Rootstock choice can dramatically affect grapevine growth

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Abstract

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

Introduction

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

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

39   Warschefsky et al., 2016).

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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

3

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, wines 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
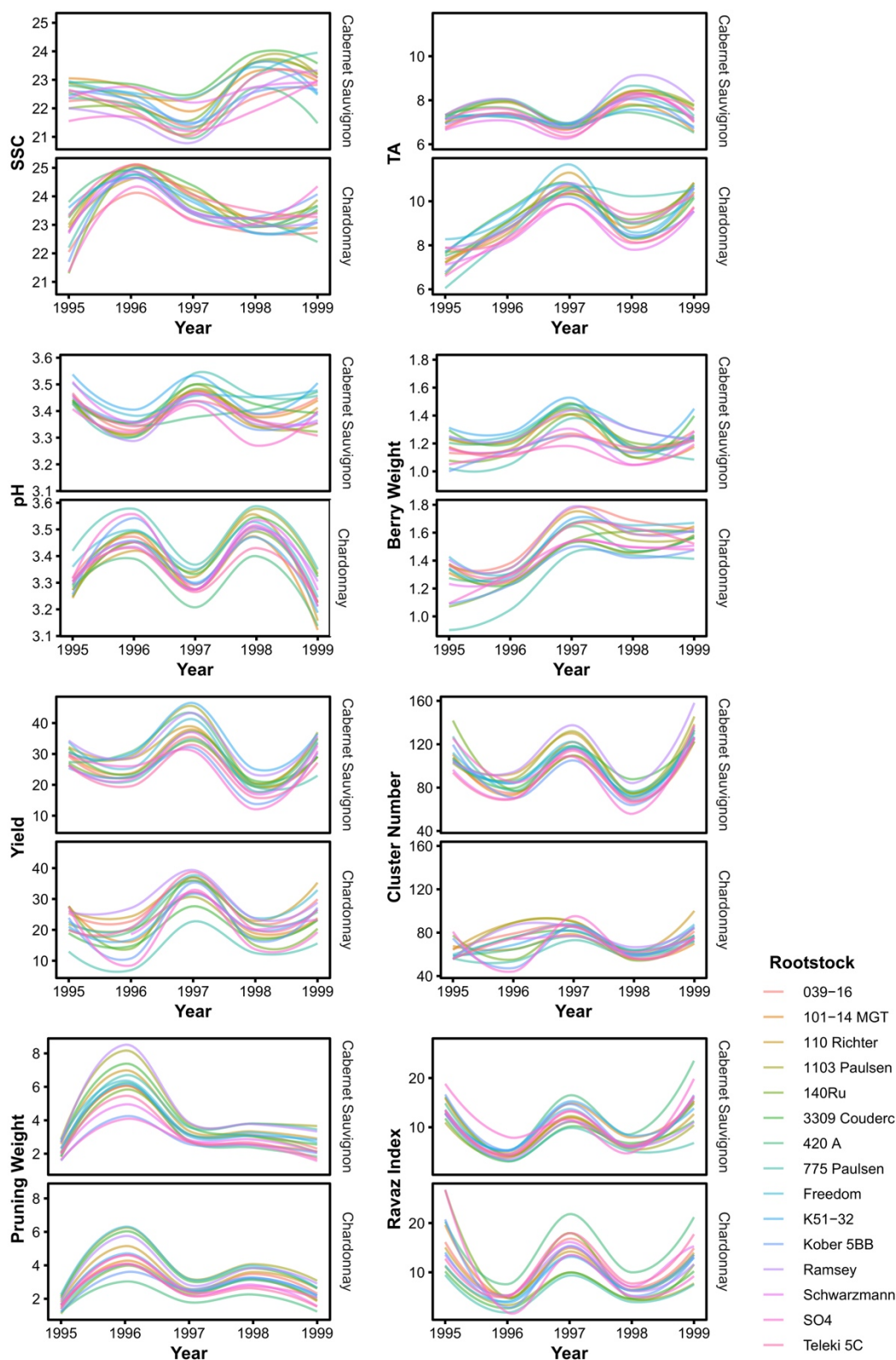
196 phenotypes measured (Figure 2).

Figure 1. Phenotypic variation across years (1995 to 1999) for each rootstock by scion combination. Loess smoothing lines are plotted.
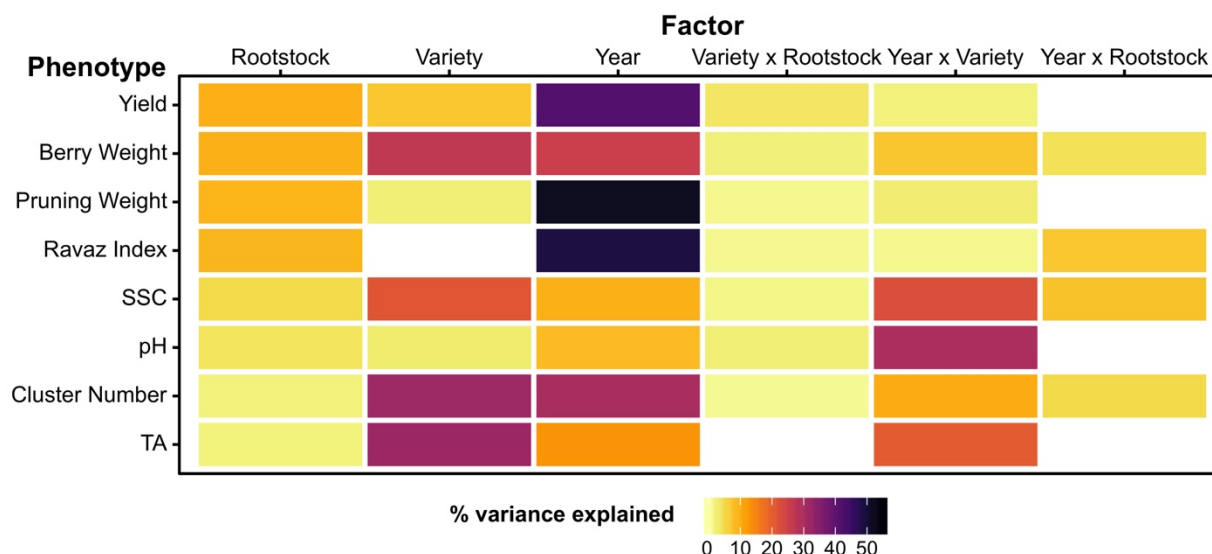
Figure 2. Phenotypic variation explained by factors of interest estimated using a linear model. For each phenotype, the linear model was optimized by removing non-significant interaction effects. For factors which explain a significant amount of variance (p < 0.05), the percent variance explained is indicated using colour. Position in the vineyard (column) was included in the model but is not plotted. Phenotypes are sorted in order of the most variance explained by rootstock.

The largest source of variation captured by our data was the effect of year, which was a significant term for all phenotypes, ranging from 8.46% (pH) to 52.08% (pruning weight). Year explained over 40% of the variation in pruning weight, Ravaz index, and yield.

Variety explained a significant amount of variation in all traits except Ravaz index, with the strongest effect for TA (32.12%), cluster number (31.98%), berry weight (26.91%), and SSC (21.32%). The interaction between year and variety was significant for all traits, and over 20% of the variation in pH, SSC, and TA could be explained by this term.

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

9

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
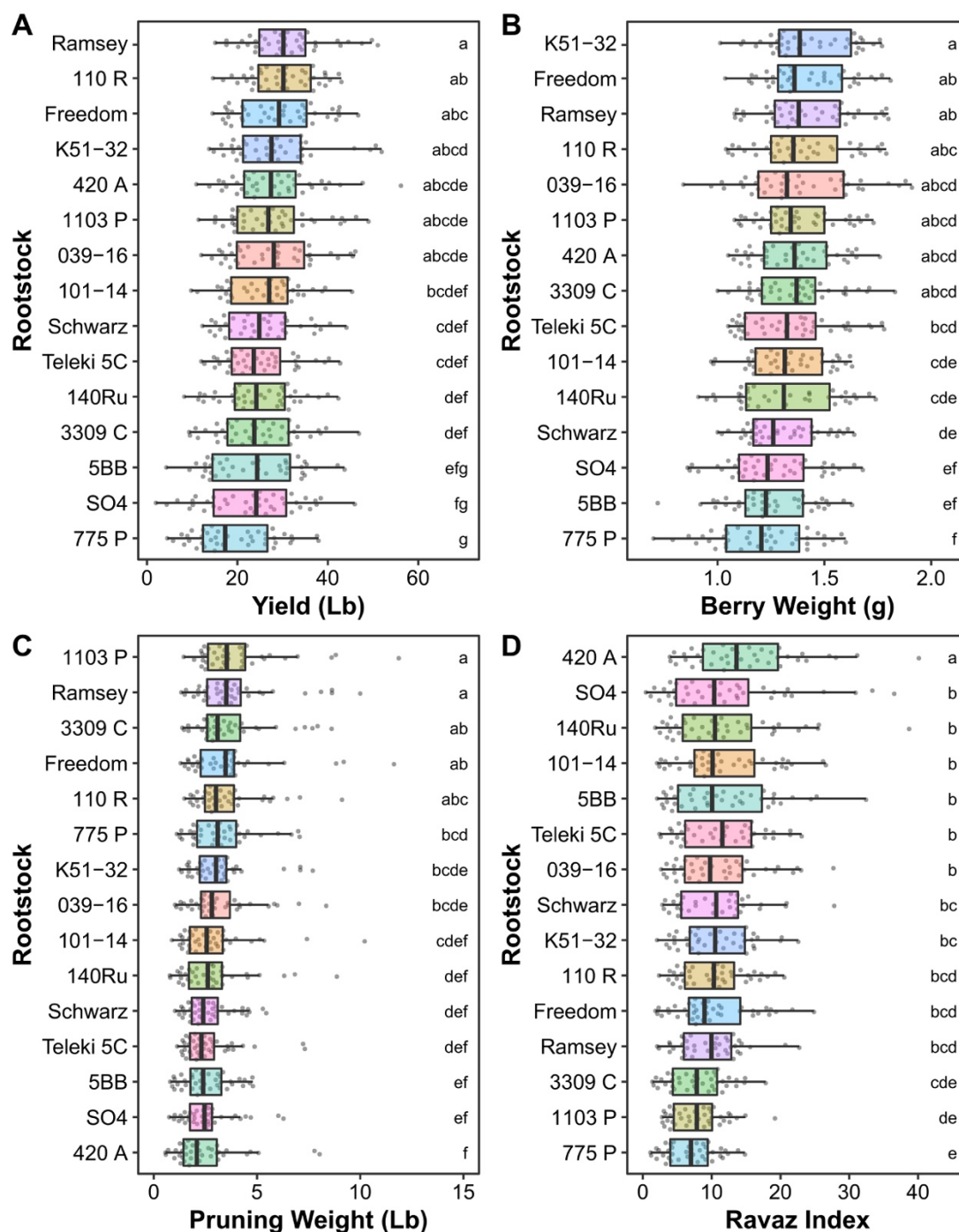
243   higher than all other rootstocks.

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

11

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

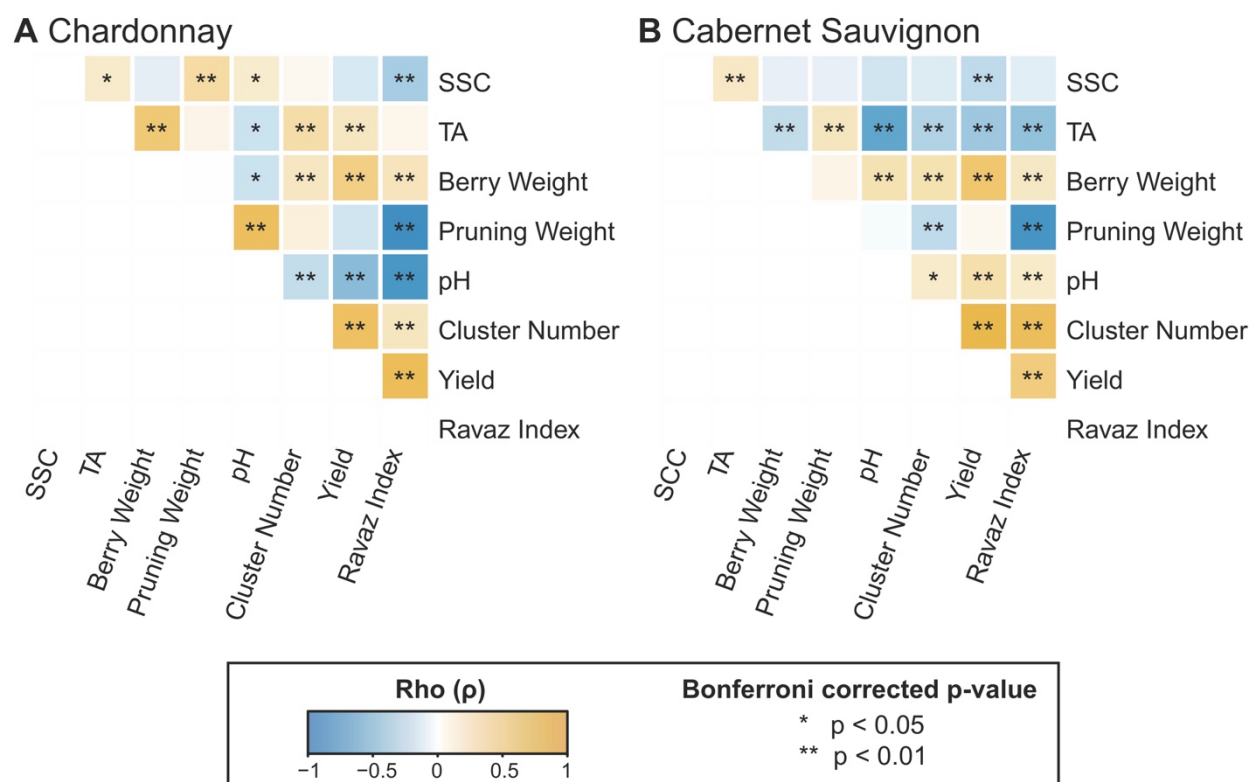258   Sauvignon': $r = 0.576$, $p < 1 \times 10^{-15}$).

259

260

Figure 4. Spearman's correlations among phenotypes for (A) Chardonnay and (B) Cabernet Sauvignon. Phenotypes were ordered using hierarchical clustering for all data. P-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%.
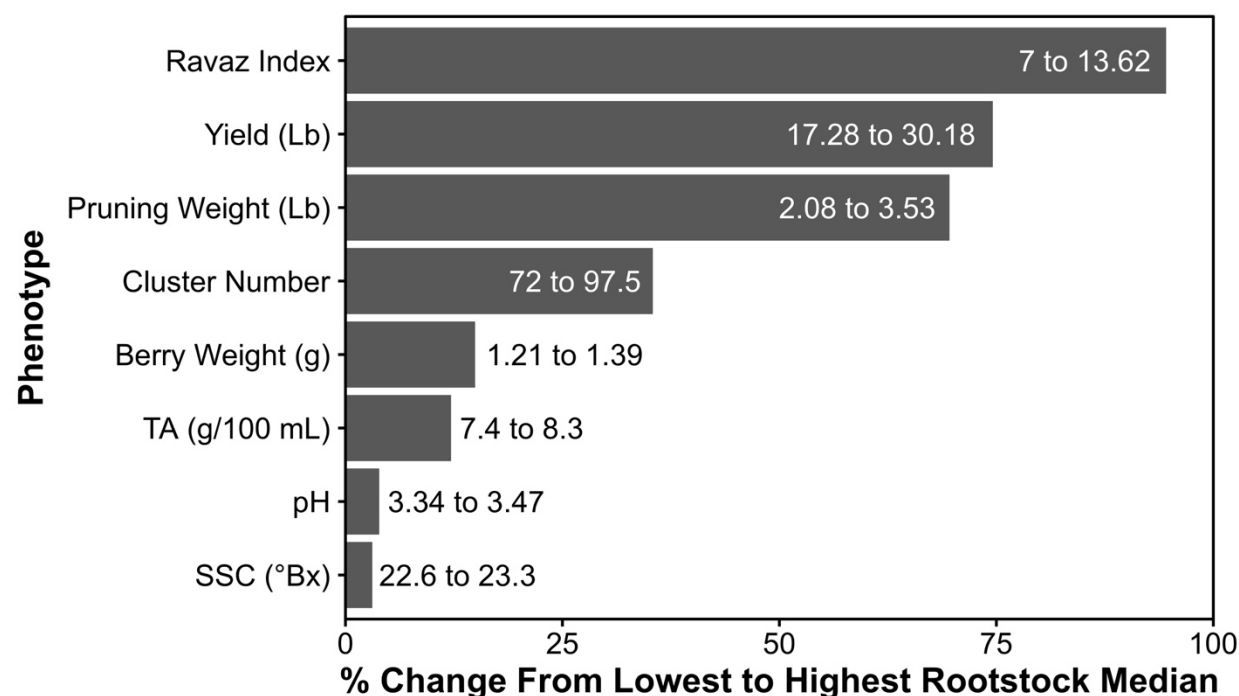
271

272

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

276

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

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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.

14

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

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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 roostock 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.

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Supplemental Data

Figure S1. Vineyard map of rootstock evaluation trial

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

Figure S3. Median values (+/- standard deviation) for each phenotype for 'Chardonnay' and 'Cabernet Sauvignon' grafted to each rootstock.

Table S1. Harvest and pruning dates for 'Chardonnay' and 'Cabernet Sauvignon' vines sampled from 1995-1999.

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

Table S3. Phenotype data collected from 1994 to 1995 for 'Chardonnay' and 'Cabernet Sauvignon' vines grafted to 15 different rootstocks.

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

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

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

Conflicts of interest

The authors declare that they have no conflicts of interest.

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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.

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