Influence of Clonal Variation, Pruning Severity, and Cane Structure on Yield Component Development in 'Cabernet Sauvignon' Grapevines

P.A. Bowed and W.M. Kliewer

Department of Viticulture and Enology, University of California, Davis, CA 95616

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Abstract. Yield components responsible for yield variation within and among three 'Cabernet Sauvignon' grape (*Vitis vinifera* L.) clones in a cane-pruned vineyard were determined over 2 years using a multivariate analysis procedure, two-dimensional partitioning (TDP). TDP analysis indicated that canes were producing at their capacity and yield per vine was limited by the number of canes retained. Yield per cane was limited by the portion of nodes at which shoots developed, and yield per shoot was limited by cluster number and fruit-set. The highest-yielding clone bore more fruit on non-cane shoots and fewer and larger clusters on cane shoots than the moderate-yielding clone. Poor fruit-set exhibited by the lowest-yielding clone resulted from inadequate or inviable pollen. In one year, thicker canes were more productive than thinner canes due to better bud burst and fruit set.

In several studies of treatment-induced differences in grapevine productivity, yield components were analyzed to pinpoint the developmental stages involved (Cawthon and Morris, 1977; May et al., 1976; Pool, 1982; Scholefield et al., 1977a, 1977b; Shaulis, 1980; Shaulis et al., 1966; Shaulis and May, 1971; Tafazoli, 1977). In these studies, the treatment responses of yield components were examined subjectively for their similarity to that of yield. This procedure gives a general idea when treatments exert their effect, but the relative importance of each yield component affected to the final yield response is not determined. Another problem with analyzing the response of yield components separately is that treatment differences in component interaction, such as compensation, are not detected.

To understand how the entire pattern of yield development is changed in response to treatments, yield components must be analyzed simultaneously by a multivariate procedure. The technique devised by Eaton et al. (1986), known as two-dimensional partitioning (TDP), uses multivariate analysis of variance to quantify the relative contributions of yield components and their interactions to treatment-induced yield variation. It was shown recently that TDP based on multivariate regression analysis can be used to analyze effects on yield development of factors expressed as continuous variables, such as vegetative characteristics or environmental conditions (Bowen, 1987).

This study was undertaken to find the reproductive stages responsible for yield differences in three clones of 'Cabernet Sauvignon' grape. TDP was used to identify the components that limited yield across clones and those that led specifically to clonal differences in yield and yield expression.

Materials and Methods

Models. In the first year of this study, two models were constructed that express yield on per-vine and per-cane bases (Fig. 1 a and b). Components in the models represent vine features considered to be important sources of grapevine yield variation.

For example, in the yield-per-vine model, pruning weight/vine is an indicator of vine size (Partridge, 1925; Scholefield et al., 1977a; Shaulis et al., 1966; Shaulis and Oberle, 1948). When the number of nodes retained per cane is constant, canes/pruning weight is a measure of pruning severity, since it is directly related to the commonly used nodes/pruning weight (Cawthon and Morris, 1977; Shaulis et al., 1966; Shaulis and Oberle, 1948). In the yield-per-cane model, burst nodes/node is the portion of cane node positions that developed at least one shoot (three are possible from a grapevine compound bud), and berries/flower is a measure of fruit-set. A model expressing yield on a per-shoot basis (Fig. 1c) was constructed for analysis in the second year.

Yield component data collection. Two of the three clones included in the study were originally collected from experimental field stations in Jackson and Oakville, Calif. The third was collected from a commercial vineyard in Livermore, Calif. Although indexed and found virus-free before planting, the three clones consistently produced high, moderate, and low yields (16.6, 12.1, and 7.5 kg/vine per year) in a 3-year trial at Davis, Calif. (C.J. Alley, unpublished data). Identified as numbers 8, 2, and 6, respectively, by the Foundation Plant Materials Service at the Univ. of California, Davis, the clones are designated here as high-, moderate-, and low-yielding, respectively.

Vines analyzed in this study were part of a g-year-old planting of seven 'Cabernet Sauvignon' clones at Davis, Calif. The own-rooted vines were planted singly in 24 complete blocks in an eight-row planting. The row $\times$ vine spacing was 3.66×2.44 m. Sixteen vines of each of the three clones in the study were selected at random from the 24 in the planting. Since vines of the three clones were not necessarily located together in blocks, data were analyzed as if from a completely randomized design.

During the winter, before the first growing season of these tests, equal numbers of vines of each clone were selected at random and pruned to four or six 15-node canes. In the second winter, all vines were pruned to four canes of about the same length, but with variable node numbers. Five two-node fruit cane renewal spurs were left on all vines in both years. The trellis training system was a four-wire double cross-arm trellis, with the canes tied to wires on the lower cross-arm. The lower and upper cross-arms were 46 and 92 cm wide, located 1.1 and 1.5 m from the ground. Other cultural practices, such as irrigation, cultivation, and disease and pest control, were the same for all clones.

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¹Present address: Agriculture Canada Research Station, Agassiz, B.C. V0M 1A0, Canada.

Fig. 1. Multiplicative yield component models of grapevine productivity.

Table 1. Clonal means for vine yield components.

Criterion	Year	Clone cropping level (kg) ^{z,y}			
		High	Moderate	Low	Mean
Pruning wt	1	9.5 a	11.0 a	11.0 a	10.5
Canes/pruning wt	1	0.57 a	0.49 a	0.50 a	0.52
Total yield	1	18.2 a	15.3 b	9.7 c	14.4
	2	13.4 a	10.7 b	5.9 c	10.0
Cane-borne yield ^x	1	10.9 a	10.6 a	6.9 b	9.5
	2	8.3 a	8.3 a	4.7 b	7.1
Non-cane yield ^w	1	7.2 a	4.7 ab	2.8 b	4.9
	2	5.1 a	2.4 b	1.2 b	2.9

^zCropping level established in a previous study (C.J. Alley, unpublished results). High-, moderate-, and low-cropping level clones correspond to U.C. Davis Foundation Plant Material Services, clone numbers 8, 2, and 6, respectively.

^yMean separation within rows by Tukey's test, $P = 0.05$.

^xEstimated as the product of cane number and yield of a single cane.

^wEstimated as the difference between total yield and cane-borne yield.

Table 2. Two-dimensional partitioning of variation in cane-borne yield per vine in the first year among yield components and clonal sources. Contributions to total yield variation expressed as R^2 percentages.

Source	Yield components			Interactions	Yield/vine
	Pruning wt	Canes/pruning wt	Yield/cane		
Clones	0	0	11**	3	14*
Residual	2	26	61	-3	86
Total	2	26**	72**		100

*,**Significant at $P = 0.05$ or 0.01 , respectively.

After pruning in each year, a single cane per vine was selected randomly for statistical analysis using the yield-per-cane model (Fig. 1b). In the second year, a single shoot was selected at random from this cane for analysis with the yield-per-shoot model (Fig. 1c). The cane length and the thinnest and thickest diameters between the first and second nodes were measured before bud burst each year. The average of the two diameters was taken as the cane thickness. Cane flatness, an indicator of shoot development under shade conditions (Antcliff et al., 1958; Kliever, 1981), was calculated as the ratio of the thickest to thinnest diameters.

During the bloom-set period, flowers aborted were collected in fine-mesh polyethylene bags (Delmet, Hercules Co., Wilmington, Del.) that were attached to the clusters just prior to

bloom. Flower numbers were calculated as the sum of aborted flowers and berries set.

Fruit was harvested when soluble solids concentration ($^{\circ}\text{Brix}$) in a mixed juice sample from the three clones was 21%. Separate harvests were made for the individual canes and shoots, then all fruit remaining on the vines was harvested the following day. Since it was impractical to harvest cane-borne fruit separately from fruit borne by shoots originating at the head of the vines, total cane-borne yield was estimated by multiplying the individual cane yield by the number of canes per vine. The difference between the estimated cane-borne yield and the measured total yield was taken as an estimate of yield borne by non-cane shoots.

After weighing and counting all clusters and berries, samples of 100 berries were used to take seed counts and $^{\circ}\text{Brix}$ measurements. The numbers of shoots and burst nodes on the canes were counted after leaf fall.

Yield component analyses. Clonal differences in yield development were analyzed by TDP using data from the first year for models a and b, and data from the second year for models b and c. Model a was not analyzed in the second year because all vines were pruned to four canes with variable node numbers. Each analysis was conducted according to the procedure of Eaton et al. (1986). Differences among clonal means for all yield components were tested with Tukey's test.

Additional TDP analyses of model b were conducted to determine the relationships between yield development and cane morphology. The continuous variables, cane diameter and flatness, were analyzed separately according to the TDP procedure using multivariate regression analysis described by Bowen (1987).

Cross-pollination study. To investigate possible causes of fruit-set differences among the three clones, a reciprocal cross-pollination study was conducted in the second year. The vines used were located in the experimental block, but were not part of the yield component study. Two replicate clusters, each on a different vine, were pollinated in each of the nine possible crosses among the three clones. Two clusters from different vines were used as pollen sources,

Emasculation was conducted 1 week before full bloom. About 200 flowers were emasculated on each cluster and all remaining flowers were removed. Both emasculated and pollen source clusters were rinsed with distilled water and bagged to prevent contamination by foreign pollen.

Pollination was conducted 4 days after emasculatation when the stigmatic surfaces of the emasculated flowers were sticky, indicating receptivity. To pollinate, the detached pollen source

Table 3. Two-dimensional partitioning of yield per cane variation among yield components and clonal sources. Contributions to total yield variation expressed as R^2 percentages.

Source	Year	Yield components								Interactions	Yield/ cane
		Cane length	Nodes/ cane length	Nodes burst/ node	Clusters/ burst node	Flowers/ cluster	Berries/ flower	Seeds/ berry	Berry weight/ seed		
Clones	1	0	0	0	0	0	3*	3**	2	10	18**
	2	0	2	1	2	0	11**	1**	0	5	22**
Residual	1	7	2	24	14	12	17	1	15	-10	82
	2	5	17	17	20	6	16	2	1	-5	78
Total	1	7*	2	24**	14**	12*	20**	4	17**		100
	2	5	19**	18**	22**	6	27**	3	1		100

*,**Significant at $P = 0.05$ or 0.01 , respectively.

Table 4. Means of cane components significantly different among clones.

Criterion	Year	Clone cropping level ^{z,y}			Mean
		High	Moderate	Low	
Berries/flower	1	0.27 a	0.28 a	0.23 b	0.26
	2	0.26 a	0.23 a	0.17 b	0.22
Seeds/berry	1	1.5 a	1.3 a	1.2 c	1.3
	2	1.6 a	1.4 b	1.2 c	1.4
Berry wt/seed (g)	1	0.71 a	0.72 a	0.73 a	0.72
	2	0.72 a	0.76 ab	0.78 b	0.75
Yield/cane (kg)	1	1.9 a	1.9 a	1.2 b	1.8
	2	1.9 a	2.0 a	1.1 b	1.6
°Brix	1	21.6 a	21.5 a	20.7 b	21.3
	2	22.3 ab	22.7 a	21.9 b	22.3

^zCropping level established in a previous study (C.J. Alley, unpublished data).

^yMean separation within rows by Tukey's test, $P = 0.05$.

Table 5. Male (pollen source) and female (emasculated cluster) clonal means for percent berry set.

Criterion	Male ^z			Female mean ^y
	Low	Moderate	High	
Female				
Low	9	20	15	18 a
Moderate	7	20	24	17 a
High	1	11	20	11 a
Male mean ^y	6 a	17 b	19 b	14

^zLow, moderate, and high refer to the relative cropping levels of the three clones.

^yMale or female clonal mean separation by Tukey's test, $P = 0.05$.

clusters were shaken over the appropriate emasculated cluster, and then all three clusters were bagged together for 1 day. Bags

were left on the pollinated clusters until after shatter to collect aborted flowers.

The number of flowers (emasculated) per cluster was determined by summing the numbers of aborted flowers and berries set. Percent set was then calculated as 100 times the ratio of berries to flowers. Differences in percent set due to male (pollen source) and female (emasculated cluster) clonal variation were determined by analysis of variance. Tukey's test was used to test differences between male and female clonal means.

Results and Discussion

Yield per vine. In both years, relative per-vine yields of the three clones were the same as those found previously by C.J. Alley (unpublished data) (Table 1). However, the cane-borne yields of the high- and moderate-yielding clones were not significantly different, indicating that they differed only in the amount of fruit produced at the head of the vine on spur shoots or shoots arising from latent buds (Table 1).

In the first year, cane-borne yield per vine was unrelated to vine size, as indicated by pruning weight (Table 2, bottom line). Pruning severity, measured as canes retained/pruning weight, was a significant contributor to yield variation, but yield/cane was more important (Table 2, bottom line). A regression of yield/cane on pruning weight/vine was insignificant (unpublished), indicating that severe pruning was not compensated for by greater per-cane yields. Individual canes were therefore yielding at their production potential, which, along with the number of canes retained, limited cane-borne yield per vine.

Clonal differences in yield/cane contributed most to the clonal differences in yield (Table 2, top line). Vine size, indicated by pruning weight, did not differ among clones, and only 3% of variation in yield was attributable to clonal differences in yield component interaction, such as compensation (Table 2, top line).

Yield per cane. In both years, nodes burst/node, clusters/burst node, and berries set contributed highly to yield-per-cane vari-

Source	Yield components								Interactions	Yield/ cane
	Cane length	Nodes/ cane length	Nodes burst/ node	Clusters/ burst node	Flowers/ cluster	Berries/ flower	Seeds/ berry	Berry weight/ seed		
Diameter	0	0	3*	0	1	2*	0	0	5	11**
Residual	7	2	21	14	11	18	4	17	-5	89
Total	7*	2	24**	14**	12*	20**	4	17**		100

Table 7. Two-dimensional partitioning of yield per-shoot variation in the second year among yield components and clonal sources. Contributions to total yield variation expressed as R^2 percentages.

Source	Clusters/ shoot	Flowers/ cluster	Berries/ flower	Seeds/ berry	Berry wt/ seed	Interactions	Yield/ shoot
Clones	4*	0	34**	0	0	-9	29**
Residual	27	0	28	4	3	9	71
Total	31**	0	62**	4	3		100

*,**Significant at $P = 0.05$ or 0.01 , respectively.

Table 8. Means of shoot components significantly different among clones

Criterion	Clone cropping level ^{z,y}			Mean
	High	Moderate	Low	
Clusters/shoot	2.3 a	2.8 b	2.6 b	0.26
Berries/flower	0.44 b	0.27 a	0.17 a	0.30
Yield/shoot (kg)	0.31 b	0.28 b	0.15 a	0.25

^zCropping level established in a previous study (C.J. Alley, unpublished data).

^yMean separation by Tukey's test, $P = 0.05$.

ation (Table 3, bottom two lines). Seeds/berry was the only component that did not influence yield in either years.

Differences between the two years in the contributions of cane length and nodes/cane length to yield variation (Table 3, bottom two lines) can be explained by the difference in pruning method used. In the first year, pruning to a constant node number meant that all variation in cane length resulted from variation in internode length. Thus, the small, but significant, positive contribution of cane length to yield variation (7%) was due to a positive relationship between yield and internode length. Little yield variation was attributed to nodes/cane length because cane length was considered first in the TDP analysis. In the second year, cane length was held fairly constant and was thus an insignificant contributor to yield variation. Nodes/cane length made a relatively large contribution to yield-variation (19%) in the second year, indicating that, unlike in the first year, canes with short internodes were more productive. The yield advantage of short internodes in the second year was probably due to more total nodes retained on canes of constant length.

The portion of the total yield variation already induced by a particular stage of development can be calculated by summing the R^2 's from the yield component analysis (bottom line in TDP tables) for all components up to that stage. Thus, in both years, by the time budbreak was complete and the number of clusters and flowers was determined, well more than half of the variation in cane productivity was already induced (Table 3, bottom line, 59% in the first year and 70% in the second year). Once fruit-set was complete, 83% of yield variation was already induced in the first year and 99% in the second year. Only a small portion of yield variation occurred during berry enlargement. This indicates that the early stages of yield development, i.e., those influenced by conditions during bud formation in the previous year (Winkler, 1974), were the most limiting to yield. May et al. (1976), in a study of light effects on yield/cane, found that high light exposure enhanced the yield components that were determined during bud formation, but not berry size or sugar concentration. This suggests that variation in shoot light exposure during the previous growing season may have been responsible for much of the yield variation among canes in this study. This possibility for the second year is further supported

by a positive relationship found between clusters/burst node and flowers/cluster (unpublished). High light exposure during bud formation has been found to enhance both the number and size of bunch primordia (Buttrose, 1969; May, 1965).

In both years, about one-fifth of the total variation in yield per cane was attributable to clonal variation (Table 3, last column). The component sources of this variation were berries/flower and seeds/berry (Table 3, top line). All earlier yield components were constant among clones, indicating that yield development was similar up to the time of set. The positive sum of interactions in both years indicates that the degree of compensation among components enhanced the clonal differences in yield.

In both years, canes of the low-yielding clone were the least productive and set the fewest berries/flower and seeds/berry (Table 4). Although the low-yielding clone had the greatest berry weight/seed in the second year (Table 4), it was insufficient to compensate for its poor set.

Results of the cross-pollination study (Table 5) show clearly that the poor set exhibited by the low-yielding clone was pollen-related, since all three clones set poorly when pollinated by the low-yielding clone. Although we did not determine whether poor pollen production or low viability was the cause, either could result from inadequate resource partitioning to flowering and fruiting. This possibility is also consistent with the almost absent compensatory increase in berry enlargement with poor set in the low-yielding clone, and its low accumulation of juice soluble solids compared with the other two clones (Table 4).

A positive relationship between yield and cane diameter in the first year resulted from better bud burst and set on thicker canes (Table 6). This relationship was not detected in the second year, and in neither year did cane thickness vary among clones. Cane flatness had no relationship with yield or yield development in either year. This result may have been due to selection of "sun"-type canes during pruning, which provided too narrow of a range in cane flatness to detect a relationship with yield.

Yield per shoot. Almost all variation in yield/shoot was accounted for by variation in cluster number per shoot and fruit-set (Table 7, bottom line). Clonal differences in yield resulted from clonal differences in both of these two yield components (Table 7, top line). The high negative sum of interactions found in the TDP analysis (Table 7, top line) indicates that final differences in yield per shoot among clones were diminished by clonal differences in compensation between the two contributing components. These differences can be discerned by examining clonal means for the two important yield components (Table 8). Shoots of the high-yielding clone bore fewer clusters than both the moderate and low-yielding clones, but compensation by a greater number of berries set resulted in a yield equal to that of the moderate-yielding clone (Table 8). Yield expression, therefore, differed between the moderate- and high-yielding clones, since the high-yielding clone bore fewer but larger clusters and

also bore more fruit on shoots arising from the head of vine, i.e., non-cane fruit.

Results of this study demonstrate that yield variation in 'Cabernet Sauvignon' may evolve throughout the 2-year span of reproductive development. Three developmental stages-flower bud induction, bud burst, and fruit set-were all decisive in obtaining high yields. Results also indicated that large vines were capable of supporting more than six fruiting canes.

Clonal differences in yield arose from several component sources, which influenced both total yield and its expression. The low-yielding clone partitioned resources inadequately to developing clusters, resulting in poor fruit set, whereas the high-yielding clone bore a significant amount of fruit at the head of the vine. Knowing these cropping characteristics may be useful in tailoring cultural techniques for existing plantings.

Literature Cited

- Antcliff, A.J., W.J. Webster, and P. May. 1958. Studies on the Sultana vine: VI. The morphology of the cane and its fruitfulness. *Austral. J. Agr. Res.* 9:328-339.
- Bowen, P.A. 1987. An analysis of sources of yield variation in three Cabernet Sauvignon clones. PhD Diss., Univ. of California, Davis.
- Buttrose, M.S. 1969. Fruitfulness in grapevines: Effects of light intensity and temperature. *Bot. Gaz.* 130:166-173.
- Cawthon, D.L. and J.R. Morris. 1977. Yield and quality of 'Concord' grapes as affected by pruning severity, nodes per bearing unit, training system, shoot positioning, and sampling date in Arkansas. *J. Amer. Soc. Hort. Sci.* 102:760-767.
- Eaton, G.W., P.A. Bowen, and P.A. Jolliffe. 1986. Two-dimensional partitioning of yield variation. *HortScience* 21:1052-1053.
- Kliewer, W.M. 1981. Grapevine physiology: How does a grapevine make sugar? *Univ. Calif. Coop. Ext. Serv. Lflt.* 21231.
- May, P. 1965. Reducing inflorescence formation by shading individual Sultana buds. *Austral. J. Biol. Sci.* 18:463-473.
- May, P., P.R. Clingeleffer, and C.J. Brien. 1976. Sultana (*Vitis vinifera* L.) canes and their exposure to light. *Vitis* 14:278-288.
- Partridge, N.L. 1925. Growth and yield of Concord grapes. *Proc. Amer. Soc. Hort. Sci.* 22:84-87.
- Pool, R.M. 1982. Effect of mepiquat chloride on the growth and yield of Concord grapevines. *J. Amer. Soc. Hort. Sci.* 107:376-380.
- Scholefield, N., P. May, and T.F. Neales. 1977a. Harvest-pruning and trellising of 'Sultana' vines: I. Effects on yield and vegetative growth. *Scientia Hort.* 115-122.
- Scholefield, N., P. May, and T.F. Neales. 1977b. Harvest-pruning and trellising of 'Sultana' vines: II. Effects on early spring development. *Scientia Hort.* 7:123-131.
- Shaulis, N. 1980. Responses of grapevines and grapes to spacing of and within canopies. *Proc. UCD Grape and Wine Symp.* p. 353-361.
- Shaulis, N., H. Amberg, and P. Crowe. 1966. Response of Concord grapes to light, exposure and Geneva double curtain training. *Proc. Amer. Soc. Hort. Sci.* 89:268-280.
- Shaulis, N.J. and P. May. 1971. Response of 'Sultana' vines to training on a divided canopy and to shoot crowding. *Amer. J. Enol. Viticult.* 22:215-222.
- Shaulis, N.J. and G.D. Oberle. 1948. Some effects of pruning severity and training on Fredonia and Concord grapes. *Proc. Amer. Soc. Hort. Sci.* 51:263-270.
- Tafazoh, E. 1977. Cane and bud number effect on yield components of nonirrigated grapes cv. 'Yaghooti'. *Scientia Hort.* 7:133-136.
- Winkler, A.J., J.A. Cook, W.M. Kliewer, and L.A. Lider. 1974. General viticulture. Univ. of California Press, Berkeley.