then used a custom automated script to measure root traits for the final networks. Using length, radius, and angle information for all the nodes in the root system network, the script estimated 12 traits: total length (sum of length for all nodes), total surface area (sum of length * π * diameter for all nodes), and total volume (sum of π * radius² for all nodes), primary and lateral root length, primary to lateral ratio (ratio of lateral to primary root length), whole root system median root diameter, primary and lateral median root diameter, number of root tips (number of terminal nodes), and root system fibrousness (number of root tips/total length) (Table 1). The average initiation angle was estimated by measuring the average angle of all nodes in a 4 cm range at the top of the image to include only the top portion of the root system, where zero degrees is vertical, and 90 degrees is horizontal. We also measured the rooting rate of each genotype (number of rooted cuttings/number of planted cuttings), where rooting was defined as formation of roots longer than 3 cm determined from the length of the longest root. Altogether, this produced 14 or 17 traits for each individual root system, depending on the propagation method (Table 1).

4. Genetic map generation

Genomic DNA was extracted from young leaf samples at the University of Minnesota Genome Center, and genotype by sequencing (GBS) was performed at the University of California, Davis Genome Center, using the Illumina NovaSeq 6000 platform with paired end (PE) 150 bp reads and an average sequencing depth of 10 \times , resulting in many

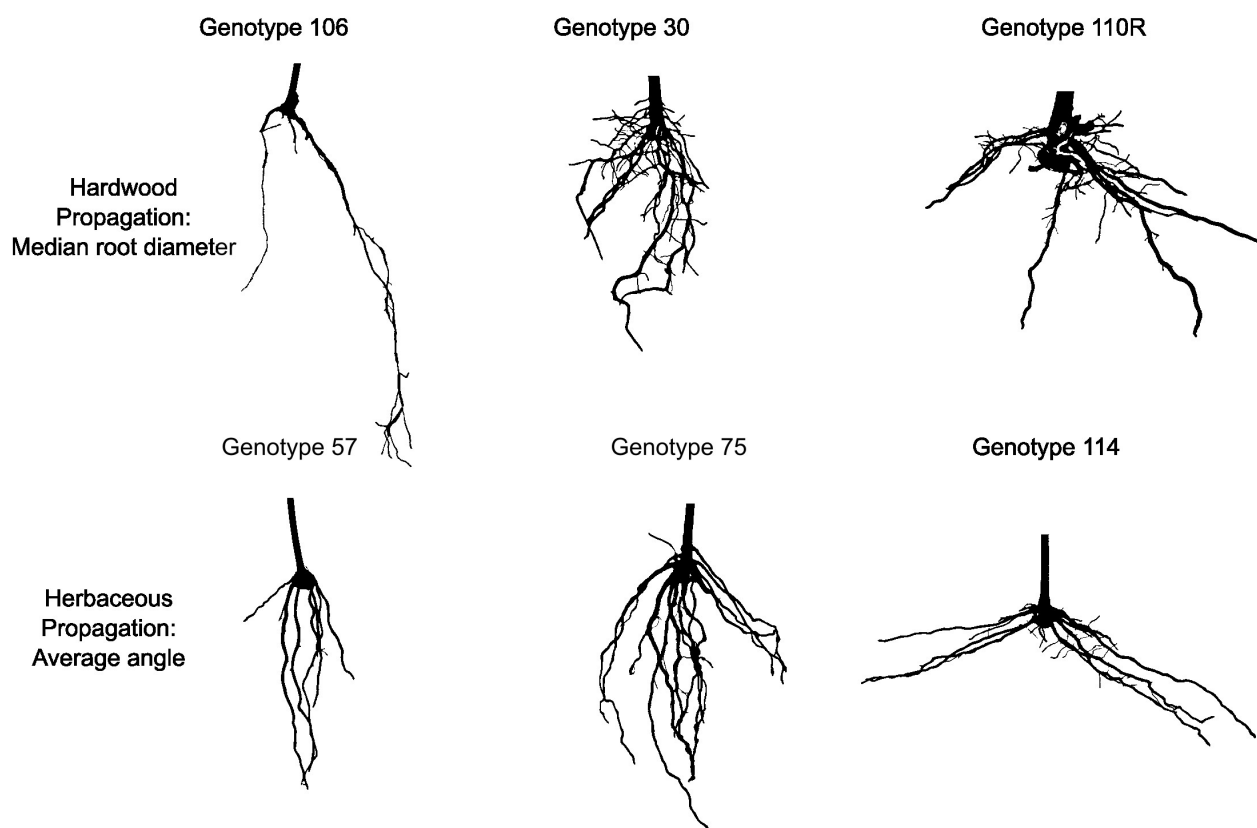


FIGURE 1. Segmented root system images.

Segmented pictures of various root systems after 35 days of growth. Hardwood root systems on the top row represent an average phenotype (middle), and two extreme genotypes for median root diameter. Herbaceous root systems on the bottom row represent an average phenotype (middle) and two extreme phenotypes for average root initiation angle. A representative individual of the mean of each genotype was chosen for each image.

TABLE 1. Measured traits, abbreviations, and units.

Trait	Abbreviation	Units	Dataset
Total length	TL	mm	HW, HB
Total area	TA	mm ²	HW, HB
Total volume	TV	mm ³	HW, HB
Number of root tips	RT	unitless	HW, HB
Average angle	AA	degrees	HW, HB
Median diameter	MD	mm	HW, HB
Fibrousness	F	mm ⁻¹	HW, HB
Median diameter primaries	MDP	mm	HW, HB
Median diameter laterals	MDL	mm	HW, HB
Primary root length	PRL	mm	HW, HB
Lateral root length	LRL	mm	HW, HB
Lateral to primary ratio	LPR	unitless	HW, HB
Length of longest root	LR	mm	HW, HB
Pooled cutting mass	CM	g	HW
Pooled leaf mass	LM	g	HW
Pooled root mass	RM	g	HW
Rooting rate	RR	unitless	HW, HB

Dataset column shows what traits were measured for each propagation method; HW signifying hardwood propagation and HB signifying herbaceous propagation.

markers with >20× coverage. TASSEL (Glaubitz *et al.*, 2014) was used for variant calling with haplotype 1 of 110R as the reference genome (Minio *et al.*, 2022). We removed markers that had less than 20× coverage, more than two alleles, were monomorphic, and were distorted as tested with chi-square test at significance level of $p < 0.10$. Two genetic maps, one for 110R and another for 101-14, were constructed using a pseudo-test cross linkage mapping strategy (Grattapaglia & Sederoff, 1994) in R using the BatchMap and ABHgenotypeR packages (Schiffthaler *et al.*, 2017).

Recombination fractions were estimated with rf.2pts, and genetic distances were obtained with the Kosambi mapping function, which was used throughout map construction. Markers were coded as lm×ll, nn×np, or hk×hk and passed to a custom imputation function as marker types D1.10, D2.15, and B3.7. The imputation function operates in two main steps. First, it builds approximate parental maps using BatchMap: it bins markers, estimates recombination fractions (rf.2pts), assigns markers to linkage groups (group), identifies the two largest pseudo-testcross groups, and orders markers with record.parallel and map.overlapping.batches to obtain preliminary marker order and linkage phase. Second, it uses these approximate phases to recode progeny genotypes into A/B states for a single parent, exports them in ABH format, and applies ABHgenotypeR (imputeByFlanks, correctStretches) to impute missing data and correct spurious recombination events. After this correction, the cleaned genotypes are filtered for missing data and segregation distortion and then used for the final map calculation. Within our custom imputation routine, the BatchMap functions were executed using LOD = 8 and max.rf = 0.1 in rf.2pts and group, and max.dist = 10, size_batches = 10, and overlap = 5 when ordering markers via map.overlapping.batches. For the final map construction outside the imputation step, BatchMap was run with LOD = 10 in both rf.2pts and group, and marker ordering employed record.parallel (times = 10) followed by map.overlapping.batches (max.dist = 10, size = 15, overlap = 10, phase.cores = 10). All remaining parameters in these functions were kept at their default values. The two resulting parental maps were merged into a composite map for QTL mapping using LPmerge in R, using the LPmerge (maps) function with the default parameters (max.interval = 1:3 and equal weights for both maps).

5. Statistical analysis

All phenotype analysis was carried out with Python 3.9.20 using the packages *scipy.stats*, *statsmodels.api*, and *sklearn*. Heritability and QTL analysis was carried out in R and R/qtl (Broman *et al.*, 2003). We cleaned the data by checking outliers and removing individuals with clear measurement error, which we defined as any individual with a trait value more than three z -scores away from the population mean. To test the assumptions for ANOVAs, we tested normality with the Anderson–Darling test and for homogeneity of variances with Levene’s test. There were some deviations from the assumptions for ANOVA. Due to plant death the

data were unbalanced, but for all traits either the ratio of variances for the largest and smallest group was within an acceptable range (<3), or the variance was coupled with group size, which would reduce statistical power rather than inflating type I error (Schielzeth *et al.*, 2020). As a result, we continued with ANOVA analysis.

Unless specified otherwise, we conducted all analyses for all traits, and separately for the herbaceous and hardwood cuttings ($N = 113$ unique genotypes, 103 for the herbaceous cuttings, and 103 for hardwood cuttings). We inspected the effect of root system size, measured with total length, on each trait for each propagation method visually and with Pearson correlations and found the responses were similar across propagation methods (Figure S1, Tables S1 and S2), so we continued with our analysis comparing propagation methods for all traits. We performed a type III ANOVA with the propagation method as the main effect and genotype as second effect to test for differences between propagation method, and we included an interaction term. For the same traits, we performed t -tests between parental genotypes for both propagation methods. To test associations between propagation methods for the shared genotype set, we calculated the mean value for each genotype and regressed the hardwood values on the corresponding herbaceous values for all traits.

We used pairwise linear regressions to test for trait correlations across genotypes. We found many significant correlations between traits, so we used principal component analysis (PCA) and unsupervised K -means clustering with three clusters to further interpret collinearity. Three clusters were chosen with the “elbow” test, by identifying the value of K where within-cluster-sum-of-squares values stopped decreasing quickly.

To estimate best unbiased linear predictions (BLUPs) and broad sense heritability for each propagation method we fit the following mixed effect model using the package *lme4* in R.

$$\begin{aligned} y_i &\sim N(\alpha_{j|i} + \beta_1(\text{block}), \sigma^2) \\ \alpha_j &\sim N(\mu_{\alpha_j}, \sigma_{\alpha_j}^2), \text{ for genotype } j = 1, \dots, j \end{aligned} \quad (1)$$

where y_i is the measured trait value for the i^{th} individual, $\alpha_{j|i}$ is the random intercept associated with genotype j , σ^2 is the residual variance, μ_{α} and σ_{α}^2 are the mean and variance of the genotype random effects, and $\beta_1(\text{block})$ is a fixed effect to account for the experiment blocking. We estimated broad sense heritability for each trait, H^2 , defined as the ratio of genotypic variance to phenotypic variance, excluding fixed effects (Visscher *et al.*, 2008). Phenotypic variance, σ_p^2 , can be split into the sum of genotypic (σ_G^2) and environmental (σ_E^2) variances, resulting in the calculation for broad sense heritability (H^2): $\sigma_G^2/(\sigma_G^2 + \sigma_E^2)$. σ_p^2 and σ_G^2 were estimated from random effect variance and residuals of the model. We estimated confidence intervals for broad sense heritability using the confint() function on the mixed effect model output in R.

There were deviations in the normality of BLUPs for some traits, however data were not transformed because deviations were generally small, and traditional parametric methods are still effective despite some non-normality (Rebai, 1997). For QTL mapping, we used BLUPs estimated from the random effects of the mixed effect model in Equation 1. To identify QTL, the whole genome logarithm of odds (LOD) significance threshold ($p < 0.05$) was determined with permutation ($N = 1,000$). Each trait was mapped to a composite map of both parents using the *scanone* function in R/qtl with Haley–Knott regression as a four-way cross. We used the 110R reference genome browser (Minio *et al.*, 2022) and BLAST (Priyam *et al.*, 2019; Altschul *et al.*, 1997; Altschul *et al.*, 2005) to identify the closest gene to the QTL peak and any associated proteins.

RESULTS

1. Population and parental traits are significantly different across genotypes and propagation methods

All the root architecture traits were significantly different across genotypes in the F1 population, for both the hardwood and herbaceous cuttings (ANOVA, $p < 0.001$) (Table 2). There were significant interactions between root system architecture and propagation methods for all measured traits (type III ANOVA, $p < 0.001$), and 7 out of 14 traits showed significant differences between propagation methods ($p < 0.05$, Table 2). Hardwood root systems were generally more fibrous, and had higher surface area and volume, more root tips, thicker primary roots, and shallower angles (Figure 2). Contrary to expectation, none of the traits were significantly correlated between the hardwood and herbaceous cuttings ($R^2 = 0.0004 - 0.03$, $p > 0.05$, $N = 93$) (Table 3).

2. Differences between parental phenotypes varies between propagation methods

Greater differences between 110R and 101-14, the parental genotypes, were seen with herbaceous cuttings ($p < 0.05$, *t*-test). The only significant difference between parental phenotypes for hardwood root systems was primary root thickness, with 110R having thicker primary roots ($p < 0.001$). Herbaceous root systems had seven traits with significant differences between parents ($p < 0.05$). For herbaceous cuttings, 110R had less fibrous root systems with shorter total lateral root length, steeper rooting angles, thicker primary roots, and thinner lateral roots. (Table 2 and Figure 3).

3. Most root architecture traits were correlated within each propagation method

Most of the root traits were significantly but weakly correlated across genotypes, in both the hardwood and herbaceous treatments ($|r| 0.19 - 0.99$, $p < 0.05$) (Tables S1 and S2, Figure S1). Positive significant trait correlations ($r = 0.19 - 0.99$), accounted for most of the correlations, except for negative correlations between root thickness traits and plant size traits (total length, total area, number of root tips, length of the longest root, primary root length, and lateral root length) as well as lateral to primary ratio ($r = -0.22 - -0.83$). The strongest relationships ($|r| > 0.7$) were positive correlations between a similar set of traits related to plant size (total length, total area, total volume, number of root tips, length of the longest root, primary root length, and lateral root length), and between traits that were functions of each other. Rooting rate was the least collinear with the other traits, with the fewest number of significant associations compared to all other traits.

TABLE 2. Population and parental trait values.

Trait	Population trait means		Parental hardwood means		Parental herbaceous means	
	Hardwood	Herbaceous	110R	101-14	110R	101-14
Total length	825.6 ± 31.8	598.5 ± 20.4	1,169.7 ± 147.5	1,557.4 ± 189	655 ± 54.5	704.8 ± 100.3
Total area	3,116.9 ± 111 *	2,350.6 ± 69.8 *	5,011.5 ± 598.5	5,915.8 ± 636.1	2,756.7 ± 209.1	2,516.4 ± 293.8
Total volume	1,339.6 ± 43.7 **	1,010 ± 27.5 **	2,415.9 ± 285.3	2,477.5 ± 247.8	1,173.7 ± 80.1	1,028.7 ± 88.6
Number of root tips	89.4 ± 4 *	50.6 ± 2.1 *	135.4 ± 17.3	177.3 ± 24.5	42.3 ± 4.6	56.1 ± 8.9
Average angle	49.7 ± 0.2 **	47.2 ± 0.3 **	51.8 ± 1.2	51.3 ± 0.7	43.4 ± 0.64 ***	48.9 ± 1.01 ***
Median diameter	1.08 ± 0.002	1.05 ± 0.004	1.21 ± 0.07	1.06 ± 0.04	1.18 ± 0.024 ***	0.91 ± 0.021 ***
Fibrousness	0.106 ± 0.0013	0.084 ± 0.0011	0.114 ± 0.004	0.11 ± 0.003	0.063 ± 0.003 ***	0.078 ± 0.004 ***
Median diameter primaries	1.422 ± 0.02 *	1.295 ± 0.01 *	1.62 ± 0.04 ***	1.354 ± 0.03 ***	1.306 ± 0.03 ***	1.138 ± 0.024 ***
Median diameter laterals	0.638 ± 0.015	0.62 ± 0.011	0.627 ± 0.006	0.634 ± 0.007	0.61 ± 0.018 *	0.657 ± 0.011 *
Primary root length	485.5 ± 17.8	424.3 ± 13	734.9 ± 88.8	956.8 ± 101.2	541 ± 44.7	443.3 ± 53.9
Lateral root length	340.1 ± 15.3	174.2 ± 8.9	434.8 ± 63.1	600.6 ± 93.3	114 ± 15.8 **	261.4 ± 50.4 **
Lateral over primary ratio	0.63 ± 0.018 *	0.4 ± 0.015 *	0.57 ± 0.06	0.6 ± 0.05	0.21 ± 0.03 ***	0.56 ± 0.05 ***
Length of the longest root	105.1 ± 2.4	97.9 ± 2.1	131.5 ± 11.9	133.8 ± 9.7	109 ± 5.7	108 ± 7.4

Significance determined by ANOVA for propagation method, and *t*-test for parental differences (significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Errors were calculated as standard error of the mean.

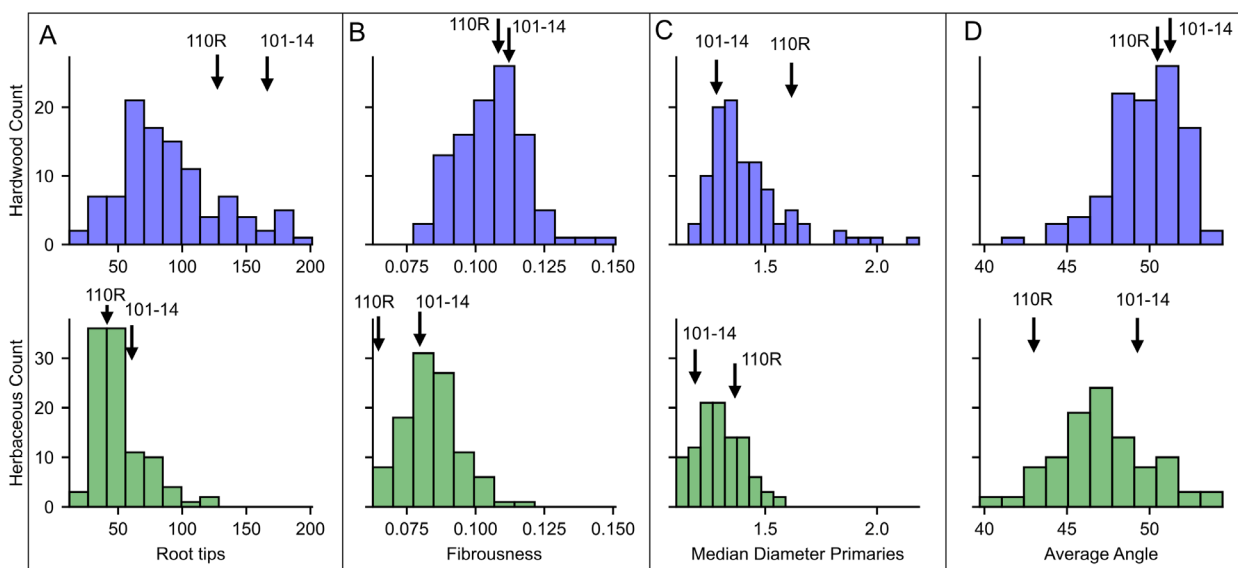


FIGURE 2. Population trait distributions.

Whole population histogram comparisons between genotypic means for each propagation method. Histograms are shown for a subset of four important root traits. The height of the bars indicates the number of genotypes in each bin. Mean of each parent is indicated for each trait and propagation method. Panels correspond to the following traits: (A) Root tips, (B) Fibrousness, (C) Median diameter, (D) Average angle.

TABLE 3. Regression results between propagation methods on the set of common genotypes.

Trait	<i>r</i>	<i>R</i> ²	<i>p</i> -value
Lateral root length	-0.145	0.021	0.167
Length of the longest root	0.037	0.001	0.723
Average angle	0.131	0.017	0.212
Lateral over primary ratio	0.029	0.001	0.781
Total area	-0.132	0.017	0.207
Total length	-0.132	0.017	0.208
Rooting rate	-0.156	0.024	0.137
Primary root length	-0.087	0.008	0.407
Total volume	-0.122	0.015	0.242
Number of root tips	-0.159	0.025	0.128
Median diameter laterals	0.1	0.01	0.342
Fibrousness	0.019	0	0.858
Median diameter primaries	0.1	0.01	0.341
Median diameter	0.092	0.008	0.382

Principal component analysis (PCA) allowed for closer investigation of collinearity of measured traits. The first four principal components accounted for 84 % and 91 % of total variance for hardwood and herbaceous cuttings, respectively (Figure 4). Principal component loadings for PC1 and PC2 were similar across propagation methods (Figure S3).

PC1 showed strong loadings for plant size traits such as total length, number of root tips, and length of the longest root, while other traits contributed to a lesser extent. PC2 was mainly characterized by median diameter, median diameter of primaries, fibrousness, and lateral to primary ratio, however fibrousness contributed positively to hardwood

root systems and negatively to herbaceous root systems. In general, PC3 and PC4 differed more significantly between propagation methods with limited contributions of total plant size. For herbaceous root systems, PC3 showed a higher contribution from average angle and root thicknesses, while PC4 was almost entirely dominated by rooting rate. For hardwood root systems, PC3 and PC4 showed contributions mainly from median diameter of laterals and rooting rate, and PC3 also had significant contributions from fibrousness (Figure S3). *K*-means cluster analysis of the first two principal components with three clusters placed F1 parents in the same cluster for hardwood cuttings (2), and in different clusters for herbaceous cuttings (0, 1) (Figure 4).

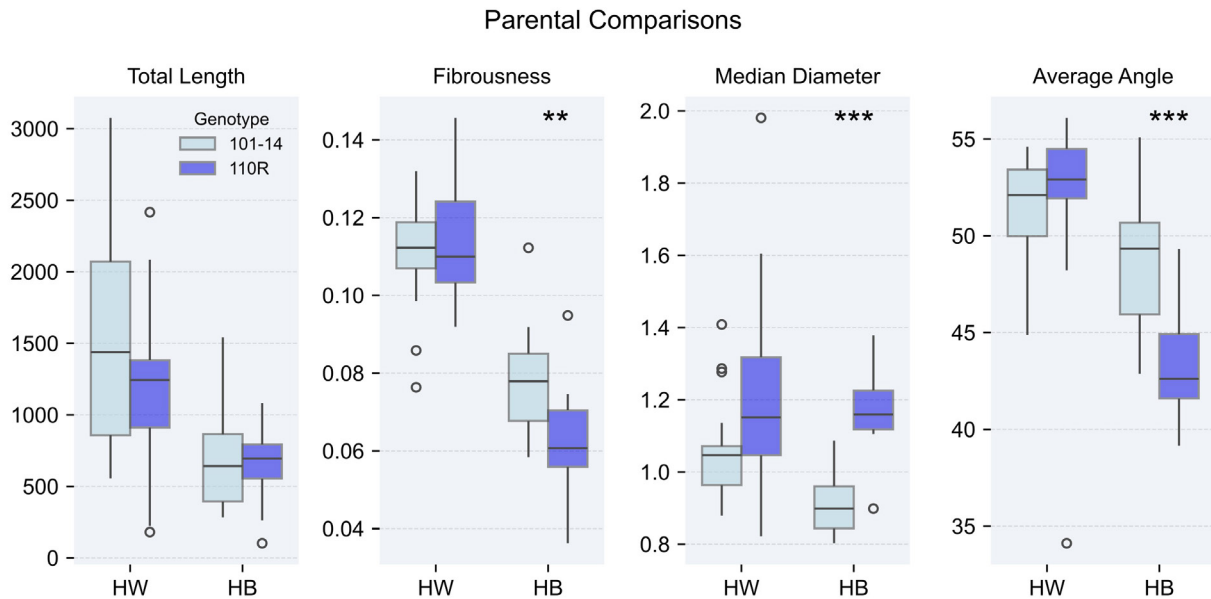


FIGURE 3. Parental trait distributions.

Box plots comparing parental phenotypes for each propagation method for a subset of four important root traits. HW signifies hardwood propagation and HB signifies herbaceous propagation. Significance is indicated by asterisks, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (two-sided t -test).

4. Environmental and genotypic variance differs between propagation methods

We calculated broad sense heritability for 13 root traits across both propagation methods. Broad sense heritability was generally low, and H^2 ranged from 0.08 to 0.34 for hardwood cuttings and 0.12 to 0.33 for herbaceous cuttings. Traits closely related to overall plant size had higher heritability than traits related to root thickness and angle (Table 4). Heritability stayed relatively constant across propagation methods for all traits. While heritability was estimated to be similar across propagation type, both genotypic and environmental variance was higher in the hardwood population.

5. Quantitative trait loci map to a variety of traits

Genotype by sequencing yielded 304,741 raw markers before filtering. Initial quality control, filtering, and binning redundant markers produced 1,017 and 1,001 unique markers for 110R and 101-14, respectively. After merging the parental maps from 367 common anchor markers, the final composite map contained 925 markers. The average distance between markers was 0.921 cM, the largest gap was 14.01 cM, the total map size was 834.31 cM, and the mean chromosome length was 43.91 cM.

Across both propagation methods, we identified two QTL for two unique root traits ($p < 0.05$) (Table 5). QTL were located on chromosomes 3 and 4 (Figure 5). We detected one QTL for each propagation method. We identified a QTL for average angle on chromosome 3 for herbaceous cuttings with a peak at 8.12 Mb and a LOD score of 4.50. We also identified a QTL for median diameter on chromosome 4 for

hardwood cuttings with a peak at 2.1 Mb and a LOD score of 5.48. After examining the nearest gene to each peak for chromosome 3 and 4 respectively, we identified genes and associated protein.3167340 (8,122,329 Mb, Chr 3) and protein.3168957 (2,052,887 Mb, Chr 4), uncategorized proteins in the *Vitis* interspecific cross – 110R V1.0 protein database (Minio *et al.*, 2022; Priyam *et al.*, 2019). There were closely related proteins identified in *Vitis vinifera* for both chromosome 3 (hypothetical protein VITISV_009065; 96.1 % similarity), and chromosome 4 (hypothetical protein VITISV_008123; 93.5 % similar), though both were identified as hypothetical proteins (Altschul *et al.*, 2005).

DISCUSSION

Results from the current study show novel QTL in grapevine root traits with useful genetic backgrounds for breeding. We also observed unexpected differences in root phenotypes between propagation methods, which provide more context for interpretation of root studies in the future. This data may assist breeding as well as guide future studies on grapevine root systems.

1. Novel QTL carry biological significance

Of the two identified significant QTL, we did not find any colocalization with previously mapped QTL or genes related to root traits from the literature, suggesting that the QTL are novel (Alahakoon & Fennell, 2023; Bert *et al.*, 2013; Blois *et al.*, 2023; Mohtasebi, 2023; Smith, 2010; Tandonnet *et al.*, 2018; Thapa, 2022). The traits with associated QTL, median diameter, and average angle, are both traits that carry biological significance.

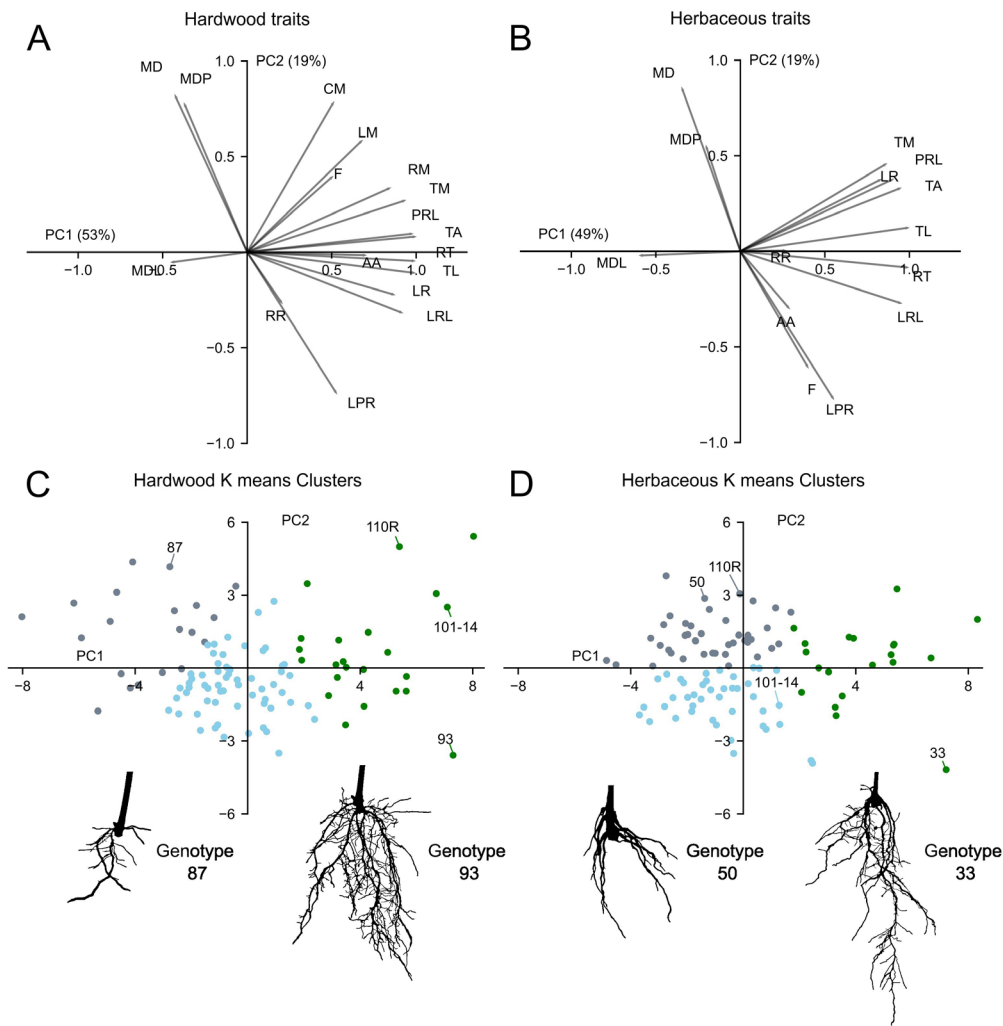


FIGURE 4. Principal component analysis.

Principal component analysis (PCA) showing biplots and cluster analysis for both propagation types. (A, B) PCA biplot for hardwood and herbaceous traits with vectors showing loadings for the first two principal components. Trait abbreviations are: total length (TL), total area (TA), total volume (TV), number of root tips (RT), average angle (AA), median diameter (MD), fibrousness (F), median diameter primaries (MDP), median diameter laterals (MDL), primary root length (PRL), lateral root length (LRL), lateral to primary ratio (LPR), length of the longest root (LR), pooled cutting mass (CM), pooled leaf mass (LM), pooled root mass (RM), rooting rate (RR). (C, D) The *K*-means cluster analysis results of hardwood and herbaceous root systems. Representative binary images of root systems that differ across both PC axes are labelled on the cluster analysis to show contrasting phenotypes are shown below. Different colours represent different clusters.

Root thickness, measured as median root diameter, may indirectly impart drought resistance through increased growth rates and penetration ability. Root thickness is associated with improved soil penetration that allows for continued root growth despite dry or hard soil (Materchera *et al.*, 1991; Materchera *et al.*, 1992). Fast growing, exploratory roots also tend to be thicker, which may assist in creating an extensive, more drought resistant root system (Lynch, 2013; Materchera *et al.*, 1991; Richards, 1983). In grapevine, root thickness has been shown to be significantly greater in drought resistant 110R than susceptible 101-14 in pots (Reingwitz *et al.*, 2021), which our results corroborated (Table 2 and Figure 3). Though previous studies have found relationships between thick roots and drought resistance, especially in annual crops (Klein *et al.*, 2020; Lynch, 2013), the effect of root thickness on long term root architecture and drought resistance in grapevine is still unknown.

Rooting angle has been extensively studied in other crops as a means of improving drought resistance (Guo *et al.*, 2024; Lynch, 2013; Trachsel *et al.*, 2013; Uga *et al.*, 2013) and in a previous study of grapevine, the drought resistant rootstocks Ramsey and 110R showed steeper root growth angles in rhizotrons than the susceptible varieties Riparia Gloire and 101-14 (Fort *et al.*, 2017). These results indicate that rooting angle is likely an important factor in drought resistance, however, the effects of root initiation angle from cuttings on long-term development of RSA of field-grown grapevine is also still unknown. The effect that root angle has on grapevine is likely more complicated than in annual crop plants due to long lived root systems and root system plasticity from year to year (Smart *et al.*, 2006; Soar & Loveys, 2007).

TABLE 4. Broad sense heritability of root traits.

Trait	Broad sense heritability H^2	
	Hardwood	Herbaceous
Total length	0.31 (0.22-0.41)	0.29 (0.21-0.40)
Total area	0.32 (0.23-0.43)	0.30 (0.21-0.40)
Total mass	0.34 (0.24-0.44)	0.32 (0.23-0.42)
Root tips	0.31 (0.22-0.41)	0.33 (0.24-0.43)
Average angle	0.17 (0.10-0.25)	0.22 (0.15-0.32)
Median diameter	0.23 (0.15-0.32)	0.29 (0.20-0.39)
Fibrousness	0.14 (0.08-0.22)	0.20 (0.13-0.29)
Median diameter primaries	0.18 (0.11-0.27)	0.12 (0.06-0.20)
Median diameter laterals	0.08 (0.03-0.14)	0.18 (0.11-0.26)
Primary root length	0.33 (0.24-0.43)	0.28 (0.20-0.38)
Lateral root length	0.30 (0.21-0.4)	0.29 (0.21-0.39)
Lateral over primary	0.23 (0.15-0.32)	0.23 (0.15-0.32)
Longest root	0.26 (0.18-0.36)	0.23 (0.15-0.32)

Heritability presented with 95 % confidence intervals.

TABLE 5. Mapped quantitative trait loci.

Trait	Chromosome	Position (cM)	Physical position (Mb)	LOD	CI low (Mb)	CI high (Mb)	% variance explained	Propagation method
Average angle	3	20	8.12	4.5	3.78	9.17	18.6	Herbaceous
Median diameter	4	2.7	2.1	5.48	0.54	2.87	22.1	Hardwood

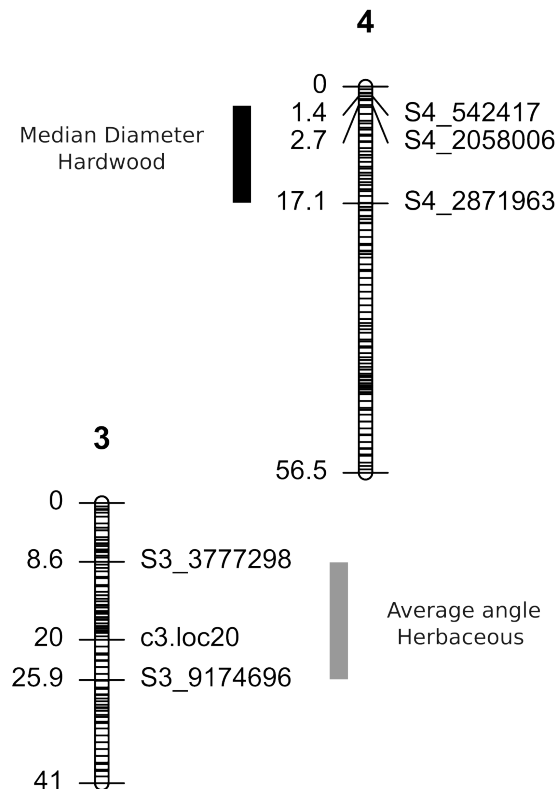


FIGURE 5. Mapped QTL.

Mapped QTL at whole genome $p < 0.05$ significance. Peak and confidence interval markers for each QTL are marked on each linkage group. Bars beside each linkage group signify QTL confidence interval. Distances are in centimorgans (cM).

After investigating the closest gene to each peak, we found they were associated with unclassified proteins in the 110R protein database. After using BLAST to explore potential protein function, we found the identified proteins were similar (93.5 % and 96.1 %) to hypothetical proteins present in *V. vinifera*. Hypothetical proteins are proteins that are expected to be expressed from the sequence, however there is yet to be any experimental evidence of translation (Desler *et al.*, 2009). To robustly identify candidate genes, more statistical power and populations that capture more recombination events are needed (*e.g.*, genome-wide association studies) to reduce confidence intervals (Myles *et al.*, 2009), so we did not expand our analysis beyond identification of the closest genes to the QTL peak.

2. Differences between propagation methods guides results interpretation of future studies

Both propagation methods have been used extensively in scientific studies, and our results more clearly highlight the scope of each propagation method. Significant differences and interaction between genotype and propagation method mean that studies using herbaceous cuttings may not be able to be directly applied to management or breeding for rootstocks. More research must be done to determine if herbaceous traits translate to hardwood propagation.

Because nurseries use hardwood propagation for commercial production of plant material, studies focused on direct management or the selection for advantageous root traits should use hardwood propagation whenever possible. While hardwood propagation may be preferable in many situations, we observed higher environmental variance in hardwood cuttings, likely due to differences in carbohydrate stores in stems affecting root system size (Larrey *et al.*, 2025; Smart *et al.*, 2006). Noisy data in the current study reduced power for QTL mapping and comparisons between genotypes and propagation methods, so care should be taken when developing a mapping population to reduce environmental variance wherever possible. Maintaining greenhouse populations for hardwood cuttings that are rotated in and out of dormancy may better control differences in cane size and development and control for variable soil, weather, or pest damage.

While interpretation of hardwood propagation is easier, despite similar heritability between propagation method, herbaceous cuttings showed clearer differences between the parent genotypes (Table 2). These genotypes are known to have different drought performance in the field and different root system architecture in adventitious root systems (Cuneo *et al.*, 2021; Hnizdor, 2023; Reingwartz *et al.*, 2021; Zhang *et al.*, 2016). This agrees with the results of the PCA *K*-means clustering, which placed parents in different clusters for herbaceous, but the same for hardwood. These results suggest that more homogeneously sized cuttings, and the ability for all genotypes to photosynthesize throughout the entire process may have reduced the dependence on carbohydrate stores to develop an adventitious root system, resulting in lower environmental variance. While herbaceous

propagation may be less suitable for direct applications to management or breeding, higher flexibility and lower environmental variance could be utilized for physiological or more basic science, like candidate gene studies.

3. Trait complexity shapes future studies and breeding

These genetic results provide novel QTL that indicate this parentage may be able to provide advantageous alleles for root architecture traits that facilitate soil exploration and water uptake. Transgressive segregation, phenotypes of progeny that are more extreme than the parental phenotypes, has been successfully leveraged in the past to make gains in plant breeding (Knapp *et al.*, 2024; Rieseberg *et al.*, 1999). Our traits showed variable transgressive segregation for all traits except for fibrousness in herbaceous cuttings, where 110R, one of the parents of the cross, was the most extreme phenotype (Figure 2). The individuals with more extreme phenotypes harbour alleles that could be useful for future breeding efforts and advance the drought resistance of rootstocks within this well-established, high performing ancestry while working on longer term projects, such as trait introgression from other genetic backgrounds.

Several previous successful family mapping studies for root traits in grapevine used crosses between *V. riparia* and *V. vinifera* (Alahakoon & Fennell, 2023; Bert *et al.*, 2013; Tandonnet *et al.*, 2018). *V. riparia* is not known for its drought resistance (Rahemi *et al.*, 2022), which could limit the applicability of these markers for breeding rootstock drought resistance. The QTL identified in the current study are from progeny derived from *V. rupestris*, *V. berlandieri*, and *V. riparia*, the most commonly used parents for rootstock breeding, which could make them more widely applicable for selecting grapevine accessions (Myles *et al.*, 2009).

Though the studied population shows promise for breeding for root traits, there are some limitations to utilise the QTL identified in this study. This study compared two propagation methods, but the experiment was not replicated in a second year, so the QTL identified would need to be verified further before use in breeding programs. Just as rootstock selection affects vigour of the scion, previous research has shown that scion selection significantly alters root diameter, density, fine root ratio, and biomass allocation of grafted rootstocks (Ferlito *et al.*, 2020; Tandonnet *et al.*, 2009). Interactions like these between scion and rootstock can result in unexpected outcomes, such as the drought resistant rootstock 1103P showing canopy collapse under drought due to excess vigour (Smart *et al.*, 2012). Additionally, the direct effects of root traits from young plants (35 days old) on drought resistance and how the traits scale to the field is still largely unknown, especially for traits with low heritability, high plasticity, and complicated effects on physiology (Bernardo *et al.*, 2025; Smart *et al.*, 2006). Drought treatments in conjunction with QTL identification could be a valuable avenue to explore in the future to directly link QTL and root traits to physiological indicators of drought resistance.

While recent studies have been successful at mapping traits with smaller effect sizes (<10 %), QTL mapping for root system traits has had mixed success (Mohtasebi, 2023; Schmitz, 2023; Smith, 2010; Thapa, 2022). In our study, low population size, collinearity of traits with plant size, high root system plasticity, and low heritability only allowed us to observe a small number of QTL with effect sizes greater than 15 %. This leads us to believe that our results agree with previous findings that root system architecture of grapevine is a complex polygenic trait, with most QTL explaining less than 20 % of variation (Alahakoon & Fennell, 2023). Marker assisted selection, while useful for QTL with larger effect sizes, may not be as helpful for many small effect markers (Bhat *et al.*, 2016). Future research on the genetics of RSA of grapevine should include higher throughput phenotyping methods to improve statistical power. Additionally, the root system of young plants may be more affected by differences in root-strike, so plants should be as well-developed as reasonably possible. Genomic selection models combined with higher throughput phenotyping methods may be a good route in the future to make selection for root traits a reality in grapevine breeding programs (Seyum *et al.*, 2022).

CONCLUSION

This study identified quantitative trait loci and the effect of propagation method on the adventitious root system architecture in a diverse *Vitis* population derived from rootstocks 110R and 101-14 MGT. The two significant identified QTL occurred in traits with biological significance for drought resistance. Significant differences and interaction between genotype and propagation method shows that propagation method affects interpretation of results from scientific studies, and each propagation method has a scope of use. Genetic control of RSA is complex and multigenic, so future efforts for breeding should focus on genomic selection models and higher throughput phenotyping to improve power of QTL and GWAS studies.

ACKNOWLEDGEMENTS

This study was funded with the California Department of Food and Agriculture Specialty Crop Block Grant Program, grant #21-0001-031-SF, the Corliss Knapp Engle Scholarship in Horticulture (Garden Club of America), ASEV Traditional Scholarship (American Society for Enology and Viticulture), Milton D. and Mary M. Miller Plant Science Award 2024 (UC Davis Plant Sciences), UC Davis Chile Scholarship (UC Davis Chile Life Sciences Innovation Center), and the Margrit Mondavi Scholarship 2024–2025 (UC Davis Viticulture and Enology).

We thank the greenhouse staff at UC Davis and Veronica Nunez for their help with experimental facilities, and students Evenie Fuentes, Jackson Grander, Vibha Venkataraman, and Felipe Suarez-Vega for their assistance with plant imaging. We thank Dr Rosa Figueroa-Balderas for assistance with genetic material collection and extraction.

REFERENCES

- Alahakoon, D., & Fennell, A. (2023). Genetic analysis of grapevine root system architecture and loci associated gene networks. *Frontiers in Plant Science*, 13, 1083374. <https://doi.org/10.3389/fpls.2022.1083374>
- Alsina, M. M., Smart, D. R., Bauerle, T., de Herralde, F., Biel, C., Stockert, C., Negron, C., & Save, R. (2011). Seasonal changes of whole root system conductance by a drought-tolerant grape root system. *Journal of Experimental Botany*, 62(1), 99–109. <https://doi.org/10.1093/jxb/erq247>
- Altschul, S. F., Madden, T. L., Schäffer, A. A., Zhang, J., Zhang, Z., Miller, W., & Lipman, D. J. (1997). Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. *Nucleic Acids Research*, 25(17), 3389–3402. <https://doi.org/10.1093/nar/25.17.3389>
- Altschul, S. F., Wootton, J. C., Gertz, E. M., Agarwala, R., Morgulis, A., Schäffer, A. A., & Yu, Y. (2005). Protein database searches using compositionally adjusted substitution matrices. *The FEBS Journal*, 272(20), 5101–5109. <https://doi.org/10.1111/j.1742-4658.2005.04945.x>
- Atkinson, C. J., Policarpo, M., Webster, A. D., & Kuden, A. M. (1999). Drought tolerance of apple rootstocks: Production and partitioning of dry matter. *Plant Soil*, 206(2), 223–235. <https://doi.org/10.1023/A:1004415817237>
- Bagniewska-Zadworna, A., Arasimowicz-Jelonek, M., Smoliński, D. J., & Stelmasik, A. (2014). New insights into pioneer root xylem development: Evidence obtained from *Populus trichocarpa* plants grown under field conditions. *Annals of Botany*, 113(7), 1235–1247. <https://doi.org/10.1093/aob/mcu063>
- Barrientos-Sanhueza, C., Zurita-Silva, A., Knipfer, T., McElrone, A. J., & Cuneo, I. F. (2024). Unique root hydraulic and mechanical properties support the resilience of grapevines adapted to the Atacama Desert. *Plant, Cell & Environment*, 47(12), 5126–5139. <https://doi.org/10.1111/pce.15085>
- Barrios-Masias, F. H., Knipfer, T., & McElrone, A. J. (2015). Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. *Journal of Experimental Botany*, 66(19), 6069–6078. <https://doi.org/10.1093/jxb/erv324>
- Bartlett, M. K., Sinclair, G., Fontanesi, G., Knipfer, T., Walker, M. A., & McElrone, A. J. (2022). Root pressure–volume curve traits capture rootstock drought tolerance. *Annals of Botany*, 129(4), 389–402. <https://doi.org/10.1093/aob/mcab132>
- Bauerle, T. L., Smart, D. R., Bauerle, W. L., Stockert, C., & Eissenstat, D. M. (2008). Root foraging in response to heterogeneous soil moisture in two grapevines that differ in potential growth rate. *New Phytologist*, 179(3), 857–866. <https://doi.org/10.1111/j.1469-8137.2008.02489.x>
- Bernardo, S., Marguerit, E., Ollat, N., Gambetta, G. A., Saint Cast, C., & de Miguel, M. (2025). Root system ideotypes: What is the potential for breeding drought-tolerant grapevine rootstocks? *Journal of Experimental Botany*, 76(11), 2970–2984. <https://doi.org/10.1093/jxb/eraf006>
- Bert, P.-F., Bordenave, L., Donnart, M., Hévin, C., Ollat, N., & Decroocq, S. (2013). Mapping genetic loci for tolerance to lime-induced iron deficiency chlorosis in grapevine rootstocks (*Vitis* sp.). *Theoretical and Applied Genetics*, 126(2), 451–473. <https://doi.org/10.1007/s00122-012-1993-5>

- Bhat, J. A., Ali, S., Salgotra, R. K., Mir, Z. A., Dutta, S., Jadon, V., Tyagi, A., Mushtaq, M., Jain, N., Singh, P. K., Singh, G. P., & Prabhu, K. V. (2016). Genomic Selection in the Era of Next Generation Sequencing for Complex Traits in Plant Breeding. *Frontiers in Genetics*, 7. <https://doi.org/10.3389/fgene.2016.00221>
- Blois, L., de Miguel, M., Bert, P.-F., Ollat, N., Rubio, B., Voss-Fels, K. P., Schmid, J., & Marguerit, E. (2023). Dissecting the genetic architecture of root-related traits in a grafted wild *Vitis berlandieri* population for grapevine rootstock breeding. *Theoretical and Applied Genetics*, 136(11), 223. <https://doi.org/10.1007/s00122-023-04472-1>
- Blum, A. (2005). Drought resistance, water-use efficiency, and yield potential—Are they compatible, dissonant, or mutually exclusive? *Australian Journal of Agricultural Research*, 56(11), 1159. <https://doi.org/10.1071/AR05069>
- Brault, C., Segura, V., Roques, M., Lamblin, P., Bouckennooghe, V., Pouzalgues, N., Cuntly, C., Breil, M., Frouin, M., Garcin, L., Camps, L., Ducasse, M.-A., Romieu, C., Masson, G., Julliard, S., Flutre, T., & Le Cunff, L. (2024). Enhancing grapevine breeding efficiency through genomic prediction and selection index. *G3: Genes, Genomes, Genetics*, 14(4), jkae038. <https://doi.org/10.1093/g3journal/jkae038>
- Broman, K. W., Wu, H., Sen, S., & Churchill, G. A. (2003). R/qtl: QTL mapping in experimental crosses. *Bioinformatics*, 19(7), 889–890. <https://doi.org/10.1093/bioinformatics/btg112>
- Cantu, D., & Walker, M. A. (2019). *The Grape Genome*. Springer International Publishing. <https://doi.org/10.1007/978-3-030-18601-2>
- Charrier, G., Delzon, S., Domec, J.-C., Zhang, L., Delmas, C. E. L., Merlin, I., Corso, D., King, A., Ojeda, H., Ollat, N., Prieto, J. A., Scholach, T., Skinner, P., van Leeuwen, C., & Gambetta, G. A. (2018). Drought will not leave your glass empty: Low risk of hydraulic failure revealed by long-term drought observations in world's top wine regions. *Science Advances*, 4(1), eaa06969. <https://doi.org/10.1126/sciadv.aao6969>
- Chen, Y., Fei, Y., Howell, K., Chen, D., Clingeffer, P., & Zhang, P. (2024). Rootstocks for Grapevines Now and into the Future: Selection of Rootstocks Based on Drought Tolerance, Soil Nutrient Availability, and Soil pH. *Australian Journal of Grape and Wine Research*, 2024, 1–23. <https://doi.org/10.1155/2024/6704238>
- Clark, L. J., Cope, R. E., Whalley, W. R., Barraclough, P. B., & Wade, L. J. (2002). Root penetration of strong soil in rainfed lowland rice: Comparison of laboratory screens with field performance. *Field Crops Research*, 76(2–3), 189–198. [https://doi.org/10.1016/S0378-4290\(02\)00039-4](https://doi.org/10.1016/S0378-4290(02)00039-4)
- Cuneo, I. F., Barrios-Masias, F., Knipfer, T., Uretsky, J., Reyes, C., Lenain, P., Brodersen, C. R., Walker, M. A., & McElrone, A. J. (2021). Differences in grapevine rootstock sensitivity and recovery from drought are linked to fine root cortical lacunae and root tip function. *New Phytologist*, 229(1), 272–283. <https://doi.org/10.1111/nph.16542>
- Cuneo, I. F., Knipfer, T., Brodersen, C. R., & McElrone, A. J. (2016). Mechanical Failure of Fine Root Cortical Cells Initiates Plant Hydraulic Decline during Drought. *Plant Physiology*, 172(3), 1669–1678. <https://doi.org/10.1104/pp.16.00923>
- Del Pozo, A., Brunel-Saldias, N., Engler, A., Ortega-Farias, S., Acevedo-Opazo, C., Lobos, G. A., Jara-Rojas, R., & Molina-Montenegro, M. A. (2019). Climate Change Impacts and Adaptation Strategies of Agriculture in Mediterranean-Climate Regions (MCRs). *Sustainability*, 11(10), 2769. <https://doi.org/10.3390/su11102769>
- Desler, C., Suravajhala, P., Sanderhoff, M., Rasmussen, M., & Rasmussen, L. J. (2009). *In Silico* screening for functional candidates amongst hypothetical proteins. *BMC Bioinformatics*, 10(1), 289. <https://doi.org/10.1186/1471-2105-10-289>
- Dry, P. R., & Coombe, B. G. (2005). *Viticulture. Volume 1: Resources* (2nd ed., reprinted with alterations). Winetitles.
- Eibach, R., & Töpfer, R. (2015). Traditional grapevine breeding techniques. In A. Reynolds (Ed.), *Grapevine Breeding Programs for the Wine Industry* (pp. 3–22). Elsevier. <https://doi.org/10.1016/B978-1-78242-075-0.00001-6>
- Farooq, M., Kakar, K., Golly, M. K., Ilyas, N., Zib, B., Khan, I., Khan, S., Khan, I., Saboor, A., & Bakhtiar, M. (2018). Comparative Effect of Potting Media on Sprouting and Seedling Growth of Grape Cuttings. *International Journal of Environmental & Agriculture Research*, 4(3), 82–89. <https://doi.org/10.5281/zenodo.1215842>
- Ferlito, F., Distefano, G., Gentile, A., Allegra, M., Lakso, A. N., & Nicolosi, E. (2020). Scion–rootstock interactions influence the growth and behaviour of the grapevine root system in a heavy clay soil. *Australian Journal of Grape and Wine Research*, 26(1), 68–78. <https://doi.org/10.1111/ajgw.12415>
- Fichtl, L., Leitner, D., Schnepf, A., Schmidt, D., Kahlen, K., & Friedel, M. (2024). A Field-to-Parameter Pipeline for Analyzing and Simulating Root System Architecture of Woody Perennials: Application to Grapevine Rootstocks. *Plant Phenomics*, 6, 0280. <https://doi.org/10.34133/plantphenomics.0280>
- Fort, K., Fraga, J., Grossi, D., & Walker, M. A. (2017). Early Measures of Drought Tolerance in Four Grape Rootstocks. *Journal of the American Society for Horticultural Science*, 142(1), 36–46. <https://doi.org/10.21273/JASHS03919-16>
- Gambetta, G. A., Fei, J., Rost, T. L., Knipfer, T., Matthews, M. A., Shackel, K. A., Walker, M. A., & McElrone, A. J. (2013). Water Uptake along the Length of Grapevine Fine Roots: Developmental Anatomy, Tissue-Specific Aquaporin Expression, and Pathways of Water Transport. *Plant Physiology*, 163(3), 1254–1265. <https://doi.org/10.1104/pp.113.221283>
- Glaubitz, J. C., Casstevens, T. M., Lu, F., Harriman, J., Elshire, R. J., Sun, Q., & Buckler, E. S. (2014). TASSEL-GBS: A High Capacity Genotyping by Sequencing Analysis Pipeline. *PLOS ONE*, 9(2), e90346. <https://doi.org/10.1371/journal.pone.0090346>
- Grattapaglia, D., & Sederoff, R. (1994). Genetic linkage maps of *Eucalyptus grandis* and *Eucalyptus urophylla* using a pseudo-testcross: mapping strategy and RAPD markers. *Genetics*, 137(4), 1121–1137. <https://doi.org/10.1093/genetics/137.4.1121>
- Guo, C., Bao, X., Sun, H., Chen, J., Zhu, L., Zhang, J., Zhang, H., Zhang, Y., Zhang, K., Bai, Z., Li, A., Liu, L., & Li, C. (2024). The crucial role of lateral root angle in enhancing drought resilience in cotton. *Frontiers in Plant Science*, 15, 1358163. <https://doi.org/10.3389/fpls.2024.1358163>
- Himmelbauer, M. L., Loiskandl, W., & Kastanek, F. (2004). Estimating length, average diameter and surface area of roots using two different Image analyses systems. *Plant and Soil*, 260(1/2), 111–120. <https://doi.org/10.1023/B:PLSO.0000030171.28821.55>
- Hnizdor, J. (2023). *Soil Matric Potential: A Drought Stress Indicator with Chardonnay and Commercial Rootstocks* [Masters thesis, University of California]. University of California, Davis. <https://www.proquest.com/openview/9a8ed60e35477b91f75a800c30c72e99/1?pq-origsite=gscholar&cbl=18750&diss=y>

- Jung, J. K. H., & McCouch, S. (2013). Getting to the roots of it: Genetic and hormonal control of root architecture. *Frontiers in Plant Science*, 4. <https://doi.org/10.3389/fpls.2013.00186>
- Keller, M. (2020). *The science of grapevines* (3rd ed.). Academic press. ISBN 978-0-12-816365-8
- Khalid, M. A., Ali, Z., Husnain, L. A., Fiaz, S., Saddique, M. A. B., Merrium, S., Attia, K. A., Ercisli, S., & Iqbal, R. (2024). GA-sensitive *Rht13* gene improves root architecture and osmotic stress tolerance in bread wheat. *BMC Genomic Data*, 25(1), 90. <https://doi.org/10.1186/s12863-024-01272-4>
- Klein, S. P., Schneider, H. M., Perkins, A. C., Brown, K. M., & Lynch, J. P. (2020). Multiple Integrated Root Phenotypes Are Associated with Improved Drought Tolerance. *Plant Physiology*, 183(3), 1011–1025. <https://doi.org/10.1104/pp.20.00211>
- Knapp, S. J., Cole, G. S., Pincot, D. D. A., Dilla-Ermita, C. J., Bjornson, M., Famula, R. A., Gordon, T. R., Harshman, J. M., Henry, P. M., & Feldmann, M. J. (2024). Transgressive segregation, hopeful monsters, and phenotypic selection drove rapid genetic gains and breakthroughs in predictive breeding for quantitative resistance to *Macrophomina* in strawberry. *Horticulture Research*, 11(2), uhad289. <https://doi.org/10.1093/hr/uhad289>
- Kolb, E., Legué, V., & Bogeat-Triboulot, M.-B. (2017). Physical root–soil interactions. *Physical Biology*, 14(6), 065004. <https://doi.org/10.1088/1478-3975/aa90dd>
- Kulkarni, M., Soolanayakanahally, R., Ogawa, S., Uga, Y., Selvaraj, M. G., & Kagale, S. (2017). Drought Response in Wheat: Key Genes and Regulatory Mechanisms Controlling Root System Architecture and Transpiration Efficiency. *Frontiers in Chemistry*, 5, 106. <https://doi.org/10.3389/fchem.2017.00106>
- Larrey, M., Tandonnet, J.-P., Saint Cast, C., Cookson, S. J., & Vivin, P. (2025). Exploring how graft length shapes root system architecture and morphology in grapevine rootstocks. *OENO One*, 59(1). <https://doi.org/10.20870/oeno-one.2025.59.1.8226>
- Levitt, J. (1980). The Nature of Stress Injury and Resistance. In J. Levitt (Ed.), *Chilling, Freezing, and High Temperature Stresses* (pp. 10–19). Elsevier. <https://doi.org/10.1016/B978-0-12-445501-6.50007-5>
- Li, B., Liu, D., Li, Q., Mao, X., Li, A., Wang, J., Chang, X., & Jing, R. (2016). Overexpression of wheat gene *TaMOR* improves root system architecture and grain yield in *Oryza sativa*. *Journal of Experimental Botany*, 67(14), 4155–4167. <https://doi.org/10.1093/jxb/erw193>
- Lyford, W., & Wilson, B. (1964). *Development of the root system of Acer rubrum L.* Harvard Forest (paper number 10), Petersham, Massachusetts, USA.
- Lynch, J. P. (2013). Steep, cheap and deep: An ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany*, 112(2), 347–357. <https://doi.org/10.1093/aob/mcs293>
- Materechera, S. A., Alston, A. M., Kirby, J. M., & Dexter, A. R. (1992). Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil*, 144(2), 297–303. <https://doi.org/10.1007/BF00012888>
- Materechera, S. A., Dexter, A. R., & Alston, A. M. (1991). Penetration of very strong soils by seedling roots of different plant species. *Plant and Soil*, 135(1), 31–41. <https://doi.org/10.1007/BF00014776>
- McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., Helmisaari, H., Hobbie, E. A., Iversen, C. M., Jackson, R. B., Leppälammil-Kujansuu, J., Norby, R. J., Phillips, R. P., Pregitzer, K. S., Pritchard, S. G., Rewald, B., & Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist*, 207(3), 505–518. <https://doi.org/10.1111/nph.13363>
- McLain, K., & Castro, H. (2017). *2015 Drought and Agriculture*. Washington State Department of Agriculture. <https://agr.wa.gov/departments/land-and-water/natural-resources/water-quantity/drought-impacts>
- Minio, A., Cochetel, N., Massonnet, M., Figueroa-Balderas, R., & Cantu, D. (2022). HiFi chromosome-scale diploid assemblies of the grape rootstocks 110R, Kober 5BB, and 101–14 Mgt. *Scientific Data*, 9(1), 660. <https://doi.org/10.1038/s41597-022-01753-0>
- Mohtasebi, P. (2023). *Morphological and Genetic Analysis of the Root System in Two American Grapevines (Vitis Species)* [Masters Thesis, Missouri State University]. Missouri State University. <https://bearworks.missouristate.edu/theses/3897>
- Morano, L. D. (1995). *An analysis of Vitis species and rootstock crosses: Vineyard root distribution patterns, root growth and metabolic response to flooding in the greenhouse and associated soil and plant communities of wild vines* [PhD Thesis, University of California]. University of California, Davis.
- Morano, L. D., & Walker, M. A. (1995). Soils and Plant Communities Associated with Three Vitis Species. *American Midland Naturalist*, 134(2), 254. <https://doi.org/10.2307/2426296>
- Myles, S., Peiffer, J., Brown, P. J., Ersoz, E. S., Zhang, Z., Costich, D. E., & Buckler, E. S. (2009). Association Mapping: Critical Considerations Shift from Genotyping to Experimental Design. *The Plant Cell*, 21(8), 2194–2202. <https://doi.org/10.1105/tpc.109.068437>
- National Weather Service. (n.d.). NOAA Online Weather Data. NOAA's National Weather Service. Retrieved February 25, 2025. <https://www.weather.gov/wrh/Climate?wfo=sto>
- Ollat, N., Bordenave, L., Tandonnet, J. P., Boursiquot, J. M., & Marguerit, E. (2016). Grapevine rootstocks: Origins and perspectives. *Acta Horticulturae*, 1136, 11–22. <https://doi.org/10.17660/ActaHortic.2016.1136.2>
- Osmont, K. S., Sibout, R., & Hardtke, C. S. (2007). Hidden Branches: Developments in Root System Architecture. *Annual Review of Plant Biology*, 58(1), 93–113. <https://doi.org/10.1146/annurev.arplant.58.032806.104006>
- Overvoorde, P., Fukaki, H., & Beeckman, T. (2010). Auxin Control of Root Development. *Cold Spring Harbor Perspectives in Biology*, 2(6), a001537–a001537. <https://doi.org/10.1101/cshperspect.a001537>
- Pouzoulet, J., Pivovarov, A. L., Scudiero, E., De Guzman, M. E., Rolshausen, P. E., & Santiago, L. S. (2020). Contrasting adaptation of xylem to dehydration in two *Vitis vinifera* L. sub-species. *VITIS – Journal of Grapevine Research*, 59(2), 53–61. <https://doi.org/10.5073/VITIS.2020.59.53-61>
- Priyam, A., Woodcroft, B. J., Rai, V., Moghul, I., Munagala, A., Ter, F., Chowdhary, H., Pieniak, I., Maynard, L. J., Gibbins, M. A., Moon, H., Davis-Richardson, A., Uludag, M., Watson-Haigh, N. S., Challis, R., Nakamura, H., Favreau, E., Gómez, E. A., Pluskal, T., ... & Wurm, Y. (2019). Sequenceserver: A Modern Graphical User Interface for Custom BLAST Databases. *Molecular Biology and Evolution*, 36(12), 2922–2924. <https://doi.org/10.1093/molbev/msz185>

- Puhe, J. (2003). Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—A review. *Forest Ecology and Management*, 175(1–3), 253–273. [https://doi.org/10.1016/S0378-1127\(02\)00134-2](https://doi.org/10.1016/S0378-1127(02)00134-2)
- Rahemi, A., Dodson Peterson, J. C., & Lund, K. T. (2022). *Grape Rootstocks and Related Species*. Springer International Publishing. <https://doi.org/10.1007/978-3-030-99407-5>
- Rebaï, A. (1997). Comparison of methods for regression interval mapping in QTL analysis with non-normal traits. *Genetical Research*, 69(1), 69–74. <https://doi.org/10.1017/S0016672396002558>
- Reingwartz, I., Uretsky, J., Cuneo, I. F., Knipfer, T., Reyes, C., Walker, M. A., & McElrone, A. J. (2021). Inherent and Stress-Induced Responses of Fine Root Morphology and Anatomy in Commercial Grapevine Rootstocks with Contrasting Drought Resistance. *Plants*, 10(6), 1121. <https://doi.org/10.3390/plants10061121>
- Richards, D. (1983). The Grape Root System. In J. Janick (Ed.), *Horticultural Reviews* (1st ed., pp. 133–135). Wiley. <https://doi.org/10.1002/9781118060728.ch3>
- Rieseberg, L. H., Archer, M. A., & Wayne, R. K. (1999). Transgressive segregation, adaptation and speciation. *Heredity*, 83(4), 363–372. <https://doi.org/10.1038/sj.hdy.6886170>
- Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allee, H., Teplitsky, C., Réale, D., Dochtermann, N. A., Gamszegi, L. Z., & Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, 11(9), 1141–1152. <https://doi.org/10.1111/2041-210X.13434>
- Schiffthaler, B., Bernhardsson, C., Ingvarsson, P. K., & Street, N. R. (2017). BatchMap: A parallel implementation of the OneMap R package for fast computation of F₁ linkage maps in outcrossing species. *PLOS ONE*, 12(12), e0189256. <https://doi.org/10.1371/journal.pone.0189256>
- Schmitz, R. (2023). *Development of root phenotyping methods and QTL analysis of root traits in grapevine mapping populations* [PhD Thesis, Universität Bonn]. Universität Bonn. <https://nbn-resolving.org/urn:nbn:de:hbz:5-69442>
- Seethepalli, A., Guo, H., Liu, X., Griffiths, M., Almtarfi, H., Li, Z., Liu, S., Zare, A., Fritschi, F. B., Blancaflor, E. B., Ma, X.-F., & York, L. M. (2020). RhizoVision Crown: An Integrated Hardware and Software Platform for Root Crown Phenotyping. *Plant Phenomics*, 2020, 2020/3074916. <https://doi.org/10.34133/2020/3074916>
- Seyum, E. G., Bille, N. H., Abteu, W. G., Munyengwa, N., Bell, J. M., & Cros, D. (2022). Genomic selection in tropical perennial crops and plantation trees: A review. *Molecular Breeding*, 42(10), 58. <https://doi.org/10.1007/s11032-022-01326-4>
- Smart, D. R., Alsina, M. M., Bauerle, T., & Zufferey, V. (2012). Can rootstocks really confer drought tolerance upon grapevine scions? A case study of Merlot on two rootstocks. *ASVO & PGIBSA*. <https://www.researchgate.net/publication/255171708>
- Smart, D. R., Kocsis, L., Walker, M. A., & Stockert, C. (2002). Dormant Buds and Adventitious Root Formation by *Vitis* and Other Woody Plants. *Journal of Plant Growth Regulation*, 21(4), 296–314. <https://doi.org/10.1007/s00344-003-0001-3>
- Smart, D. R., Schwass, E., Lakso, A., & Morano, L. (2006). Grapevine Rooting Patterns: A Comprehensive Analysis and a Review. *American Journal of Enology and Viticulture*, 57(1), 89–104. <https://doi.org/10.5344/ajev.2006.57.1.89>
- Smith, B. P. (2010). *Genetic and molecular mapping studies on a population derived from Vitis vinifera x Muscadinia rotundifolia and genetic diversity of wild Muscadinia rotundifolia* [PhD Thesis, University of California]. University of California, Davis. <https://www.proquest.com/dissertations-theses/genetic-molecular-mapping-studies-on-population/docview/808569602/se-2>
- Smith, B. P., Wheal, M. S., Jones, T. H., Morales, N. B., & Clingeleffer, P. R. (2013). Heritability of adventitious rooting of grapevine dormant canes. *Tree Genetics & Genomes*, 9(2), 467–474. <https://doi.org/10.1007/s11295-012-0570-z>
- Soar, C. J., & Loveys, B. R. (2007). The effect of changing patterns in soil-moisture availability on grapevine root distribution, and viticultural implications for converting full-cover irrigation into a point-source irrigation system. *Australian Journal of Grape and Wine Research*, 13(1), 2–13. <https://doi.org/10.1111/j.1755-0238.2007.tb00066.x>
- SoilWeb. (n.d.). SoilWeb. Retrieved February 25, 2025. <https://casoilresource.lawr.ucdavis.edu/gmap/>
- Song, X., Gao, X., Wu, P., Zhao, X., Zhang, W., Zou, Y., & Siddique, K. H. M. (2020). Drought responses of profile plant-available water and fine-root distributions in apple (*Malus pumila* Mill.) orchards in a loessial, semi-arid, hilly area of China. *Science of The Total Environment*, 723, 137739. <https://doi.org/10.1016/j.scitotenv.2020.137739>
- Swanepoel, J. J., & Southey, J. M. (1989). The Influence of Rootstock on the Rooting Pattern of the Grapevine. *South African Journal of Enology & Viticulture*, 10(1). <https://doi.org/10.21548/10-1-2295>
- Tandonnet, J.-P., Cookson, S. J., Vivin, P., & Ollat, N. (2009). Scion genotype controls biomass allocation and root development in grafted grapevine. *Australian Journal of Grape and Wine Research*, 16(2), 290–300. <https://doi.org/10.1111/j.1755-0238.2009.00090.x>
- Tandonnet, J.-P., Marguerit, E., Cookson, S. J., & Ollat, N. (2018). Genetic architecture of aerial and root traits in field-grown grafted grapevines is largely independent. *Theoretical and Applied Genetics*, 131(4), 903–915. <https://doi.org/10.1007/s00122-017-3046-6>
- Thapa, S. (2022). *Analysis of Root System Architecture and QTL Identification in Grapevines* [Masters Thesis, Missouri State University]. Missouri State University. <https://bearworks.missouristate.edu/theses/3778>
- Thomas, P., Lee, M. M., & Schiefelbein, J. (2003). Molecular identification of proline-rich protein genes induced during root formation in grape (*Vitis vinifera* L.) stem cuttings. *Plant, Cell & Environment*, 26(9), 1497–1504. <https://doi.org/10.1046/j.1365-3040.2003.01071.x>
- Trachsel, S., Kaeppler, S. M., Brown, K. M., & Lynch, J. P. (2013). Maize root growth angles become steeper under low N conditions. *Field Crops Research*, 140, 18–31. <https://doi.org/10.1016/j.fcr.2012.09.010>
- Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, H., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J., Matsumoto, T., Takai, T., Okuno, K., & Yano, M. (2013). Control of root system architecture by *DEEPER ROOTING 1* increases rice yield under drought conditions. *Nature Genetics*, 45(9), 1097–1102. <https://doi.org/10.1038/ng.2725>
- van Leeuwen, C., & Darriet, P. (2016). The Impact of Climate Change on Viticulture and Wine Quality. *Journal of Wine Economics*, 11(1), 150–167. <https://doi.org/10.1017/jwe.2015.21>

- Viana, A. P., de Resende, M. D. V., Riaz, S., & Walker, M. A. (2016). Genome selection in fruit breeding: Application to table grapes. *Scientia Agricola*, 73(2), 142–149. <https://doi.org/10.1590/0103-9016-2014-0323>
- Visscher, P. M., Hill, W. G., & Wray, N. R. (2008). Heritability in the genomics era—Concepts and misconceptions. *Nature Reviews Genetics*, 9(4), 255–266. <https://doi.org/10.1038/nrg2322>
- Waite, H., Whitelaw-Weckert, M., & Torley, P. (2015). Grapevine propagation: principles and methods for the production of high-quality grapevine planting material. *New Zealand Journal of Crop and Horticultural Science*, 43(2), 144–161. <https://doi.org/10.1080/01140671.2014.978340>
- Wells, C. E., & Eissenstat, D. M. (2001). Marked differences in survivorship among apple roots of different diameters. *Ecology*, 82(3), 882–892. [https://doi.org/10.1890/0012-9658\(2001\)082\[0882:MDISAA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0882:MDISAA]2.0.CO;2)
- White, R. G., & Kirkegaard, J. A. (2010). The distribution and abundance of wheat roots in a dense, structured subsoil – implications for water uptake. *Plant, Cell & Environment*, 33(2), 133–148. <https://doi.org/10.1111/j.1365-3040.2009.02059.x>
- Yuan, Y., Bai, M., Ni, P., Li, Y., Chang, X., He, J., Yang, G., & Li, S. (2024). Comparative transcriptome profiling reveals that light coordinates auxin to inhibit adventitious root formation in grapevine. *Horticultural Plant Journal*, 11(4), 1453–1468. <https://doi.org/10.1016/j.hpj.2024.02.003>
- Zhang, L., Marguerit, E., Rossdeutsch, L., Ollat, N., & Gambetta, G. A. (2016). The influence of grapevine rootstocks on scion growth and drought resistance. *Theoretical and Experimental Plant Physiology*, 28(2), 143–157. <https://doi.org/10.1007/s40626-016-0070-x>