Effect of Preveraison Water Deficits on the Yield Components of 15 Winegrape Cultivars

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Effect of Preveraison Water Deficits on the Yield Components of 15 Winegrape Cultivars

Alexander D. Levin, 1,2* Mark A. Matthews, 3 and Larry E. Williams 3, 4

Abstract: Accurate information regarding crop reproductive development and yield formation in response to water deficits is needed for informed vineyard irrigation management decisions, particularly when water supply is limiting. Fifteen red wine grape cultivars grown in the San Joaquin Valley of California were subjected to two regulated deficit irrigation (RDI) treatments for four years to determine yield component responses to water deficits (no applied water) preveraison (ED) and postveraison (LD). In the fifth year, the cultivars were kept well-watered to determine carryover effects. In the first four years, early water deficits (ED) consistently and significantly reduced yields compared to the control (sustained deficit, SD; applied water at 50% of estimated crop evapotranspiration (ETc) throughout the growing season) across all years and cultivars, but the late (postveraison) deficit (LD) treatment vines were not different from the control. The reduction in yield with ED was primarily due to a significant reduction in berry fresh weight (FW) and clusters per vine, with little change in berries per cluster. Neither flowers per cluster nor percent berry set were affected by the treatments, although flowers per cluster varied significantly among cultivars. Berries per cluster increased linearly with flowers per cluster until saturation at ~150 berries per cluster as percent berry set declined at ~250 flowers per cluster. In the fifth year, yields of the two RDI treatments recovered somewhat because of increases in berry FW and a small, but significant, increase in clusters per vine. These results show that berry size, because of a reduction in FW, is the most sensitive yield component to water deficits, followed by clusters per vine and berries per cluster, with sensitivity maximum preveraison and few differences among cultivars.

Key words: grape yield, regulated deficit irrigation, yield components

Reproductive development of grapevine (Vitis vinifera L.) occurs over the course of two seasons, as with most woody perennials (Mullins et al. 1992). Consequently, yield at harvest is the product of various yield components (e.g., clusters per vine, berries per cluster, and berry fresh weight [FW]), whose development can be either directly or indirectly affected by cultural practices (e.g., pruning and irrigation) (Freeman et al. 1979, Matthews and Anderson 1989, Williams et al. 2010b) or environmental conditions (e.g., light and temperature) (Buttrose 1969, Sanchez and Dokoozlian 2005). Thus, changing cultural practices or environmental conditions during key stages of reproductive development for each yield component can have an adverse effect on yield and ultimate vineyard profitability.

The number of clusters per vine and potential cluster size are determined in the year prior to harvest with the initiation of inflorescence primordia in latent buds following anthesis in the current growing season (Mullins et al. 1992). The percentage of latent buds with inflorescence primordia (i.e., bud fruitfulness) increases to a maximum near veraison (Williams 2000). Following the initiation of an inflorescence primordium, differentiation of flower primordium takes place prior and just subsequent to budbreak the following year (Mullins et al. 1992). During inflorescence development, aspects of the vine’s environment such as temperature, light intensity, and water status have been shown to both positively and negatively affect bud fruitfulness (Matthews and Anderson 1989, Sanchez and Dokoozlian 2005, Williams et al. 2010b, Uriarte et al. 2015).

Water deficits during floral initiation the year prior to anthesis have been shown to reduce both the number of clusters per vine and the number of flowers per inflorescence (i.e., flowers per cluster) the following year (Matthews and Anderson 1989, Dayer et al. 2013, Uriarte et al. 2015). Matthews and Anderson (1989) demonstrated that flower development and, subsequently,
the number of berries per cluster of Cabernet franc, was dependent on vine water status before veraison. Moreover, the authors show that berries per cluster was the yield component most responsive to water deficits after berry FW. Conversely, Santesteban et al. (2011) and Williams et al. (2010b) show that clusters per vine was the yield component most responsive to water deficits early in the season. Thus, early season (preveraison) water deficits can inhibit reproductive development, but it is unclear which yield component is most sensitive. Genotypic differences play a large role in bud fruitfulness, with a high degree of variability in fruitfulness and, ultimately, in yield among cultivars (Sanchez and Dokoozlian 2005, Keller et al. 2012). Therefore, it is possible that the sensitivity of yield components to water deficits depends on cultivar.

To evaluate the interactive effects of cultivar and water deficits on reproductive development, this study capitalized on an established cultivar trial and was conducted over a five-year period coinciding with the most recent regional drought cycle. Deficit irrigation treatments were applied for the first four years of the study to impose equivalent water deficits during two phenological periods—pre- or postveraison—to the same vines in each year. To evaluate carryover effects, vines were kept well watered in the fifth year. Two hypotheses were tested in this study: (1) that clusters per vine is more sensitive to water deficits than berries per cluster, and (2) that the sensitivity of reproductive development and yield formation to water deficits is cultivar dependent.

Materials and Methods

Experimental vineyard site and management. The experimental vineyard site used in this study was an existing cultivar trial planted with 1103 Paulsen (Vitis berlandieri × Vitis rupestris) rootstock in June 2003 at the University of California Kearney Agricultural Research and Extension Center near Parlier, California (36°48′N; 119°30′W). Twenty red wine grape cultivars were field grafted in May 2004. Detailed descriptions of the vineyard site, soil type, design, and plant materials (e.g., source of budwood and clone) have been previously reported (Levin et al. 2019).

Irrigation treatments. Every year before berry set, all vines were irrigated at 100% of estimated crop evapotranspiration (ETc) to maintain midday leaf water potential (Ψl) at or above -1.0 MPa. After berry set, irrigation treatments were imposed once Ψl reached the threshold value of -1.0 MPa (averaged across cultivars). Three irrigation treatments were imposed from 2012 to 2015: late deficit (LD): irrigated at 100% of estimated ETc from berry set until the onset of ripening (veraison), with no water applied from veraison until harvest; sustained deficit (SD; control): irrigated at 50% of estimated ETc throughout the entire growing season; and early deficit (ED): no applied water from berry set until veraison, irrigated at 50% of estimated ETc from veraison until harvest.

In 2016, LD and ED plots were irrigated at 100% of estimated ETc from berry set until harvest to evaluate potential carryover effects of the deficit irrigation treatments on reproductive development. The SD plots remained unchanged and were irrigated as described above.

Drip emitters were plugged or unplugged to impose the irrigation treatments, and inline water meters were used to quantify applied water amounts. Anthesis, berry set, and veraison were determined by visual ratings and time points defined as 50% cap fall, 50% berry set (berry size ~1 to 2 mm in diameter), and 50% cluster coloration, respectively. After harvest, all vines were irrigated at 50% of estimated ETc until leaf fall. Methods for vineyard ETc estimation and irrigation scheduling are given in a related study (Levin et al. 2019).

Vine water status measurements. Vine water status (midday leaf water potential; Ψl) was measured periodically throughout the growing season as described in Levin et al. (2019). Briefly, Ψl measurements were taken using a pressure chamber on fully expanded sunlit leaves between 1230 and 1330 hr, Pacific Daylight Time. A single leaf per plot was measured and used for data analysis. There were 9, 12, 11, 7, and 16 preveraison measurements, and 22, 8, 10, 1, and 8 postveraison measurement dates in 2012, 2013, 2014, 2015, and 2016, respectively.

Soil water content measurements. In 2015, volumetric soil water content (SWC) was measured in the Cabernet Sauvignon-SD plots at budbreak (24 March). SWC was measured at four depths: 0.3, 0.6, 0.9, and 1.2 m; and at three distances from the vine trunk into the alley: 0.35, 0.75, and 1.5 m. The soil was augered to the appropriate depth and samples were taken with a Soil Conservation Service “Madera” soil sampler. Samples were then brought back to the laboratory, weighed, dried at 75°C for 72 hrs, then weighed again. SWC was calculated as the difference between dry and fresh samples relative to the sample volume.

Harvest protocol and determination of yield components. In 2012 and 2015, all cultivars and treatments were harvested at the same time (11 to 12 Oct and 9 Sept, respectively). In 2013, 2014, and 2016, fruit across cultivars and irrigation treatments was harvested at commercial maturity (24 Brix). Berry FW at harvest was determined the day prior to harvest each year. Samples were taken from both sides of the canopy. Berry samples were 150 berries per plot in 2012 and 2013 and 50 berries per plot in 2014, 2015, and 2016.

Vine yield was recorded as the average of the three-vine plots. Berries per vine was estimated as the quotient of the plot average vine yield and plot average berry FW. Clusters per vine were counted at harvest in 2013, 2014, 2015, and 2016, and cluster FW was estimated as the quotient of the plot average vine yield and plot average clusters per vine. Berries per cluster was estimated as the quotient of the plot average cluster FW and plot average berry FW.

Prior to anthesis in 2014 and 2015, select cultivars were chosen that had a broad range of berries/cluster (from 2013 data) for the determination of percent berry set. Cultivars chosen in 2014 were Cabernet Sauvignon, Malbec, Refosco, Tempranillo, and Tinta Madeira; while those in 2015 were Cabernet Sauvignon, Petit Verdot, Refosco, Tannat, Tempranillo, and Tinta Madeira. Two representative inflorescences were selected and flagged in each plot, and flowers were visually counted by hand in the field on the first branch of the main axis of each inflorescence. The number of flowers on...
the primary branch has been shown to be highly correlated with total number of flowers per inflorescence (Bennett et al. 2005). After berry set, the number of berries was counted on the flagged branches, and percent berry set was calculated as the proportion of counted berries to counted flowers. Percent berry set was assumed to be the same for the whole cluster. The average percent berry set for the two clusters per plot was assumed to be representative for the whole plot.

**Experimental design and data analyses.** The experimental design was a randomized complete block design with a split-block factorial treatment structure and four replications of three vines per replicate (n = 4). Details on the field design and treatment structure are given in Levin et al. (2019). All statistical analyses and graphics were done using R statistical software (ver. 3.6; www.R-project.org), and the critical significance level was designated as α = 0.05. Linear models were fit with the `lmer()` function from the package `lme4` (Kuznetsova et al. 2017), and all analysis of variance (ANOVA) were conducted using the `anova()` function. For soil water content analysis, the two-way ANOVA included depth and distance from vines (and their interaction) as fixed factors. For vine water status analysis, all `Ψl` measurement dates were first binned into pre- and postveraison data sets. Three-way ANOVAs were conducted for each data set separately with cultivar, irrigation treatment, and year (and all interactions) as fixed factors. For yield and yield component analyses, three-way ANOVAs were conducted with cultivar, irrigation treatment, and year (and all interactions) as fixed factors. Data were transformed as needed to meet assumptions of ANOVA, thus back-transformed data and standard errors are reported. Estimated marginal means (i.e., least-squares means) were computed using the `emmeans()` function in the `emmeans` package (Lenth 2019). Multiplicity adjustments for p values of pairwise comparisons between means were made using the Tukey method. For responses of percent berry set and berries per cluster to flowers per cluster, regression analyses were conducted using the functions `lm()` and `nls()` from the base R package `stats`.

### Results

**Environmental conditions, applied water amounts, soil water content, and vine water status.** Across all five years of the study, accumulated growing degree days (GDD) and reference ET (ET₀) remained relatively stable year-to-year, while rainfall was much more variable (Table 1). The across-year coefficients of variation (CV) for GDD and ET₀ were 5% and 2%, respectively, although both variables were higher than their 30-year averages in each year—particularly for GDD in 2014 and 2015. In contrast to the stable evaporative conditions among years, variability in total rainfall among years was high (CV = 50%) and was even more variable during the dormant season (CV = 71%). As is typical for the region, a majority of the rainfall occurred during the dormant season (58 to 85% of the total), with the exception of 2012, in which only 36% of the total occurred during the dormant season.

Irrigation commenced on 31, 13, 15, 11, and 23 May in 2012, 2013, 2014, 2015, and 2016, respectively. Termination of irrigation for LD plots occurred on 17, 8, 14, and 6 July in 2012, 2013, 2014, and 2015, respectively. Initiation of irrigation for ED plots occurred on 25, 8, and 12 July, and 26 June in 2012, 2013, 2014, and 2015, respectively. Vines in the SD and LD treatments received more water compared to ED in each year except 2016, when LD and ED vines were irrigated at 100% ET₀ all season long (Table 1). From 2012 to 2015, ED vines received 234 to 306 mm (28 to 40% ET₀), SD vines received 351 to 461 mm (52 to 60% ET₀), and LD vines received 349 to 528 mm (43 to 63% ET₀). At budbreak in 2015, SWC was lowest 1.2 m below the soil surface, increased towards 0.6 m, and then decreased slightly towards 0.3 m (Figure 1). The average SWC (± 1 standard error; SE) measured in the top 1.8 m² transect of soil was 13.8 ± 0.6 v/v, and in the top 0.68 m² transect it was 16.5 ± 0.9 v/v.

The irrigation treatments consistently and significantly influenced midday leaf water potential (Ψ₇) in each year of the study (Table 2). From 2012 to 2015, the treatments established three levels of vine water status preveraison and two levels postveraison. In 2016, when LD and ED vines were irrigated

<table>
<thead>
<tr>
<th>Year</th>
<th>GDD (mm)</th>
<th>ET₀ (mm)</th>
<th>ET₉ (mm)</th>
<th>Dormant (mm)</th>
<th>Growing (mm)</th>
<th>Total (mm)</th>
<th>LD (mm)</th>
<th>SD (mm)</th>
<th>ED (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>2671 (105)</td>
<td>1185 (101)</td>
<td>769</td>
<td>62</td>
<td>110</td>
<td>172 (68)</td>
<td>383</td>
<td>461</td>
<td>306</td>
</tr>
<tr>
<td>2013</td>
<td>2732 (108)</td>
<td>1202 (102)</td>
<td>816</td>
<td>110</td>
<td>20</td>
<td>130 (46)</td>
<td>447</td>
<td>438</td>
<td>240</td>
</tr>
<tr>
<td>2014</td>
<td>2990 (118)</td>
<td>1255 (107)</td>
<td>841</td>
<td>80</td>
<td>57</td>
<td>137 (46)</td>
<td>528</td>
<td>444</td>
<td>234</td>
</tr>
<tr>
<td>2015</td>
<td>2904 (114)</td>
<td>1210 (103)</td>
<td>813</td>
<td>54</td>
<td>28</td>
<td>82 (27)</td>
<td>349</td>
<td>421</td>
<td>301</td>
</tr>
<tr>
<td>2016</td>
<td>2758 (109)</td>
<td>1244 (106)</td>
<td>833</td>
<td>245</td>
<td>54</td>
<td>299 (99)</td>
<td>702</td>
<td>351</td>
<td>702</td>
</tr>
</tbody>
</table>

*LD, late deficit: irrigated at 100% of estimated crop evapotranspiration (ET₀) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated ET₀ throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated ET₀ from veraison until harvest.

Am. J. Enol. Vitic. 71:3 (2020)
at 100% of estimated ET, there were no significant differences among the treatments preveraison, and small significant differences postveraison driven by a reduction in SD vine \(\Psi_l\). There was a strong, significant main effect of cultivar in both time periods, but no significant interactions between cultivar and treatment or cultivar and year. Accordingly, mean \(\Psi_l\) ranged ~0.23 to 0.24 MPa across all cultivars during each phenological time period, but with broad overlapping confidence intervals (Supplemental Table 1).

**Yield and yield components ANOVAs.** ANOVAs on the large data set that included 15 cultivars and three irrigation treatments over four to five years resulted in many highly statistically significant main and interaction effects for each tested variable (Table 3). There were strong, significant year effects across all variables with the exception of the three-way interaction for clusters per vine \((p = 0.092)\). In general, the relative magnitude of \(F\) values and associated significance tests for yield and berry FW trended together, whereas those results for clusters per vine and berries per vine ANOVAs were different. There were large treatment effects on yield and berry FW, and the cultivar main effect was larger on berry FW than on yield. However, the cultivar-by-treatment interaction terms for both yield and berry FW trended together. Clusters per vine was strongly affected by treatment and less so by cultivar, while berries per cluster was strongly affected by cultivar and less so by treatment.

**Yield.** Yields ranged more than ten-fold from 3.9 tons/ha for the Syrah-ED treatment in 2015 to 39.6 tons/ha for Cinsault-LD treatment in 2012 (Figure 2). Yields generally increased to their highest values in 2013, then decreased to their lowest values in 2015, before increasing slightly in 2016. Yields were highest for Cinsault, Grenache, and Refosco, and lowest for Malbec, Syrah, and Freisa.

Yields were significantly reduced by 35 to 45% in ED vines compared to SD vines in each year except 2016 when averaged across cultivars. In contrast, there were no significant differences in yield between LD vines and SD vines in each year, although yields were slightly lower in LD vines in 2015. Results were similar when cultivars were analyzed individually—many statistically significant differences \((p < 0.05)\) between ED and SD vines in most years and few differences between LD and SD vines (Supplemental Table 2). In 2016, there were few significant differences in yield between either ED and SD or LD and SD vines across all cultivars, although it is notable that yields of SD vines were 15% higher than in 2015.

**Table 2** Midday leaf water potential (\(\Psi_l\)) for vines subjected to different irrigation treatments in each season of the study. Data are treatment means \((\pm 1\ SE)\) for samples taken preveraison and postveraison (averaged across cultivars). Means within a column for each year followed by a different letter are significantly different at \(p < 0.05\). Analysis of variance (ANOVA) results for each time period are given below.

<table>
<thead>
<tr>
<th>Year/treatment</th>
<th>Preveraison</th>
<th>Postveraison</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>-0.95 ± 0.04 a</td>
<td>-1.57 ± 0.04 b</td>
</tr>
<tr>
<td>SD</td>
<td>-1.25 ± 0.04 b</td>
<td>-1.43 ± 0.05 a</td>
</tr>
<tr>
<td>ED</td>
<td>-1.62 ± 0.04 c</td>
<td>~b</td>
</tr>
<tr>
<td>2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>-0.96 ± 0.04 a</td>
<td>-1.69 ± 0.02 b</td>
</tr>
<tr>
<td>SD</td>
<td>-1.27 ± 0.04 b</td>
<td>-1.51 ± 0.02 a</td>
</tr>
<tr>
<td>ED</td>
<td>-1.60 ± 0.04 c</td>
<td>-1.48 ± 0.02 a</td>
</tr>
<tr>
<td>2014</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>-1.02 ± 0.04 a</td>
<td>-1.62 ± 0.02 b</td>
</tr>
<tr>
<td>SD</td>
<td>-1.29 ± 0.04 b</td>
<td>-1.38 ± 0.02 a</td>
</tr>
<tr>
<td>ED</td>
<td>-1.64 ± 0.04 c</td>
<td>-1.42 ± 0.02 a</td>
</tr>
<tr>
<td>2015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>-0.99 ± 0.04 a</td>
<td>-1.81 ± 0.05 b</td>
</tr>
<tr>
<td>SD</td>
<td>-1.12 ± 0.04 b</td>
<td>-1.35 ± 0.05 a</td>
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<tr>
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<td>-1.46 ± 0.04 c</td>
<td>-1.29 ± 0.05 a</td>
</tr>
<tr>
<td>2016</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>-1.07 ± 0.06 a</td>
<td>-1.06 ± 0.04 a</td>
</tr>
<tr>
<td>SD</td>
<td>-1.16 ± 0.06 a</td>
<td>-1.21 ± 0.04 b</td>
</tr>
<tr>
<td>ED</td>
<td>-1.05 ± 0.07 a</td>
<td>-0.95 ± 0.06 a</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Term</th>
<th>F-value</th>
<th>(Pr(&gt;F))</th>
<th>F-value</th>
<th>(Pr(&gt;F))</th>
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<tr>
<td>Cultivar</td>
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<td>&lt;0.001</td>
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<td>0.002</td>
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<tr>
<td>Treatment</td>
<td>153.0</td>
<td>&lt;0.001</td>
<td>56.10</td>
<td>&lt;0.001</td>
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<td>Year</td>
<td>4.45</td>
<td>0.023</td>
<td>25.30</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(C\times T)</td>
<td>1.10</td>
<td>0.320</td>
<td>0.709</td>
<td>0.885</td>
</tr>
<tr>
<td>(C\times Y)</td>
<td>0.977</td>
<td>0.526</td>
<td>0.912</td>
<td>0.658</td>
</tr>
<tr>
<td>(T\times Y)</td>
<td>10.40</td>
<td>&lt;0.001</td>
<td>13.40</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(C\times T\times Y)</td>
<td>0.535</td>
<td>1.000</td>
<td>0.645</td>
<td>0.996</td>
</tr>
</tbody>
</table>

\(a\)LD, late deficit: irrigated at 100% of estimated crop evapotranspiration (ET\(_c\)) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated ET\(_c\) throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated ET\(_c\) from veraison until harvest.

\(b\)Data not collected.

\(c\)Vines were irrigated at 100% ET\(_c\) all season long.
Berry FW. Berry FW ranged more than six-fold from 0.64 g for Durif-LD in 2015 to 3.94 g for Cinsault-ED in 2016 (Figure 3). Berry FW trends followed the same pattern as was observed for vine yield. Berry FW was highest for Cinsault, Montepulciano, and Refosco, and lowest for Petit Verdot, Tannat, and Durif. It should be noted that the grand mean berry FW for Cinsault was 50% (0.95 g) larger than the next highest mean berry FW (Montepulciano).

Treatment differences in berry FW also followed the same trends as for vine yields when cultivars were analyzed individually: large, significant differences between ED and SD vines for most cultivars, but almost no significant differences between LD and SD vines for any cultivar during that same period (Supplemental Table 3). Berry FW was significantly reduced by 21 to 36% in ED vines compared to SD vines in each year except 2016 when averaged across cultivars. In contrast, berry FW was only significantly different between LD and SD vines in 2015 when it was reduced by 23% in LD vines. Finally, berry FW of SD vines was 17% higher in 2016 relative to 2015, but differences between the two years were only statistically significant for about half of the cultivars. There were few differences in berry FW between either ED and SD or LD and SD vines across all cultivars in 2016.

Clusters per vine. The number of clusters per vine ranged approximately three-fold from 24 clusters per vine for the Syrah-ED irrigation treatment in 2015 to 74 clusters per vine for the Petit Verdot LD irrigation treatment in 2013 (Figure 4). Clusters per vine decreased from 2013 to 2015, before increasing slightly (although significantly) in 2016. Clusters per vine was highest in Petit Verdot, Cabernet Sauvignon, and Montepulciano, and was lowest in Freisa, Syrah, and Malbec.

Clusters per vine were significantly reduced by 11 to 22% in ED vines compared to SD vines in each year except 2016 when averaged across cultivars. In contrast, there were no significant differences in clusters per vine between LD and SD vines in each year. When cultivars were analyzed individually, there were few significant differences in clusters per vine between ED and SD vines from 2012 to 2015, and there were almost no significant differences in clusters per vine between LD and SD vines for any cultivar except for Tinta Madeira and Freisa) during that same period (Supplemental Table 4). Finally, while there were similarly few significant differences in clusters per vine between either ED and SD or LD and SD vines for most cultivars in 2016, the aforementioned significant increase in clusters per vine from 2015 to 2016 was driven by that of ED vines (p < 0.001).

Berries per cluster. Berries per cluster ranged more than three-fold from 69 berries per cluster for the Malbec-ED irrigation treatment in 2015 to 226 berries per cluster for the Tannat-SD irrigation treatment in 2013 (Figure 5). Berries per cluster decreased significantly from 2013 to 2015 and did not change from 2015 to 2016. Berries per cluster was highest in Tannat, Durif, and Grenache, while it was lowest in Malbec, Touriga Nacional, and Cinsault.

Averaged across cultivars, berries per cluster was not significantly affected by the irrigation treatments in any year, and only varied 7% among treatments and years. Similarly, there were few significant differences in berries per cluster between ED and SD vines from 2012 to 2015 for individual cultivars, and there were almost no significant differences in berries per cluster between LD and SD vines for any cultivar during that same period (Supplemental Table 5). In 2016, there were similarly few significant differences in berries per cluster between either ED and SD or LD and SD vines for most cultivars, and there was no change from 2015 in any treatment.

Flowers per cluster and percent berry set. Flowers per cluster ranged more than four-fold from 116 to more than 550 across years, cultivars, and treatments. Percent berry set similarly ranged almost three-fold from ~29% to more than 76% across years, cultivars, and treatments. Although there was a highly significant main effect of cultivar on flowers per cluster and percent berry set (p < 0.001) across years, there was no significant irrigation treatment effect for either variable.

There were significant nonlinear relationships between berries per cluster and flowers per cluster, as well as between percent berry set and flowers per cluster (Figure 6). Berries per cluster increased linearly with increasing flowers per cluster up to ~250 flowers per cluster, then saturated at ~150 berries per cluster (Figure 6A). The asymptote (± 1 SE) of the sigmoidal function fit to the data was estimated to be 153 ± 5 berries per cluster.

Conversely, percent berry set generally decreased with increasing flowers per cluster (Figure 6B). Although there were few data points below 250 flowers per cluster, there was a large degree of vertical scatter in the data at low flower numbers. A simple linear regression analysis of percent berry set on flowers per cluster using the constrained

<p>| Table 3 Analysis of variance results (F and p values) for four response variables. Significance level was α = 0.05. FW, fresh weight. |
|---|---|---|---|---|---|---|---|---|</p>
<table>
<thead>
<tr>
<th>Source</th>
<th>Yield</th>
<th>Berry FW</th>
<th>Clusters/ vine</th>
<th>Berries/cluster</th>
<th>Yield</th>
<th>Berry FW</th>
<th>Clusters/ vine</th>
<th>Berries/cluster</th>
</tr>
</thead>
<tbody>
<tr>
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Am. J. Enol. Vitic. 71:3 (2020)
data set of points below 250 flowers per cluster resulted in a nonsignificant slope, but a highly significant intercept of $63 \pm 12\% \ (p < 0.001)$.

**Sensitivity of yield components to water deficits.** Berry FW was the yield component most sensitive to water deficits, followed by clusters per vine, and then berries per cluster—and this effect was most pronounced before veraison (Figure 7). On average, berry FW was reduced by preveraison water deficits from 19 to 35% calculated across cultivars, although some reductions were greater for an individual cultivar (data not shown). Conversely, postveraison water deficits had little effect on berry FW in each year, except in 2015 when it was significantly reduced by more than 20%. Preveraison water deficits also significantly reduced clusters per vine, although by a relatively smaller degree compared to reductions of berry FW. Clusters per vine were reduced from 11 to 20% across cultivars from 2012 to 2015. Similar to berry FW, postveraison water deficits had a minimal effect on clusters per vine with no significant differences from zero. Finally, berries per cluster changed little with pre- or postveraison

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**Figure 2**  Response of yield (tons/ha) to irrigation treatments in each year of the study. Cultivar panels are arranged in order from top-left to bottom-right by their grand mean yield value. LD, SD, and ED refer to the different irrigation treatments: LD, late deficit: irrigated at 100% of estimated crop evapotranspiration (ETc) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated ETc throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated ETc from veraison until harvest.
water deficits relative to the control, ranging ± 10% across cultivars, treatments, and years.

**Discussion**

Across 15 cultivars and five years spanning the most recent drought cycle, it was found that the development of clusters per vine was more sensitive to water deficits compared to berries per cluster—supporting the first hypothesis—but the sensitivity was not cultivar dependent, rejecting the second hypothesis. Overall, berry FW was the most sensitive yield component in response to water deficits such that sensitivity of response was ordered thusly: berry FW > clusters per vine > berries per cluster. However, the sensitivity of berry FW and clusters per vine to water deficits was limited to the preveraison period. Conversely, berries per cluster changed little through the study period, despite large fluctuations in vine water status during the growing season as well as in winter rainfall during the dormant season. As a consequence, yield was strongly influenced by berry FW and clusters per vine, and preveraison water deficits reduced yield over multiple seasons by reducing berry FW in the current season and inhibiting development of clusters per vine for the following season.

**Yield and berry FW.** Vine yield responded similarly to the irrigation treatments across cultivars and years from 2012 to 2015, with consistently large reductions in yield due to

![Figure 3](image_url)

*Figure 3* Response of berry fresh weight (FW) at harvest (g/berry) to irrigation treatments in each year of the study. Data are mean values ± 1 SE (n = 3 to 4). Cultivar panels are arranged in order from top-left to bottom-right by their grand mean yield value. LD, SD, and ED refer to the different irrigation treatments: LD, late deficit: irrigated at 105% of estimated crop evapotranspiration (ETc) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated ETc throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated ETc from veraison until harvest. Data not collected for Cinsault in 2012.
preveraison water deficits that reduced berry size together with clusters per vine. In contrast, postveraison water deficits during that time had an inconsistent effect on final yield across cultivars and years. There was a strong seasonal yield response as well, with yields generally declining from high to low from 2012 to 2013, to 2015.

When comparing preveraison and postveraison water deficit effects on yield, the reduction of yield due to preveraison water deficits is the most consistent observation in the literature despite relatively variable preveraison weather conditions (Matthews and Anderson 1989, Williams et al. 1994, Romero et al. 2010, Santesteban et al. 2011, Junquera et al. 2012, Intrigliolo et al. 2012, Uriarte et al. 2015). In contrast, previously reported effects of postveraison water deficits on yield are inconsistent, with yields either lower (Junquera et al. 2012), the same (Matthews and Anderson 1989), or even higher (Intrigliolo et al. 2012), compared to well-watered controls. Furthermore, there were substantial interyear inconsistencies of yield responses to postveraison water deficits within the aforementioned studies, despite relatively stable interyear weather conditions late in the season. Similar interyear inconsistencies among LD yields were found in this study.

Figure 4 Response of clusters per vine to irrigation treatments from 2013 to 2016. Data are mean values ± 1 SE (n = 3 to 4). Cultivar panels are arranged in order from top-left to bottom-right by their grand mean clusters per vine value. LD, SD, and ED refer to the different irrigation treatments: LD, late deficit: irrigated at 100% of estimated crop evapotranspiration (ETc) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated ETc throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated ETc from veraison until harvest.
Berry FW was more responsive to the irrigation treatments across all years and cultivars, and it largely drove the differences in vine yield. In addition, berry FW response to the irrigation treatments was more consistent and less variable than that of berries per vine (the product of clusters per vine and berries per cluster) across years and cultivars. Berry FW is highly sensitive to vine water deficits—particularly between anthesis and veraison—which limit berry growth through reduced cell enlargement in the berry mesocarp (Matthews and Anderson 1989, Ojeda et al. 2001), whereas postveraison water deficits have a more limited effect on berry growth, due to the shift in water source at veraison from xylem to phloem (Greenspan et al. 1994). Accordingly, berries grown on vines subjected to postveraison water deficits often have a similar FW to that of the controls (Matthews and Anderson 1989, Castellarin et al. 2007).

In this study, preveraison water deficits of $\Psi_l < -1.3$ MPa in ED vines consistently and significantly reduced berry FW relative to the SD and LD irrigation treatments for many cultivars, which ultimately reduced their final yield. By comparison,

**Figure 5** Response of berries per cluster to irrigation treatments from 2013 to 2016. Data are mean values ± 1 SE (n = 3 to 4). Cultivar panels are arranged in order from top-left to bottom-right by their grand mean berries per cluster value. LD, SD, and ED refer to the different irrigation treatments: LD, late deficit: irrigated at 100% of estimated crop evapotranspiration ($ET_c$) from berry set until the onset of ripening (veraison); no water was applied from veraison until harvest. SD (control): irrigated at 50% of estimated $ET_c$ throughout the entire growing season. ED: no applied water from berry set until veraison; irrigated at 50% of estimated $ET_c$ from veraison until harvest.
berry FW (and ultimately yield) was less affected by the LD treatment, with few significant differences among cultivars between SD and LD vines. It should be noted that without well-watered vines postveraison, interpretation is made more difficult considering that this may have somewhat limited the maximum potential yield and berry FW. However, as mentioned above, several other studies that included a well-watered control have shown limited to no effects of postveraison water deficits. The results of this study indicate that the potential to maximize yield across all cultivars is greatest before veraison by avoiding water deficits of $\Psi_l < -1.3$ MPa.

Sensitivity of clusters per vine versus berries per cluster. In addition to reducing berry FW, preveraison water deficits also reduced yield through a reduction in clusters per vine that drove the overall reduction in total berries per vine. In contrast, berries per cluster did not respond strongly to the irrigation treatments, despite the treatments’ strong impact on vine water status both pre- and postveraison. Finally, the lack of any significant differences among cultivars in response sensitivity to pre- or postveraison water deficits for either yield component provides evidence that these traits are under tight genetic control and that this control is highly conserved across $V. vinifera$ L. cultivars.

Temporally, inflorescence (cluster) primordia must be induced in the bud prior to any differentiation of floral primordia, and this occurs mid-summer between anthesis and veraison (Williams 2000). Accordingly, clusters per vine response to water deficits was only observed preveraison, during primordia development, with reductions in clusters per vine due to preveraison water deficits but little effect due to postveraison water deficits. The significant reductions in clusters per vine were observed in ED vines (relative to SD vines) whose preveraison $\Psi_l$ averaged -1.5 to -1.6 MPa. This suggests that preveraison water deficits of $\Psi_l \leq -1.5$ MPa are significant enough to disrupt development of cluster primordia in the bud. On the other hand, the lack of differences in clusters per vine between LD and SD vines suggests that inhibition of cluster primordia development is likely unaffected at preveraison water deficits down to $\Psi_l = -1.3$ MPa and that severe postveraison water deficits ($\Psi_l << -1.3$ MPa) do not affect primordia development at all, presumably because this process is completed by veraison. Therefore, an average preveraison vine water status of $\Psi_l = -1.3$ MPa may be considered a preliminary critical value below which bud fruitfulness is negatively affected.

The inhibition of cluster primordia development under the water deficits in this study is more likely due to changes in shoot carbon partitioning as opposed to simple shoot growth inhibition. In general, plant cell expansive growth is more sensitive to water deficits compared to net photosynthesis (Hsiao 1973). However, while grapevine shoot elongation is
typically inhibited at $\Psi_l = -1.0$ MPa (Schultz and Matthews 1988, Williams et al. 2010a), net photosynthesis is only reduced by 9% (Williams 2012b). However, at $\Psi_l = -1.3$ MPa, Williams (2012b) showed that net photosynthetic rate was reduced by 49%, and at $\Psi_l = -1.5$ MPa, it was reduced by 94%. Recently, a water deficit-induced inhibition of photosynthesis was reported to negatively affect floral differentiation (Dayer et al. 2013). Thus, the inhibition of cluster primordia development—as inferred from the reduction in clusters per vine—in ED vines relative to SD vines and the lack of differences in clusters per vine between LD and SD vines—can be at least partially explained by a change in the carbon economy of the developing shoot.

There is some disagreement in the literature about whether clusters per vine or berries per cluster is more sensitive to water deficit, although this may have been due to cultivar, rootstock, and/or site differences across studies. For example, Matthews and Anderson (1989) and Keller et al. (2016) showed that berries per cluster was more sensitive to water deficits compared to clusters per vine in Napa-grown Cabernet franc (grafted) and in eastern Washington-grown Cabernet Sauvignon (own-rooted), respectively. In contrast, Williams (2010) showed that clusters per vine is more sensitive to water deficits in Cabernet Sauvignon across multiple rootstocks in the Central Coast region of California (Paso Robles), suggesting that rootstock may have limited effect on sensitivity differences between the two yield components when that factor was controlled.

Other work has also shown that clusters per vine is more sensitive to water deficits compared to berries per cluster in Thompson Seedless (Williams et al. 2010b) and Merlot (Williams 2012a) grown in the southern San Joaquin Valley (SJV) of California. In addition, Keller et al. (2012) found fewer differences in berries per cluster compared to clusters per vine among three cultivars: Syrah, Chardonnay, and Merlot grown in eastern Washington. Those studies took place across varied regions of the western United States, potentially confounding direct comparisons, but their evidence supports the notion that clusters per vine is the yield component that is more sensitive to water deficits.

In this study, there were many more statistically significant differences among treatments in the response of clusters per vine compared to berries per cluster, and these responses were consistently observed across all 15 cultivars grown on the same rootstock over several years. Although rootstock has been shown to significantly influence yield formation in *V. vinifera* L. scion cultivars, the scion effect is typically much stronger (Keller et al. 2012); therefore, the cultivar comparisons are valid. There were also significant differences among cultivars for each yield component variable on an absolute basis, but when cultivars were compared on a relative basis, there were no differences in response sensitivity for either variable. This analysis may be somewhat confounded by the facts that (1) ED and LD treatments were not perfectly mirrored pre- and postveraison, and (2) the SD treatment designated as the control was not well watered. Future studies should aim to compare cultivars, taking these factors into account. Nevertheless, the results of this study coupled with evidence from previous research suggests it is unlikely that the sensitivity of yield components’ response to water deficits is cultivar dependent.

**Interrelationships among flowers per cluster, percent berry set, and berries per cluster.** To ensure that the lack of significant differences in berries per cluster among irrigation treatments was not due to differences in percent berry set, several representative cultivars were chosen in 2014 and 2015 for the determination of percent berry set. The selected cultivars were chosen based on a range of berries per cluster measured in 2013. The irrigation treatments did not have a significant effect on percent berry set either year. This was not surprising considering that all vines across treatments were irrigated similarly and had the same water status until after berry set (Levin et al. 2019). The irrigation treatments imposed the previous year may have affected starch reserves in the vines because of a water deficit-induced inhibition of photosynthesis that can inhibit floral differentiation (Dayer et al. 2013). However, it is unlikely that there would be a carryover effect of the irrigation treatments on set, considering that floral differentiation is highly controlled by environmental and physiological factors the current year (Skinner and Matthews 1989, Dokoozlian 2000). Based on the mean temperatures during the period of anthesis and berry set in both years (data not shown), it did not appear that set was negatively affected by environmental conditions in this study.

The interrelationships between flowers per cluster, percent berry set, and berries per cluster obtained in this study demonstrated that berry set was relatively high (~60%) at very low numbers of flowers per cluster (~150) and remained stable as flower number increased until ~250 flowers per cluster, at which point it began to decrease. Keller et al. (2010) reported a nearly linear relationship with berry set at ~55% at ~500 flowers per shoot across three years in Cabernet Sauvignon. In that study, there was an average of just under two clusters per shoot across all years and treatments, which would equate to comparable percent berry set values found in this study on a per cluster basis (i.e., ~250 flowers per cluster). Furthermore, Keller et al. (2012) also found significant differences among cultivars in percent berry set and flowers per cluster with no significant interactions between cultivar and rootstock. The authors reported higher percent berry set values with lower flower numbers and also an across cultivar percent berry set of ~50% at 250 flowers per cluster (Keller et al. 2012). Thus, the data in this study corroborate other findings regarding percent berry set in winegrape cultivars grown across different climates; namely, that flowers per cluster is strongly cultivar dependent, and that percent berry set levels much higher than 60% are unattainable in cultivated winegrapes.

Interestingly, it appears that across several cultivars with widely varying numbers of flowers per cluster, berries per cluster reached a maximum at ~150 and would not increase significantly with increasing flower number either year. Although grapevines have been previously reported to exhibit compensatory responses with respect to reproductive
development (Keller et al. 2012), there were no significant relationships found in this study between berries per cluster and clusters per vine (data not shown). Data from multiple studies across different regions, years, cultivars, rootstocks, and experimental treatments show that berries per cluster is almost always ~150 or below and rarely above 200 (Skinner and Matthews 1989, Matthews and Anderson 1989, Keller et al. 2008, 2010, Santesteban et al. 2011, Intrigliolo et al. 2012, Junquera et al. 2012, Keller et al. 2012, Dayer et al. 2013, Romero et al. 2013, Guilpart et al. 2014, Mendez-Costabel et al. 2014, Uriarte et al. 2015, Nelson et al. 2016).

Consequently, ~150 berries per cluster may represent somewhat of a physiological limit to the number of berries per cluster in *V. vinifera* L. cultivars under nonlimiting environmental conditions. From a mechanistic perspective, this would likely be a function of photoassimilate partitioning among flower sinks, whereby at low numbers of flowers per cluster, percent berry set is sink limited, while at high numbers of flowers per cluster percent berry set is source limited. From a management perspective, cane pruning can be employed as a management tool to increase flowers per cluster in cultivars that consistently set fewer than 150 berries per cluster, as more fruitful mid-cane buds are retained with this technique (Williams 2000, Sanchez and Dokoozlian 2005).

**Carryover effects and year-to-year variation.** In 2016, the treatments in the ED and LD plots were altered such that vines received 100% of estimated ET, to evaluate any potential carryover effects on reproductive development after several years of either early or late-season water deficits. Congruently, the SD plots were unchanged to account for any year effects. Yields were significantly increased across all treatments from 2015 to 2016 (including SD), mainly due to larger berries, and to a smaller degree, due to more berries per vine. Although berry sizes were similar across treatments in 2016, the lower yields in ED vines in 2015 were not made up for in 2016 when water was returned.

The general year-to-year reduction in berries per vine over the course of the study was primarily due to the reduction in clusters per vine, and to a much lesser extent, in berries per cluster. The largest year-to-year reduction in clusters per vine (and concomitant reduction in yield) across all cultivars was from 2013 to 2014, with little change from 2014 to 2015, and was increased slightly in 2016. While it is difficult to draw definitive conclusions about the cause of year-to-year variation in yield components (outside of the effects of the experimental treatments), it has been shown that dry conditions during the winter can reduce grapevine yield in the following season by primarily reducing the number of clusters per vine (Mendez-Costabel et al. 2014). That study was conducted in the SJV of California over two average rainfall winters in which the soil surface was covered to prevent absorption of water into the soil profile.

While most assume a full soil water profile at the beginning of the growing season, the measured values of SWC prior to the beginning of the 2015 growing season were below the soil type’s typical field capacity rating of 18.2% v/v (websoilsurvey.sc.egov.usda.gov). In addition, the values measured were also below those previously observed for well-watered grapevines grown on this soil type (Williams et al. 2010a). Thus, the low amount of dormant season rainfall in the winters of 2013 to 2014 and 2014 to 2015 did not fill the soil to field capacity, and vines were potentially under slight water deficit during dormancy. Reductions in clusters per vine and yield of Zinfandel grown on two rootstocks in the SJV were also reported by Nelson et al. (2016) from 2013 to 2014. The maintenance of cluster primordia during the dormant season has been shown to be sensitive to environmental conditions (Skinner and Matthews 1989). Therefore, it is possible that dry conditions during dormancy led to water deficits that caused an abortion of cluster primordia, reducing clusters per vine from 2013 to 2014 in this study as well.

Finally, it should be noted that SD vines also had significantly larger berries in 2016 compared to 2015 across all cultivars. Midday Ψᵣ was also greater in SD vines throughout the 2016 growing season compared to the 2015 growing season. While it is commonly understood that berry size is primarily a function of the current season’s growing conditions (May 2000), berry size may be largely determined well before the season begins, or at least before fruit set. Because the berry is the result of a fertilized ovary that itself developed in the flower, environmental conditions during the final stages of floral differentiation—such as temperature (Keller et al. 2010) or precipitation (Mendez-Costabel et al. 2014)—may significantly affect ovary size and thus final berry size. When Mendez-Costabel et al. (2014) excluded winter precipitation and kept soil dry during dormancy, berries were significantly smaller than controls at two weeks postanthesis. Accordingly, the significant rainfall during dormancy from 2015 to 2016 may have increased the water status of the dormant vines, influenced respiration, and ultimately encouraged more growth and development of primordial floral structures that ultimately led to larger berries in 2016.

**Conclusions**

The results of this study provide clear evidence that berry FW is the most sensitive yield component in response to water deficits, followed by clusters per vine, and then berries per cluster—with no differences in sensitivity among cultivars. The former two yield components also showed sensitivity to the timing of water deficits during the growing season, whereas berries per cluster did not. Both berry FW and clusters per vine were consistently and negatively affected by preveraison water deficits compared to postveraison across all years and cultivars.

Comparatively, berries per cluster was relatively unresponsive to growing season water deficits throughout the study. The relative lack of berries per cluster response to irrigation treatments was not associated with differences in percent berry set, suggesting that flowers per cluster was also relatively unresponsive to water deficits during the growing season, regardless of their timing. Consequently, berries per cluster was the yield component that was more genetically fixed compared to clusters per vine across cultivars. In contrast, clusters per vine was more sensitive to cultural practices that...
affected vine physiology and/or vine environment under the conditions of this study.

Nevertheless, flowers per cluster (and thus berries per cluster) depended strongly on cultivar and influenced percent berry set such that percent berry set was highest below 250 flowers per cluster (~50 to 60%), then decreased inversely with flowers per cluster at flower numbers greater than 250. Because of this relationship, berries per cluster increased linearly up to 250 flowers per cluster, then saturated at ~150 berries per cluster. A tentative across-cultivar flower number per cluster of 250 is proposed to optimize percent berry set in the SJV.

Preveraison water deficits not only reduced yield in the current season by reducing berry size but will also reduce yield the following season by reducing bud fruitfulness through a reduction in clusters per vine. Thus, to maximize grapevine yields, water should be applied early to avoid preveraison water deficits that can inhibit berry growth in the current season and bud fruitfulness for the following season.

**Literature Cited**


Effect of Water Deficits on Yield Components across 15 Cultivars – 221


