

1 **Rootstock choice can dramatically affect grapevine growth**

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3 Zoë Migicovsky^{1*}, Peter Cousins², Lindsay M. Jordan³, Sean Myles¹, Richard Keith Striegler³,
4 Paul Verdegaal⁴, Daniel H. Chitwood^{5,6*}

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6 ¹Department of Plant, Food and Environmental Sciences, Faculty of Agriculture, Dalhousie
7 University, Truro, NS B2N 5E3, Canada

8 ²E. & J. Gallo Winery, Modesto, CA, 95354, USA

9 ³E. & J. Gallo Winery, Acampo, CA 95220, USA

10 ⁴University of California Cooperative Extension, San Joaquin Valley, Stockton, CA, 95206,
11 USA

12 ⁵Department of Horticulture, Michigan State University, East Lansing, Michigan, 48824, USA

13 ⁶Department of Computational Mathematics, Science and Engineering, Michigan State
14 University, East Lansing, Michigan, 48824, USA

15
16 *Corresponding authors: zoe.migicovsky@dal.ca (ZM) and dhchitwood@gmail.com (DHC)

17 **Abstract**

18
19
20 Grape growers use rootstocks to provide protection against pests and pathogens and to modulate
21 viticulture performance such as shoot growth. Our study examined two grapevine varieties
22 (‘Chardonnay’ and ‘Cabernet Sauvignon’) grafted to 15 different rootstocks and determined the
23 effect of rootstocks on eight traits important to viticulture. We assessed the vines across five
24 years and identified both year and variety as contributing strongly to trait variation. However, the
25 effect of rootstock was relatively consistent across years and varieties, explaining between 9%
26 and 10% of the variation in growth-related traits including yield, pruning weight, berry weight,
27 and Ravaz index (yield to pruning weight ratio). Increases in yield due to rootstock were
28 generally the result of increases in berry weight, likely due to increased water uptake by vines
29 grafted to a particular rootstock. We determined that it is possible to achieve an over 50%
30 increase in yield, pruning weight, and Ravaz index by choosing the optimal rootstock, indicating
31 that rootstock choice is crucial for grape growers looking to improve vine performance.

32 **Introduction**

33
34
35 Grafting joins two distinct plant parts: a scion (shoot system) from a donor plant and a rootstock
36 (root system) from a second plant to which the scion is attached. The practice of grafting chiefly
37 enables clonal propagation but can also have many other benefits, such as reducing the juvenility

38 period (increasing precocity) or size (dwarfing) in fruit trees (Webster, 1995; Fazio et al., 2014;
39 Warschefsky et al., 2016).

40

41 In grapevines (*Vitis vinifera* L.), widespread use of grafting began in the late 1800s, following
42 the introduction of phylloxera (*Daktulosphaira vitifoliae* Fitch) to Europe from North America.
43 While *V. vinifera* is highly susceptible to phylloxera, which feeds on the roots of grapevines,
44 eastern North American *Vitis* species evolved in the presence of phylloxera and are tolerant
45 and/or resistant to it. By grafting *V. vinifera* scions to rootstocks of other *Vitis* species, *V. vinifera*
46 could be grown in European soils containing phylloxera, rescuing the wine industry (Ollat et al.,
47 2016).

48

49 Ten years after its detection in Europe, own-rooted (ungrafted) grapevines with phylloxera were
50 first identified in California. The inter-continental spread of the pest was likely due to the
51 importation of vines from European nurseries or from eastern North America (Lider et al., 1995).
52 However, due to the sandy soils of California's Central Valley (or San Joaquin Valley,
53 specifically), phylloxera infections were not as severe and did not require the immediate use of
54 rootstocks (Riaz et al., 2019). By the 1950s, less than 30% of California grapevines were grafted
55 onto phylloxera-resistant rootstocks (Lider, 1959). Still, over time, the California grapevine
56 industry transitioned primarily to grafted vines. Currently, more than 80% of vineyards
57 worldwide grow grafted vines (Ollat et al., 2016).

58

59 In addition to allowing *V. vinifera* vines to grow in phylloxera-infested soils, grapevine
60 rootstocks can provide tolerance to several other damaging pests and diseases including root-
61 knot and dagger nematodes (Cousins and Walker, 2002; Hwang et al., 2010; Ferris et al., 2012).
62 Rootstocks may also be used to improve resilience to abiotic stresses such as salinity (Zhang et
63 al., 2002) and drought (Serra et al., 2014). Grafting grapevines to a particular rootstock can
64 influence a wide range of traits in the scion including mineral composition (Migicovsky et al.,
65 2019), berry chemistry (Cheng et al., 2017), and berry maturation (Walker et al., 2000).

66

67 Of particular interest to grape growers is the observation that rootstock choice can affect vine
68 size and yield (Jones et al., 2009). While an increase in yield is desirable, increasing vine size or

69 vegetative growth also increases the cost of managing the vine, due to additional labour for vine
70 training, pruning, and fruit thinning. An ideal rootstock will increase reproductive growth, or
71 yield, without an accompanying increase in vegetative growth, which is assessed by measuring
72 pruning weight or the amount of one-year-old dormant cuttings removed during the winter. The
73 Ravaz index, or yield divided by pruning weight from the following dormant season, can be
74 calculated to determine the relative ratio of reproductive to vegetative growth.

75
76 With all the potential benefits offered by a rootstock, deciding which one to use is an important
77 choice. While other changes to vineyard management can be made throughout the lifespan of the
78 vines—such as altering irrigation, fertilizer, pesticides, and pruning—rootstock choice is made only
79 once. In this study, we assessed eight traits of viticultural importance across two scion varieties
80 (‘Chardonnay’ and ‘Cabernet Sauvignon’) grafted to 15 different rootstocks. The vines were
81 grafted near Lodi in San Joaquin County, California, in 1992 and evaluated from 1995 to 1999 in
82 order to determine the relative contributions of variety, year, and rootstock to phenotypic
83 variation.

84

85 **Materials and Methods**

86

87 *Experimental design*

88

89 In 1991, dormant field grown rootstocks were planted in a Tokay fine sandy loam soil (UC-
90 Davis, 2019). On April 10th, 1992, scionwood was whip-grafted to the planted rootstock. Rows
91 were oriented east-west with vine spacing of 2.13 m by 3.05 m (Figure S1). The trellis system
92 was a bilateral cordon with fixed foliage wires. The cordon wire was at 1.07 m height with single
93 foliage wire about 40.6 cm above. There were two wires 45.7 cm above the foliage catch wire at
94 either ends of a 63.5 cm cross arm. The vines were cordon trained and spur pruned.

95

96 Prior to vineyard establishment, wine grapes were grown at the site for over 75 years. Initial
97 plantings on this site were ungrafted *V. vinifera* vines. Because of this production history,
98 various pests were considered to be endemic. These included several species of nematodes,
99 phylloxera (*Daktulospharia vitifoliae*), many grape associated viruses, and oak root fungus

100 (*Armillaria mellea*) (Bettiga, 2013). All of these soil pests and pathogens can cause considerable
101 economic losses to growers. For this reason, ungrafted vines were not included as a control in
102 this study.

103 Vines were grafted to the following rootstocks: ‘Freedom’, ‘Ramsey’, ‘1103 Paulsen’, ‘775
104 Paulsen’, ‘110 Richter’, ‘3309 Couderc’, ‘Kober 5BB’, ‘SO4’, ‘Teleki 5C’, ‘101-14 Mgt’, ‘039-
105 16’, ‘140 Ruggeri’, ‘Schwarzman’, ‘420 A’, and ‘K51-32’. The two scion varieties were
106 ‘Chardonnay’ (selection FPS 04) and ‘Cabernet Sauvignon’ (selection FPS 07).

107 The experimental design was a randomized complete block design, split between ‘Chardonnay’
108 and ‘Cabernet Sauvignon’. There were four replications per treatment (rootstock). Each plot
109 consisted of eight or nine vines per plot, except for ‘Kober 5BB’ and ‘SO4’, which had four or
110 five vines each, to fit all treatments in the block. Data were collected for five years from 1995-
111 1999.

112 *Vine management*

113
114 Canopy management practices were consistent with regional guidelines and included shoot
115 thinning and leaf removal. Shoot thinning was performed pre-bloom and consisted of removal of
116 non-count shoots (shoots not originating from spur positions). Leaf removal was performed at
117 berry set only on the north side of the vine. Four to six leaves were removed to open a window in
118 the fruiting zone.

119 Irrigation and vine nutrition programs were standard Best Management Practice (BMP) for the
120 Lodi District. The irrigation strategy followed a moderate Regulated Deficit Irrigation (RDI)
121 program of about 80% estimated crop evapotranspiration losses, from berry set to veraison
122 (Prichard et al., 2004). During the post-harvest period, vineyard irrigation was increased to 100%
123 Etc. The vine nutrition program consisted of the application of approximately 30 lbs of actual
124 nitrogen (N) and 60 lbs of actual potassium (K) per acre at post bloom annually. Zinc (Zn) was
125 applied in some years, as local soils tend to be low in native levels of Zn (Christensen et al.,
126 1978). All irrigation and nutrients were applied through a drip system, comprised of two 0.5 gph
127 emitters per vine.

128

129 *Data collection*

130

131 Prior to harvest, a 100 berry sample was collected for each plot. The berries were counted and
132 weighed to determine average berry weight. Berries were crushed by hand in plastic collection
133 bags, then strained through cheesecloth to provide juice for analysis of soluble solids content
134 (SSC) (°Brix), pH, and titratable acidity (TA) (g/L). Juice samples were titrated to an endpoint of
135 pH 8.2 to determine TA (Amerine and Ough, 1980). SSC was determined by a temperature
136 compensating Atago N1 refractometer and pH was determined using Beckman 200 pH meter
137 with a dual KCl electrode. For each variety, all vines were harvested on the same day (Table S1).
138 The number of clusters per vine and total fruit yield were collected. In late winter, vines were
139 pruned to retain two node fruiting spurs with a target of 50 nodes retained per vine (Table S1).
140 Dormant pruning weights were measured.

141 Weather data from 1994 to 1999 were downloaded from the National Environmental Satellite,
142 Data, and Information Service for Lodi, California, US (USC00045032) on September 30, 2019
143 (Table S2).

144

145 *Statistical analysis*

146

147 We calculated Ravaz index, a measurement of crop load, by dividing yield by pruning weight
148 from the following dormant season. As a result, our dataset consisted of eight traits, measured
149 across five years, for two scion varieties grafted to 15 different rootstocks (Table S3).

150

151 Minimum temperature, maximum temperature, and cumulative precipitation for 1994 to 1999
152 were also visualized (Figure S2).

153

154 The following linear model was evaluated for each phenotype:

155

156 Phenotype ~ Year + Variety + Rootstock + Column + Year x Rootstock + Variety x
157 Rootstock + Year x Variety + Year x Variety x Rootstock

158

159 The model was optimized for each phenotype, which included the removal of the three-way
160 interaction in all cases as well as non-significant two-way interactions. All main effects were
161 retained. The percent variation was calculated for all terms by calculating the Sum of Squares for
162 a particular term, divided by the Total Sum of Squares, then multiplied by 100. The results for
163 significant terms ($p < 0.05$), except column (position in the vineyard), were plotted. We included
164 column in our model to account for variation due to position in the vineyard, but we do not
165 discuss those results here. They are included in our supplemental files and explain up to 10.72%
166 of the variation in a trait (Table S4).

167
168 We visualized phenotype data for ‘Chardonnay’ and ‘Cabernet Sauvignon’ separately using a
169 loess smoothing line to plot variation across years. For the four traits where rootstock explained
170 the largest amount of variation (i.e. yield, berry weight, pruning weight, and Ravaz index),
171 rootstocks were compared using a Tukey Test on the model results. For each phenotype, the raw
172 data and a corresponding boxplot were plotted for each rootstock. To visualize the variety-
173 specific rootstock effects, we plotted the median values (+/- standard deviation) for ‘Cabernet
174 Sauvignon’ and ‘Chardonnay’ separately for each phenotype (Figure S3).

175
176 Since there are large differences between the two grape varieties used in this study, we calculated
177 the correlation between phenotypes for ‘Chardonnay’ and ‘Cabernet Sauvignon’ separately,
178 using a Spearman’s correlation in R v.3.60 (R Core Team, 2019). To correct for multiple testing,
179 p-values within a particular variety were Bonferroni-corrected. Heatmaps were generated using
180 the heatmap.2 function in the gplots R package (Warnes et al., 2016). The order of phenotypes in
181 the heatmap was determined by performing hierarchical clustering using the hclust function with
182 the ward.D2 method on a distance matrix with all phenotype data. Besides the heatmap, all
183 remaining figures were plotted using ggplot2 in R (Wickham, 2016).

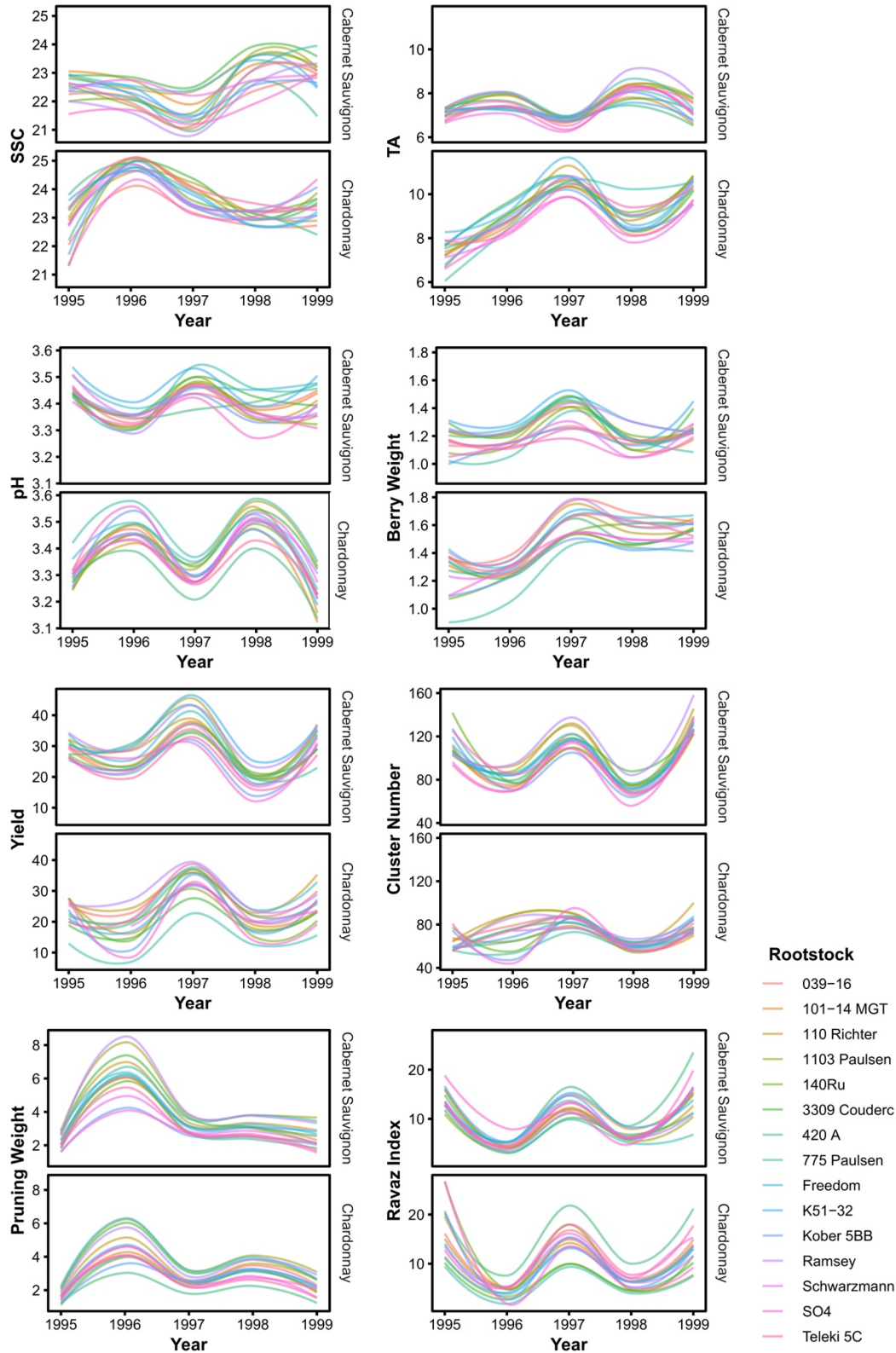
184
185 Lastly, we determined the potential range of variation induced by rootstock choice by calculating
186 the percent change possible from the lowest rootstock median value to the highest rootstock
187 median value within a particular phenotype. These results were visualized with phenotypes
188 ordered from highest to lowest possible percent change.

189

190 **Results**

191

192 There was strong variation in phenotypes across the years of the study, with reduced yield and
193 fewer clusters in 1996 and 1998. Vines generally had higher pruning weights in 1991. However,
194 the relative rankings of the rootstocks were generally consistent across years (Figure 1). We used
195 a linear model to determine which factors described the most variation for each of the 8
196 phenotypes measured (Figure 2).

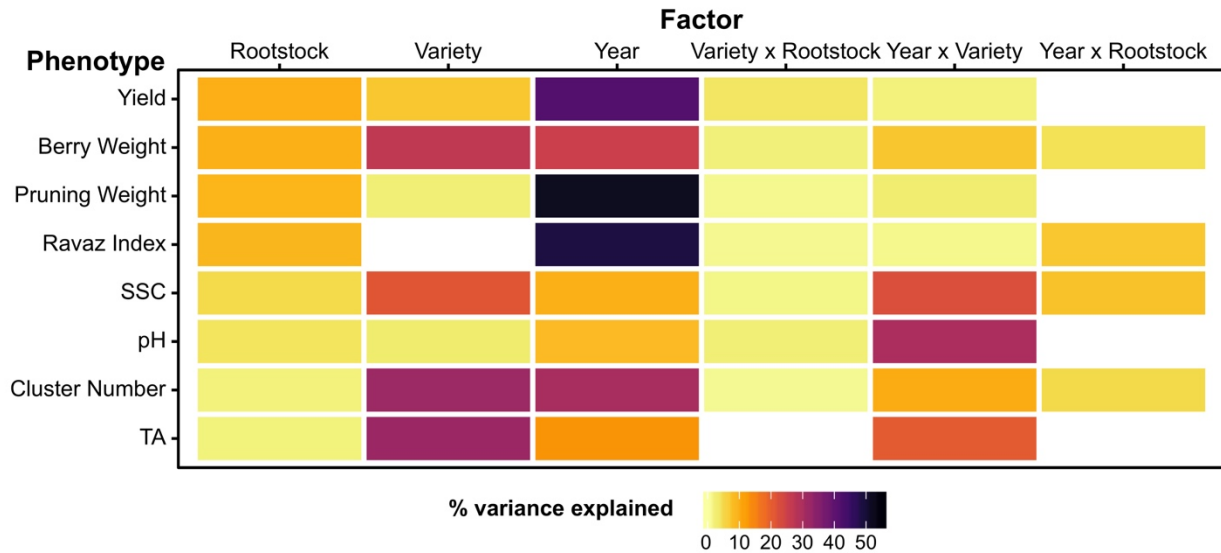


197

198

199

Figure 1. Phenotypic variation across years (1995 to 1999) for each rootstock by scion combination. Loess smoothing lines are plotted.



200
 201 **Figure 2. Phenotypic variation explained by factors of interest estimated using a linear**
 202 **model.** For each phenotype, the linear model was optimized by removing non-significant
 203 interaction effects. For factors which explain a significant amount of variance ($p < 0.05$), the
 204 percent variance explained is indicated using colour. Position in the vineyard (column) was
 205 included in the model but is not plotted. Phenotypes are sorted in order of the most variance
 206 explained by rootstock.

207
 208
 209 The largest source of variation captured by our data was the effect of year, which was a
 210 significant term for all phenotypes, ranging from 8.46% (pH) to 52.08% (pruning weight). Year
 211 explained over 40% of the variation in pruning weight, Ravaz index, and yield.
 212 Variety explained a significant amount of variation in all traits except Ravaz index, with the
 213 strongest effect for TA (32.12%), cluster number (31.98%), berry weight (26.91%), and SSC
 214 (21.32%). The interaction between year and variety was significant for all traits, and over 20% of
 215 the variation in pH, SSC, and TA could be explained by this term.

216
 217 Rootstock had a significant effect on all phenotypes and explained between 9% and 10% of the
 218 variation in yield, berry weight, pruning weight, and Ravaz index. For half the phenotypes
 219 assessed, the interaction between rootstock and year was removed from the model because it did
 220 not explain a significant amount of variation in the trait. For the remaining traits, the interaction
 221 between rootstock and year explained 4.31% to 7.68% of the variation (Figure 2).

222

223

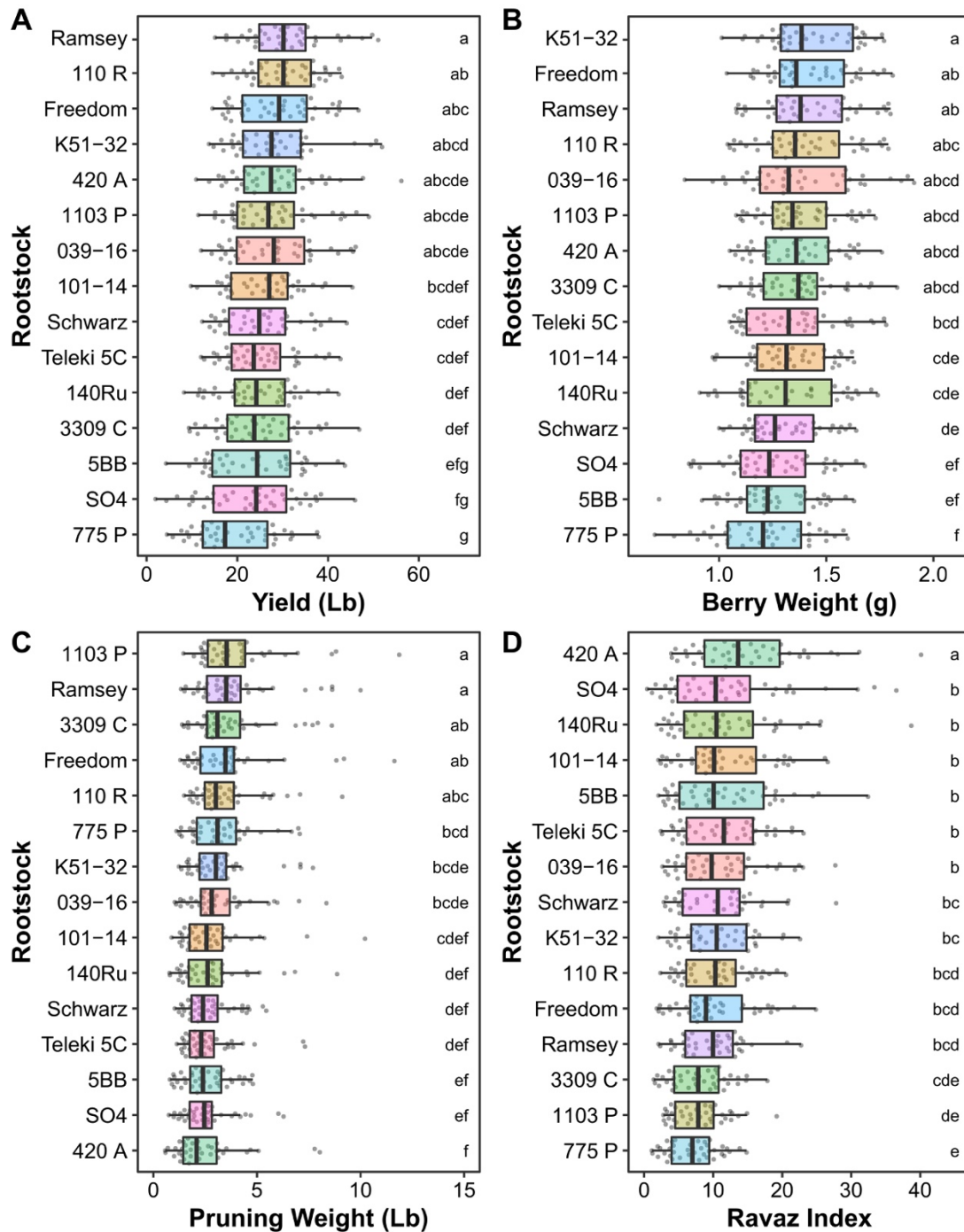
224 While the interaction between variety and rootstock was retained as a significant term for all
225 phenotypes except TA, it explained less than 4% of the variation in any given phenotype.

226

227 Focusing on the phenotypes in which rootstock showed the strongest effect, we plotted the
228 distributions for yield (9.73%), berry weight (9.62%), pruning weight (9.08%), and Ravaz index
229 (9.01%) and compared each of the 15 rootstocks using a Tukey test (Figure 3). Across these
230 phenotypes, ‘Ramsey’ had among the highest yields, berry weights, and pruning weights, and
231 one of the lowest Ravaz indexes. The yield for ‘Ramsey’ was significantly higher than eight of
232 the other rootstocks evaluated. Similarly, ‘Freedom’ ranked within the top four for yield, berry
233 weight, and pruning weight measurements, but ranked 11th for Ravaz index. However,
234 ‘Freedom’ and ‘Ramsey’ were only significantly lower in Ravaz index when compared to ‘420
235 A’, and were significantly higher than ‘3309 C’, ‘1103 P’, and ‘775 P’.

236

237 The roostock ‘775 P’ generally generated the lowest yields and smallest berries, with only ‘SO4’
238 and ‘5BB’ not differing significantly for these two phenotypes. In contrast, ‘775 P’ was ranked
239 6th for pruning weight, which resulted in a significantly lower Ravaz index than all other
240 rootstocks except ‘3309 C’ and ‘1103 P’, although this trend is likely due primarily to the low
241 yield of ‘Chardonnay’ grafted to ‘775 P’ (Figure S3). In comparison, ‘420 A’ ranked 5th for
242 yield and had the lowest pruning weight, thus resulting in a Ravaz index which was significantly
243 higher than all other rootstocks.

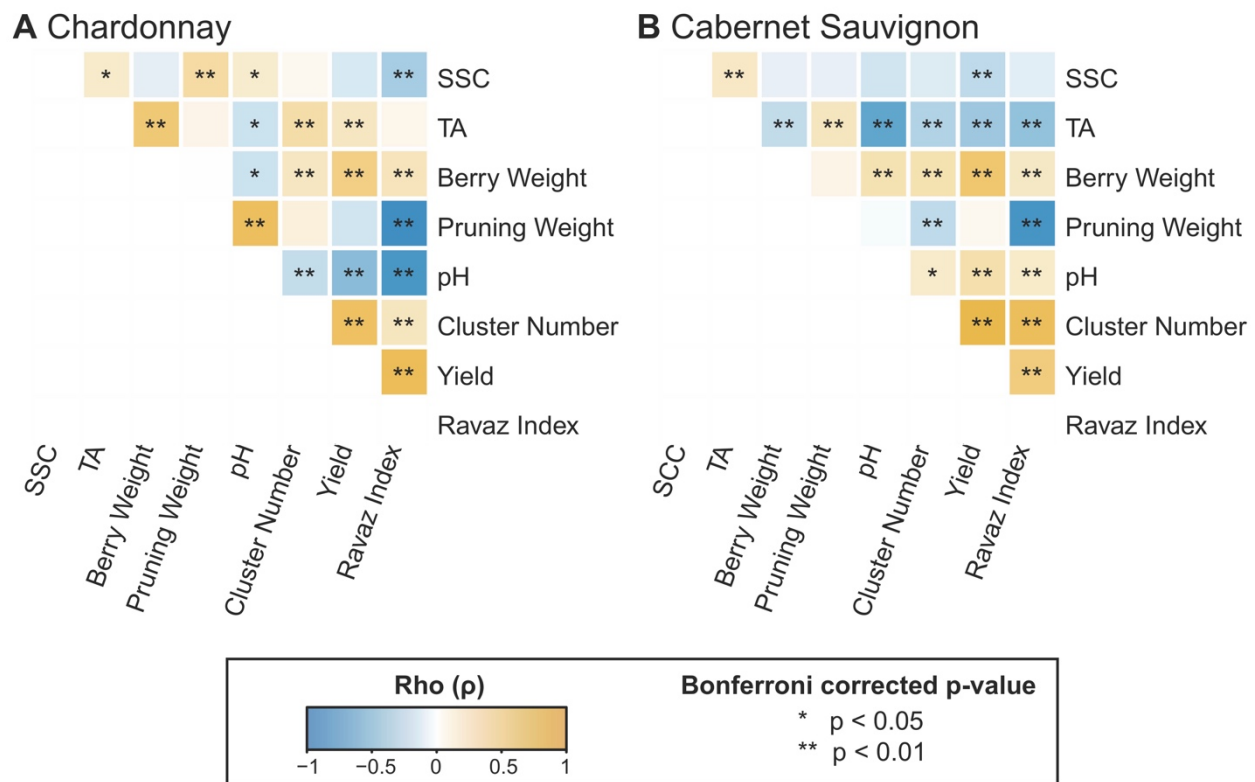


244

245 **Figure 3. Variation in (A) yield, (B) berry weight, (C) pruning weight, and (D) Ravaz index**
 246 **across vines grafted to 15 different rootstocks.** Rootstocks are ordered from highest to lowest
 247 median values. Tukey test results are reported from a linear model accounting for variation in
 248 variety, year, position in the vineyard (column), and interaction effects. Rootstocks with the
 249 same letter (indicated inside the plot) are not significantly different from each other.

250

251 For both ‘Chardonnay’ and ‘Cabernet Sauvignon’, Ravaz index was significantly correlated with
 252 most other phenotypes with the exception of TA (‘Chardonnay’) and SSC (‘Cabernet
 253 Sauvignon’) (Figure 4, Table S5). Ravaz index was positively correlated with cluster number for
 254 ‘Chardonnay’ ($r = 0.250$, $p = 3.847 \times 10^{-4}$) and ‘Cabernet Sauvignon’ ($r = 0.672$, $p < 1 \times 10^{-15}$).
 255 Yield was not significantly correlated with pruning weight for either variety but it was positively
 256 correlated with cluster number (‘Chardonnay’: $r = 0.634$, $p < 1 \times 10^{-15}$; ‘Cabernet Sauvignon’: $r =$
 257 0.726 , $p < 1 \times 10^{-15}$) and berry weight (‘Chardonnay’: $r = 0.489$, $p < 1 \times 10^{-15}$; ‘Cabernet
 258 Sauvignon’: $r = 0.576$, $p < 1 \times 10^{-15}$).
 259
 260

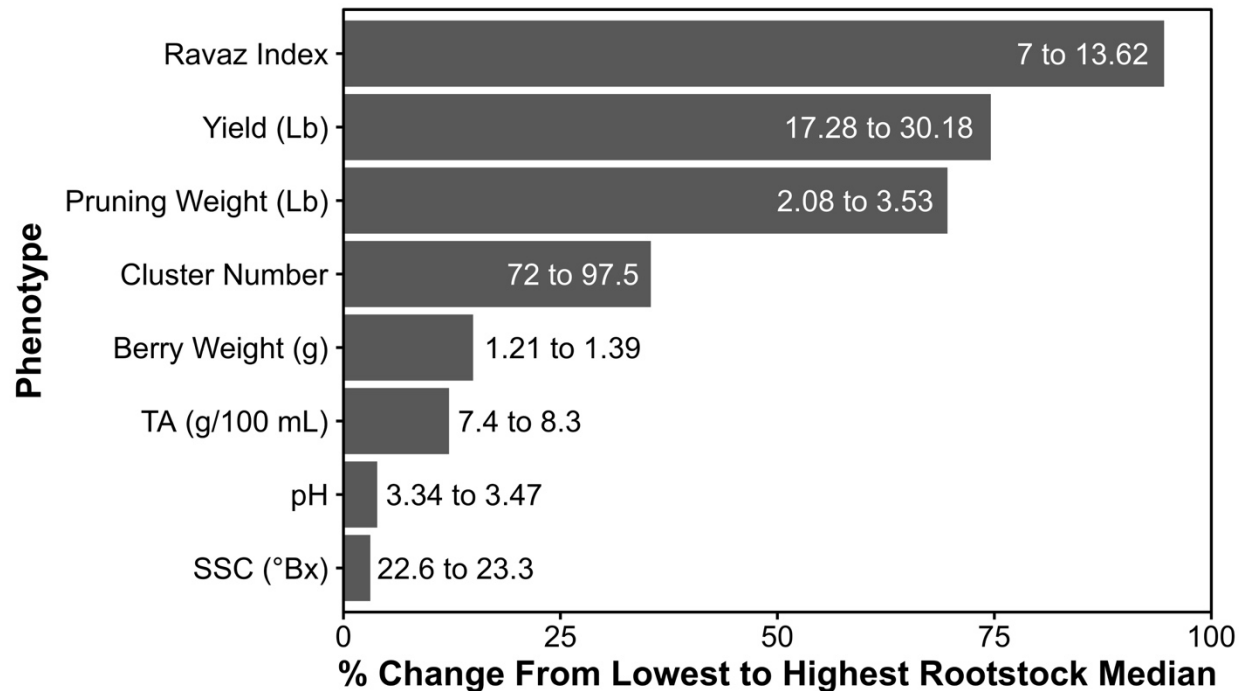


261
 262 **Figure 4. Spearman’s correlations among phenotypes for (A) Chardonnay and (B)**
 263 **Cabernet Sauvignon.** Phenotypes were ordered using hierarchical clustering for all data. P-
 264 values were Bonferroni-corrected for multiple comparisons with a particular variety.
 265

266
 267 Lastly, we evaluated the percent change between the best and worst performing rootstocks for
 268 each phenotype (Figure 5, Table S6). The percent change ranged from 3.10% for SSC to 94.56%

269 for Ravaz index. Cluster number (35.42%), pruning weight (69.6%), and yield (74.59%) all
270 increased by over 30%, while the remaining phenotypes increased by less than 15%.

271



272

273 **Figure 5. Percent change in each phenotype from rootstock with the lowest median to the**
274 **rootstock with the highest median.** Phenotypes are ordered from largest percent change to
275 lowest percent change. Raw values are also listed.

276

277 Discussion

278

279 In California, most wine regions annually receive sufficient rainfall during the dormant season to
280 support desired canopy growth. However, there are years where low dormant season rainfall may
281 reduce canopy growth (Mendez-Costabel et al., 2014). Across the years of this study, vines had
282 lower yield and fewer clusters in 1996 and 1998. Previous work examining ‘Merlot’ vines across
283 two years in California found that soil moisture level during the dormant season impacted both
284 vegetative and reproductive growth, even when irrigation is applied after budbreak (Mendez-
285 Costabel et al., 2014). In our study, there was less rainfall during the 1994 and 1997 dormant
286 seasons when floral initiation would have occurred. While the reduction in yield we observed in
287 1998 may be due to a dry 1997 dormant season, the dormant season prior to 1996 had higher

288 rainfall and it's unclear why the yield was not higher. Previous work also found that the
289 reduction to pruning mass due to dormant season rainfall was more severe than the reduction to
290 yield, increasing the Ravaz index for vines which did not receive rainfall (Mendez-Costabel et
291 al., 2014). In contrast, the years with lower yield in our study had either similar or higher pruning
292 weight values, leading to a decrease in the Ravaz index for those years. Overall, our results
293 confirm that the variable environmental conditions between years, such as access to water during
294 the dormant season, plays a crucial role in plant growth and development. Indeed, year was the
295 largest source of variation in growth-related traits assessed in this study.

296
297 During the growing season, grape growers can use management practices such as irrigation to
298 partly buffer against year-to-year variation (Medrano et al., 2003). The vines in this study were
299 all irrigated using the same management practices across five years, with a moderate RDI
300 program of 80% from berry set to veraison, therefore reducing the impact of weather fluctuations
301 during the growing season. When included in a linear model, variety explained over 20% of the
302 variation we observed for TA, berry weight, and SSC, indicating that there is a strong variety-
303 specific effect on many berry characteristics, which is at least partially due to the developmental
304 stage at which the grapevines were harvested. Year, or vintage, had a significant interaction with
305 variety for all phenotypes and explained over 20% of the variation in berry chemistry
306 measurements such as pH, SSC, and TA. Even with consistent water management, berries from
307 each variety responded differently to environmental conditions. In comparison, for growth
308 measurements such as yield and pruning weight there was less variation explained by year by
309 variety interaction, indicating the years with low or high growth for 'Chardonnay' had a similar
310 impact on 'Cabernet Sauvignon'. Thus, the effect of year on growth was relatively similar across
311 different grapevine varieties, while the effect on berry chemistry differed between varieties.

312
313 In contrast to variety, the effect of rootstock rarely varied across years: the interaction between
314 rootstock and year explained less than 8% of the variation for any phenotype. In addition, we
315 found that the effect of a rootstock was generally consistent between 'Chardonnay' and
316 'Cabernet Sauvignon'. This suggests that grape growers should place great emphasis on
317 rootstock choice as a critical decision during vineyard planning as performance of one rootstock,
318 relative to others, is generally consistent over time and between varieties.

319

320 The choice of rootstock is particularly important for growth-related traits such as yield, pruning
321 weight, berry size, and Ravaz index, where rootstock effects explained at least 9% of the
322 variation. In contrast to our study, previous work examining nine grape varieties grown
323 ungrafted and grafted to four different rootstocks found that yield and berry weight were not
324 affected by rootstock. However, similar to our work, the study identified that vine and yield
325 components were more responsive to rootstock than fruit composition variables (Reynolds and
326 Wardle, 2001). Our results are also consistent with previous work identifying a significant
327 difference in yield, pruning weight, and berry weight of ‘Shiraz’ vines grafted to different
328 rootstocks and measured across six years (Jones et al., 2009).

329

330 In long-lived perennial plants where significant year-to-year variation can occur, the collection
331 of data across multiple years is a valuable tool for untangling the effect of environment. By
332 evaluating the vines in this study across five years, we were able to account for the variation due
333 to year in our model and determine how much of the variation was due to rootstock. Similarly, a
334 recent seven year study examined ‘Cabernet Sauvignon’ grafted to three different rootstocks
335 (‘*Riparia*’, ‘101-14 Mgt’, and ‘420 A’). The study found no significant effect of rootstock on
336 pruning weight, although yield and berry weight did differ significantly (Hickey et al., 2016).
337 When comparing the rootstocks which overlapped with our study, the authors found similar
338 results: ‘101-14 Mgt’ and ‘420 A’ did not differ significantly for yield and berry weight, but ‘420
339 A’ had a significantly higher Ravaz index (Hickey et al., 2016). Another study that measured
340 ‘Cabernet Sauvignon’ grafted to three different rootstocks across 25 years also found that Ravaz
341 index was significantly affected by rootstock choice, but only after 7 years of planting. Similarly,
342 yields across rootstocks only differed after 15 years (Ollat et al., 2003). Although we detect
343 variation in vines which have only been planted for three to eight years, our dataset includes a
344 much broader representation of rootstocks. Given that grapevines may remain in the ground for
345 at least 20 years, additional long term studies are needed in order to determine how the effect of
346 rootstocks differs over time.

347

348 Generally, rootstocks resulting in large values of one growth-related phenotype also resulted in
349 large measures of other growth-related phenotypes. For example, rootstocks that generated

350 higher yields generally also produced larger berries. While cluster number was more highly
351 correlated with yield than berry weight, much more variation in berry weight could be explained
352 by rootstock, indicating that increased yields due to rootstock were primarily a result of
353 increased berry weight and not additional clusters. This suggests that rootstock choice does not
354 influence floral initiation, but rather influences water uptake, which leads to variation in berry
355 weight. While high yields are generally desirable, the ratio of skin-to-pulp is an important
356 consideration for vinification, and this ratio is reduced when berries take on more water.
357 Previous work also demonstrated that in addition to decreasing fruit size, reducing water in
358 ‘Cabernet Sauvignon’ increased desirable characteristics such as the concentrations of skin
359 tannin and anthocyanins (Roby et al., 2004). Therefore, while the use of a rootstock to increase
360 yields is beneficial, this has to be balanced with ensuring that the berries maintain a desirable
361 size, possibly through a reduction in irrigation for more vigorous rootstocks.

362

363 While increased reproductive growth leading to increased yields is economically beneficial, if
364 the vegetative growth increases at the same rate, the Ravaz index, or crop load, of the vine will
365 remain consistent. Increased vegetative growth results in higher vine management costs, such as
366 pruning and leaf thinning. We demonstrated that Ravaz index was correlated with most of the
367 other phenotypes we measured. This suggests that the balance between reproductive and
368 vegetative growth in a vine is associated with many other characteristics of that vine. However,
369 pruning weight and yield were not correlated, likely because all vines were pruned to a similar
370 size and shoot number to prevent overcropping, but the number of clusters per shoot differed. As
371 a result, higher yields were positively correlated with both berry weight and cluster number, but
372 the strengths of these correlations indicate that the primary source of increased yield was more
373 clusters and not larger berries. In some instances, therefore, rootstock choice may increase
374 reproductive growth of a vine without an increase in vegetative growth and its associated costs.

375

376 It is likely that much of the variation in growth that can be attributed to rootstock in our study is
377 due to increased water uptake by vines grafted to certain rootstocks. Variation in water uptake is
378 generally the result of some combination of water uptake efficiency, the size and surface area of
379 the root system, and stomatal regulation to reduce water loss, among other factors (Serra et al.,
380 2014). For example, ‘Ramsey’ and ‘Freedom’ generally had high yields, large berries, and high

381 pruning weights. Similarly, in an Australia study, ‘Shiraz’ vines grown with irrigation and
382 grafted to ‘Ramsey’ or ‘Freedom’ rootstocks yielded more fruit than ungrafted vines and than
383 vines grafted on the other five rootstock varieties assessed, indicating that these rootstocks tend
384 to increase yield and pruning weight (Mccarthy et al., 1997). Other work found a rootstock-
385 dependent effect of irrigation on some yield components such as cluster number and berry
386 weight, but not on yield itself (Stevens et al., 2010). In our study, all vines were irrigated equally,
387 which may have lead to a rootstock-specific effect on water uptake which ultimately contributed
388 to variation in yield and could be further controlled with rootstock-specific irrigation regimes.

389
390 In addition to variation water uptake, it is possible some variation in growth is due to variation in
391 disease resistance. While phylloxera is a concern in the region, all vines were grafted to
392 rootstocks which should provide protection. Additionally, there is the potential for grapevine
393 fanleaf virus at this site. One of the key symptoms of fanleaf degeneration is a decrease in fruit
394 set which leads to a lower yield (Walker et al., 1994). Given that only vines grafted to ‘039-16’
395 would have fanleaf protection in this study, and the yield of vines grafted to ‘039-16’ is not
396 significantly higher than other rootstocks which do not offer protection, indicating that it is likely
397 not a severe concern in this vineyard. Thus, while there may be some variation in rootstock
398 tolerance to other pests and pathogens, this is unlikely to be a major factor in this study.

399
400 Lastly, we determined that the choice of one rootstock over another has little effect on berry
401 chemistry, but can result in nearly a two-fold difference in growth-related traits like yield, Ravaz
402 index and pruning weight. Increasing yield, especially during the early years of production, can
403 have a dramatic influence on the profitability of a vineyard and the results of this study clearly
404 indicate that selection of the right rootstock is a valuable tool that grape growers can use to help
405 control vine size and yield. These results should be taken into account when considering which
406 rootstock to select, particularly in the San Joaquin Valley where this study was performed.
407 Future work can explore if the early advantage provided by rootstock is maintained throughout
408 the life of a vineyard.

409
410
411

412 **Supplemental Data**

413

414 **Figure S1. Vineyard map of rootstock evaluation trial**

415

416 **Figure S2. Variation in maximum temperature (°F), minimum temperature (°F) and**
417 **cumulative precipitation (inches) measured from January 1994 to December 1999.**

418

419 **Figure S3. Median values (+/- standard deviation) for each phenotype for ‘Chardonnay’**
420 **and ‘Cabernet Sauvignon’ grafted to each rootstock.**

421

422 **Table S1. Harvest and pruning dates for ‘Chardonnay’ and ‘Cabernet Sauvignon’ vines**
423 **sampled from 1995-1999.**

424

425 **Table S2. Weather data from 1994 to 1999 downloaded from the National Environmental**
426 **Satellite, Data, and Information Service for Lodi, California, US (USC00045032) on**
427 **September 30, 2019.**

428

429 **Table S3. Phenotype data collected from 1994 to 1995 for ‘Chardonnay’ and ‘Cabernet**
430 **Sauvignon’ vines grafted to 15 different rootstocks.**

431

432 **Table S4. Linear model results for each phenotype.** Each model was optimized for each
433 phenotype: the main effects were retained in all cases but non-significant interactions were
434 removed.

435

436 **Table S5. Results of Spearman’s correlation between phenotypes for ‘Chardonnay’ and**
437 **‘Cabernet Sauvignon’.** P-values were Bonferroni-corrected for comparison within each variety.

438

439 **Table S6. Variation across phenotypes based on median rootstock values.** The maximum
440 median, minimum median, average median are included as well as the maximum percent change
441 (from minimum to maximum median) and average percent change across rootstocks.

442

443 **Conflicts of interest**

444

445 The authors declare that they have no conflicts of interest.

446

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448

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454

455 **Authors' Contributions**

456

457 PV conceived this work and led the collection of the data. LMJ organized the data. ZM analyzed
458 the data and wrote the manuscript. PC, SM, and DHC provided feedback in data analysis and
459 interpreting the results. PC, RKS, and DHC provided project oversight and guidance. All authors
460 reviewed the manuscript.

461

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463

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