INFLUENCE OF DEFOLIATION, LEAF DARKENING, AND CLUSTER SHADING ON THE GROWTH AND COMPOSITION OF SULTANA GRAPES

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ABSTRACT

One half of the total leaf area of 'Sultana' vines was eliminated by either physical leaf removal (defoliation) or by covering the leaves with aluminum bags (darkening). Treatments were applied about a month after anthesis either to all leaves on every other shoot per vine or to leaves on the basal or apical half on all shoots per vine. Half of the fruit clusters on each vine were covered to protect the fruit from direct solar radiation. A further series of vines receiving the defoliation treatments above, including no defoliation, were completely defoliated at véraison.

All leaf elimination treatments reduced berry weight and soluble solids concentration significantly, the reductions being already pronounced in the early stages of ripening and not increasing as the fruit matured. Elimination of apical leaves reduced both variables more than did elimination of basal leaves. Defoliation reduced berry weight more, and soluble solids concentration less, than did darkening. Covered clusters had a slightly higher soluble solids concentration in all treatments and a slightly higher berry weight in the control and defoliation treatments. They had a considerably higher berry weight in the darkening treatments, and this accounted for the difference in this respect between darkening and defoliation, the berry weight for uncovered clusters being the same for both.

All leaf elimination treatments led to a higher total acidity in the fruit in the early stages of ripening, but only when apical leaves were eliminated did it remain higher until maturity. At maturity, fruit from leaf darkened vines was slightly more acidic than fruit from defoliated vines, and fruit from covered clusters was slightly more acidic than fruit from uncovered clusters.

Fruit from vines completely defoliated at véraison had a drastically lower soluble solids concentration but less severely reduced berry weight by the end of the ripening period, than did corresponding vines not further defoliated at véraison. Acidity was scarcely affected. Berry weight and °Brix of fruit were significantly greater for covered clusters on vines entirely defoliated at véraison than for uncovered clusters.

Removal of apical leaves increased the total number of nodes per vine and per shoot over all other treatments. The percentage of mature nodes was greater on defoliated vines than on leaf-darkened vines. Shoots with no leaves always had fewer mature nodes than shoots with leaves, and vines with basal leaves removed had considerably higher percentages of mature nodes than vines with apical leaves removed.

Approximately 10 square centimeters of leaf tissue per gram of fruit was required to mature the crop fully without decreasing the total soluble solids in the berries.

The relationship between leaf area, fruit and vine growth, and fruit composition of grapevines has been studied by several investigators (1, 9, 12, 13). May et al. (9), in recent field defoliation studies with 'Sultana', found that removal of one-third to two-thirds of the leaves on fruitful shoots in various combinations after all unfruitful shoots had been removed decreased berry weight, total soluble solids, and sugar per berry at harvest by 3 to 36%. They further showed that carbohydrates are readily translocated between shoots on the same cane, and to a much less extent between canes. Winkler (13) found that 'Muscat of Alexandria' clusters (40 berries) on girdled shoots required from 1300 to 1800 cm^2 of leaf area (12-16 leaves) to mature the fruit properly, and Buttrose (1) reported that 12 leaves (1500 cm^2) were necessary for unhindered development of all the organs in potted 'Muscat of Alexandria' plants. May et al. (9) found that about 6 square centimeters of leaf tissue per gram of fruit was required to mature 'Sultana' grapes fully.

In none of the investigations mentioned above was the physical removal of leaves compared with leaf removal by natural abscission as to effects on berry growth and sugar accumulation, nor was the effect of increased exposure of fruit to solar radiation caused by reduction in leaf area on growth and composition of fruit measured. Answers to these questions were sought by means of leaf and cluster darkening (covering with aluminum coated bags). A further objective was to compare the effect of removing basal and apical leaves on berry weight and composition.

MATERIALS AND METHODS

Used in the experiments were eighteen-year-old own-rooted vines of *Vitis vinifera* L., var. 'Sultana' (syn. 'Thompson Seedless'), growing in an irrigated vineyard at the CSIRO Division of Horticultural Research, Merbein, Victoria, Australia. In the winter of 1968 the vines were pruned to eight canes with 12 to 14 buds per cane. Weak vines were not used; however, pruning was not balanced according to pruning weights nor was adjustment made for number of clusters per vine. The average number of clusters per vine was 56. The clusters were about at full bloom on November 5th, and the fruits reached véraison during the last two to three days in December.

Two experiments were designed, randomized blocks replicated seven (Experiment I) and six (Experiment II) times, each replicate being a single vine except for treatments B and E, which were represented by two vines per replicate. There were seven treatments in experiment I.

A) Control; all foliage left on all shoots.
B) All foliage removed (all except one or two apical leaves) from alternate shoots on each cane; half of all other shoots not on canes were also defoliated.
C) All foliage removed from the basal half of each shoot on the vine.
D) All foliage removed from the apical half of each shoot on the vine.
E) Same as B except leaves were covered with bags instead of removed.
F) Same as C except leaves were covered with bags instead of removed.
G) Same as D except leaves were covered with bags instead of removed.

The clusters on all vines in all treatments were split into two equal groups, uncovered and covered. The leaves and fruit were covered with 6-½-by-7-¾-inch aluminum-coated paper bags, which were fastened with staples around the petiole or peduncle. Bags covering fruit clusters were open at the bottom to simplify sampling. The initial defoliation was done December 6 and 7 (treatments B-D) and the initial leaf covering was done from December 9 through 13 (treatments E-G). Newly arising leaves were removed from B-D vines on December 27, January 23, February 7, and February 24. Additional bags were placed on new leaves in treatments E-G on December 30 and January 27. Bags were put on clusters at the time of initial defoliation and leaf covering. Covered leaves remained attached to the shoots for 3 to 4 weeks, by which time they had completely turned yellow and abscissed from the vines.

Experiment II consisted of four treatments (A, B, C and D), the same as in experiment I except that all leaves remaining after initial removal were taken off at or near véraison. The date of initial leaf removal was the same as in experiment I; dates of complete leaf removal were January 2 (Treatment A) and January 15 (Treatments B, C, D). As in experiment I, half the clusters on each vine were covered with aluminum-coated bags at the time leaves were first removed. All new leaves on each vine were subsequently removed on four separate occasions at about 2-week intervals.

Three to five berries were taken randomly from each cluster on a vine at five different dates (Figures 1-9). The fruits from uncovered and covered clusters were kept separate. In treatments B and E, berries were taken separately from both foliated and defoliated shoots. The berries were weighed, counted, and homogenized in a grinder immediately after being sampled. The expressed juice was analyzed for total soluble solids (degree Brix) with a refractometer, and total titratable acidity by titration with 0.1 NaOH to a phenolphthalein end point. Total sugar per berry was estimated by multiplying °Brix by weight per berry.

All remaining fruits from each vine were harvested March 13. Beginning March 26, the fresh weight of all leaf blades per vine was measured. The ratio of cm² of leaf per gram dry weight was also determined, and from this ratio was estimated the total leaf area per vine from the total leaf dry weight per vine. Shoot growth was estimated by counting the number of mature and immature nodes in the autumn of 1969. Nodes and adjacent internodes that were hardened and brown in color were designated mature.

RESULTS

Statistical analysis of the data for berry weight and sugar concentration showed significant effects from the pattern of leaf elimination (i.e. which leaves were selected for elimination), method of elimination (i.e. defoliation or darkening), and whether the clusters were covered or not. On the other

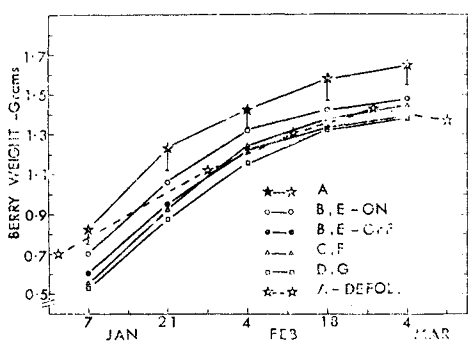

Figure 1. Effect of defoliation and leaf darkening on berry weight of 'Sultana' fruits sampled at various times during the ripening period. See Materials and Methods for identification of treatments. ON and OFF refer to fruits sampled from shoots with all leaves on or all leaves off. Brackets indicate the difference between treatment means required for significance of the 5% level.

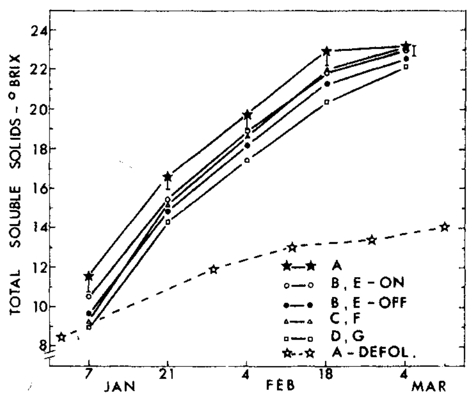

Figure 2. Effect of defoliation and leaf darkening on total soluble solids in 'Sultana' fruits sampled at various times during the ripening period. See Materials and Methods for identification of treatments. ON and OFF refer to fruits sampled from shoots with all leaves on or all leaves off. Brackets indicate the difference between treatment means required for significance at the 5% level.

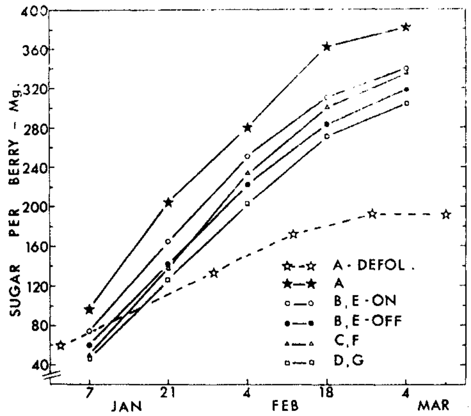

Figure 3. Effect of defoliation and leaf darkening on total sugar per berry in 'Sultana' fruits sampled at various times during the ripening period. See Materials and Methods for identification of treatments. ON and OFF refer to fruits sampled from shoots with all leaves on or all leaves off.

hand, there were no significant interactions between the pattern and method of elimination, and the interaction of cluster covering with the other factors was small in comparison with the primary effect. The data are therefore combined as appropriate to illustrate the primary comparisons.

Figures 1 to 3 show the effects of the various patterns of leaf elimination on berry weight, total soluble solids, and sugar per berry at each sampling date. Each point in these figures combines the mean of samples from covered and uncovered clusters for corresponding defoliation and darkening treatments. All leaf elimination treatments significantly reduced berry weight and total soluble solids (except for the last date of sampling) but did not always differ significantly among themselves. Reductions were greatest where leaves on the apical half of all shoots had been eliminated, and the reductions due to the elimination of basal leaves were in many cases significantly less. Shoots with all leaves eliminated, on vines with alternate shoots treated, showed an intermediate effect while the corresponding untreated shoots were the least af-

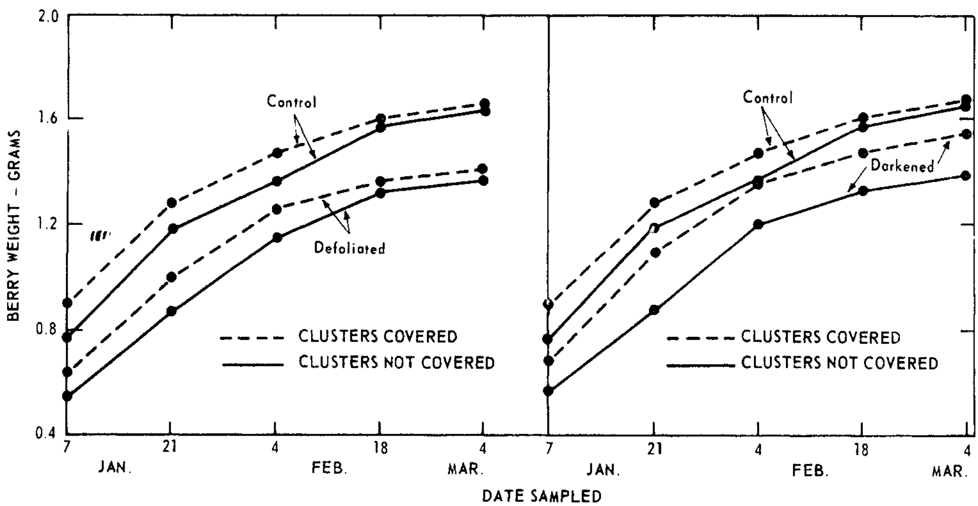

Figure 4. Effect of covering fruit clusters on weight of berries from partially defoliated (mean of samples from treatments B, C, and D, left figure) or leaf darkened (mean of samples from treatments E, F, and G, right figure) 'Sultana' vines sampled at various times during the ripening period. Weight of berries was significantly ($P<0.01$) greater from covered clusters than from uncovered clusters in all cases.

fected. The reduction in berry weight, total soluble solids, and sugar per berry, respectively, ranged from 9 to 36%, 1 to 23%, and 10 to 51%, for the various treatments and sampling dates (Table 1). Generally, the effects of defoliation and leaf darkening were well established at the first time of sampling and did not increase as maturation progressed.

Cluster covering and method of leaf elimination interacted significantly in their effects on berry weight, and the effects of cluster covering are therefore shown separately for the defoliated and the darkened treatments in figure 4. Covered clusters had heavier berries in all cases ($P<0.01$), but whereas the differences are similar for treatments A, B, C, and D (leaf-defoliated treatments) they are significantly larger for treatments E, F, and G (leaf-darkened treatments).

The effect of method of leaf elimination on total soluble solids is shown in figure 5. Each point combines the mean of samples from covered and uncovered clusters for all treatments with the same method of leaf elimination. There was a greater reduction by darkening than by defoliation, and the difference was significant ($P<0.05$) at all times of sampling except the first.

The effect of covering clusters on total soluble solids is shown in figure 6. Each point is the mean of all samples from covered or uncovered clusters. The covered clusters had a higher total soluble solids at all times of sampling. Although the differences were not very great they were all significant ($P<0.001$, except Jan. 21 ($P<0.01$).

Complete defoliation at about véraison of vines in treatments A, B, C, and D, experiment II, reduced the total soluble

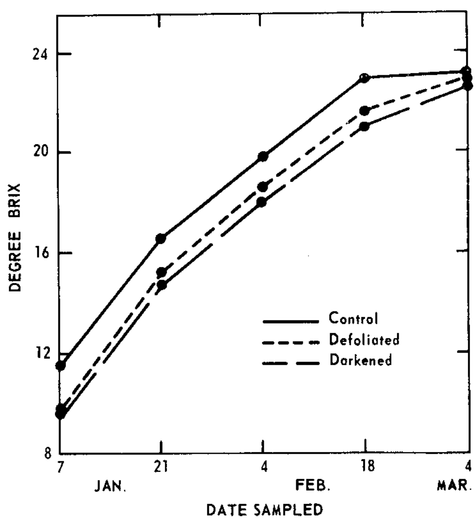

Figure 5. Effect of leaf elimination by manual defoliation or by leaf darkening on total soluble solids (°B) of berries from 'Sultana' vines sampled at various times during the ripening period. Leaf darkening significantly ($P<0.05$) decreased the °B of the fruit to a greater extent than defoliation at all sampling times except on January 7.

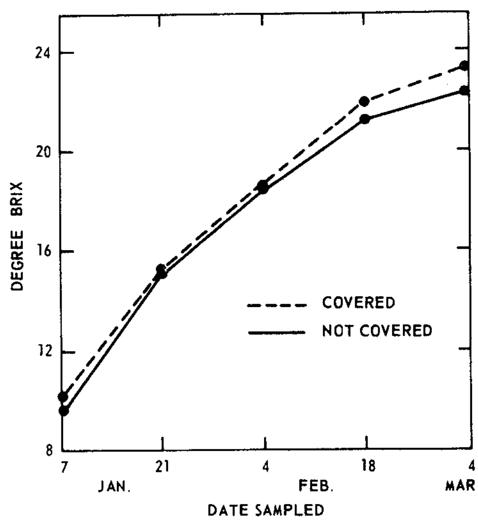

Figure 6. Effect of covering fruit clusters on total soluble solids of berries from 'Sultana' vines sampled at various times during the ripening period. Each point represents the mean of all treatments and replicates from covered and uncovered clusters in experiment I. The ° Brix of berries was significantly greater ($P<0.001$ except for Jan. 21, $P<0.01$) from covered clusters than from uncovered clusters at all sampling dates.

solids of mature fruit by 34 to 40% (Figure 7) and berry weight by 12 to 16% (Figure 8) compared with vines of corresponding treatments not defoliated at véraison, i.e. treatments A, B, C, and D, experiment I. Berry weight and total soluble solids of fruits were significantly greater ($P<0.01$) for covered clusters than for uncovered, exposed clusters in experiment II (Figure 9). Each point in this figure represents the combining of means of samples from covered and uncovered clusters from all treatments.

Table 2 shows that all leaf elimination treatments led to a higher total acidity in fruits at early stages of ripening (January 7th and 21st samples) than when no leaves were removed (treatment A), but acidities remained higher until maturity only if apical leaves were eliminated (treatments D and G). Mature fruit was slightly more acidic from leaf-darkened vines than from defoliated vines, and berries from covered clusters during the last three sampling dates were significantly ($P<0.001$) higher in total acidity than were berries from uncovered clusters.

Manual defoliation of the apical half of leaves on shoots (treatment D) greatly increased ($P<0.01$) the total number of nodes per vine and per shoot over the mean for all other treatments (Table 3). Differences in total nodes per vine between individual pairs of treatment means did not differ significantly. The number of nodes per shoot, however, was sigificantly higher for treatment D than for control vines (treatment A). The mean percentage of mature nodes of all defoliated treatments was considerably greater ($P<0.01$) than the mean of all leaf-defoliated treatments

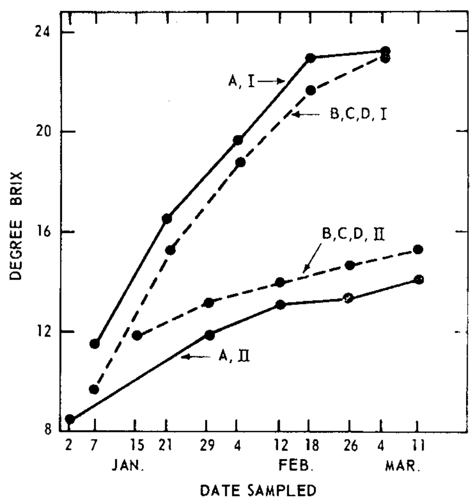

Figure 7. Effect of 50% leaf removal (treatments B, C, D-I) and complete leaf removal (B, C, D-II and A-II) of 'Sultana' vines on total soluble solids of fruits. Treatment A, I served as a control with no leaves removed. Data from treatments B, C, and D in experiment I have been combined as has data from treatments B, C, and D in experiment II. See Materials and Methods for further explanation of treatments and for time of leaf removal in experiments I and II.

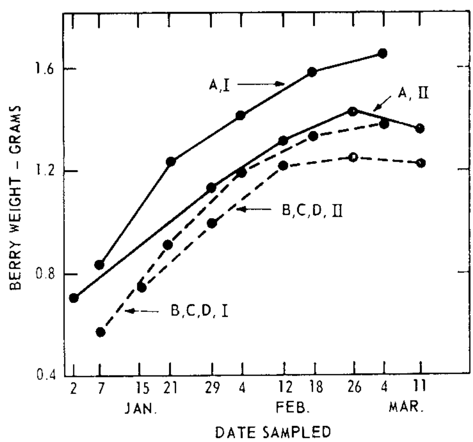

Figure 8. Effect of 50% (B, C, and D-I) and complete (B, C, D-II and A, II) leaf removal of 'Sultana' vines on berry weight. Treatment A, I served as a control with no leaves removed. Data from treatments B, C, and D, in experiment I have been combined and averaged together as has data from treatments B, C, and D in experiment II. See Materials and Methods for explanation of treatments and for time of leaf removal in experiments I and II.

TABLE I

Effects of Defoliation and Leaf Darkening on Total Soluble Solids, Berry Weight, and Sugar Per Berry at Various Times During the Ripening Period[a]

	Total soluble solids					Berry weight					Sugar per berry				
Treatment[b]	Jan. 7	Jan. 21	Feb. 4	Feb. 18	Mar. 4	Jan. 7	Jan. 21	Feb. 4	Feb. 18	Mar. 4	Jan. 7	Jan. 21	Feb. 4	Feb. 18	Mar. 4
A	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
B-ON	92.9	93.8	96.3	95.3	100	84.9	83.4	91.2	90.5	88.5	78.5	77.8	87.6	86.4	88.4
B-OFF	85.1	89.2	92.4	93.4	98.1	72.5	76.2	83.6	82.6	83.9	62.1	67.6	77.3	77.2	82.2
C	81.9	94.2	98.1	97.2	101.4	63.8	75.5	83.8	84.0	83.9	52.0	69.5	82.2	81.5	85.2
D	77.4	88.1	90.5	90.9	97.4	63.5	68.7	81.3	81.4	80.9	49.1	61.0	73.6	74.1	78.8
E-ON	88.9	92.4	94.9	94.4	98.9	86.5	88.8	95.7	89.2	90.3	77.2	82.3	90.8	84.3	89.3
E-OFF	82.3	89.6	91.9	91.8	97.8	75.0	77.7	89.2	85.7	85.8	61.3	69.7	81.9	78.8	84.0
F	77.0	88.2	92.2	93.4	99.1	68.4	76.1	92.4	90.4	90.9	52.7	67.0	85.2	84.5	90.0
G	77.8	84.4	85.9	86.9	94.1	70.7	73.8	82.9	87.6	86.7	54.6	62.7	71.1	76.2	81.6

[a] Data are the average of covered and uncovered clusters for seven replicates and are expressed as per cent of treatment A (control).

[b] See Materials and Methods for identification of treatments. ON and OFF refer to fruit sampled from shoots with all leaves on or all leaves off.

(Table 3). Likewise, shoots in treatments B and E, with all leaves on, had significantly more ($P<0.001$) mature nodes than shoots in treatments B and E, with all leaves off (Table 3), and shoots with basal leaves removed (treatments C and F) had a strikingly higher ($P<0.001$) percentage of mature nodes than shoots with apical leaves removed (treatments D and G). There were no significant interactions between treatments in percentage of mature nodes.

Figure 10 shows the relationship between total soluble solids of fruits at harvest and cm^2 of leaf area per gram of fruit for all defoliated-leaf darkened vines. The regression curve followed the equation $Y=24.47—15.37/X$, where $Y=°Brix$ and $X=cm^2$ leaf area per gram fruit. A correlation coefficient of $r=0.815$ was obtained. The data indicate that about 9 to 10 cm^2 of leaf area per gram of fruit was required to mature the grapes fully, i.e. to a degree Brix of about 23.

DISCUSSION

Berries were heavier from covered clusters on leaf-darkened vines than from covered clusters on defoliated vines (Figure 4). This may have been due to the greater protection provided fruit clusters against direct solar radiation during the first few weeks of growth by the shading effect of the bagged leaves. Uncovered clusters on leaf-darkened vines did not differ significantly from uncovered clusters on defoliated vines in weight of berries (Figure 4), though the former fruit usually had slightly lower total soluble solids (Figure 5). The net effect was that total sugar per berry was about the same in defoliated and darkened vines. In this regard, then, it appears to make little difference whether leaf area per vine is reduced by leaf removal or by darkening of the laminae. The covered leaves abscissed about 3 weeks after bagging, and there-

TABLE 2

Effects of Defoliation and Leaf-Darkening Treatments of 'Sultana' Vines with Covered and Uncovered Clusters on Total Titratable Acidity at Five Different Sampling Dates

Treatment[f]	Jan. 7	Jan. 21	Feb. 4	Feb. 18	Mar. 4
		(g tartaric acid/100 ml juice)			
A	2.31	1.060	0.614	0.500	0.429
B + E (ON & OFF)	2.90[a]	1.193[a]	0.640	0.509	0.424
C + F	3.10[a]	1.244[a]	0.629	0.499	0.423
D + G	3.12[a]	1.293[a]	0.675[b]	0.534[b]	0.444[b]
Defoliated (B, C, D)	2.99	1.225	0.640	0.505	0.425
Darkened (E, F, G)	3.02	1.236	0.653	0.521[c]	0.433[d]
Uncovered (All treatments)	3.04	1.210	0.626	0.494	0.415
Covered (All treatments)	2.81[e]	1.213	0.660[e]	0.529[e]	0.443[e]

[a] Significantly different from control, A ($P<0.001$).

[b] Significantly different from C + F ($P<0.001$).

[c] Significantly different from defoliated ($P<0.001$).

[d] Significantly different from defoliated ($P<0.05$).

[e] Significantly different from uncovered ($P<0.001$).

[f] See Materials and Methods for identification of treatments. ON and OFF refer to fruit sampled from shoots with all leaves on or all leaves off. 'Defoliated' and 'Darkened' refer to the method of leaf removal and 'Covered' and 'Uncovered' refer to fruit clusters that have been protected or left unprotected from solar radiation.

after became essentially the same as in corresponding defoliated treatments. Chemical analysis of covered leaves revealed that at abscission almost all the chlorophylls, sugars, and starch had disappeared (unpublished data of Kliewer and Kriedemann). Respiration undoubtedly accounted for a large percentage of the losses of these compounds. However, some of these carbohydrates may have been translocated out of the leaves and into the parent vine. Kliewer and Kriedemann observed no translocation of C^{14}-labeled photosynthate from uncovered mature leaves to covered fully expanded leaves, indicating that artificially darkened leaves do not act as parasites on the vine.

The reduction in berry growth and sugar concentration of fruits is attributable to both reduction in leaf area and to the increased exposure of clusters to solar radiation (Figures 1-9). Removal of about 50% of the foliage was generally more detrimental to berry weight than to the increase of sugars in the fruit (Figures 4 and 5), in agreement with results of May et al. (9). On the other hand, complete defoliation at véraison reduced berry sugar concentration much more than the berry weight (Figures 7 and 8). Radler (10) found that clusters held 3 months at 33°C, beginning shortly after flowering, developed mature berries that were considerably smaller and had slightly less sugar than berries developed under lower temperatures. Kliewer and Lider (6) showed that fruits from 'Thompson Seedless' vines exposed to direct solar radiation had lower berry weight and less titratable acidity than fruit from shaded parts of vines. They also found that berries in the sun were usually 1 to 11°C warmer than shaded berries and that the total accumulated heat received daily was 43 to 62% greater for sun fruits than for shade fruits. May et al. (9) reported that removing one-third to two-thirds of the leaves from 'Sultana' vines reduced berry weight at harvest by 7 to 21%, and Buttrose (1) found that reducing leaf numbers of potted 'Muscat of Alexandria' vines from 20 to 6 also reduced berry growth by about 20%. In our experiments, covered leaves and fruit clusters were usually 1 to 4°C cooler than uncovered during daylight hours, and 0.5 to 3°C warmer at night.

The time at which leaves are removed appears to have an important bearing on berry development (Figures 1 and 8). In experiment II, vines in treatments B, C, and

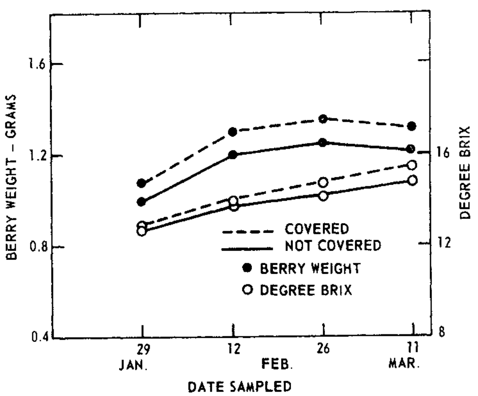

Figure 9. Effect of covering 'Sultana' fruit clusters on the total soluble solids and berry weight of fruits from vines completely defoliated at véraison (Experiment II). Each point represents the mean of all covered and uncovered samples for each sampling date. The berry weight and °B of fruit were significantly greater ($P<0.05$) from covered clusters than from uncovered clusters at each sampling date.

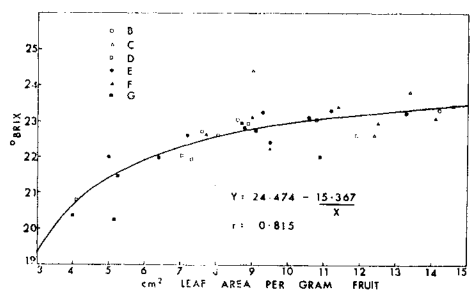

Figure 10. Regression of sugar concentration (°B) of 'Sultana' berry juice at harvest (March 4) on leaf area per unit crop (cm^2/g).

D were partially defoliated December 7, about one month after anthesis, at which time 'Sultana' berries enter the lag phase of their double-sigmoid growth curve (3). Treatment A vines were completely defoliated on January 2, by which time the second growth period had commenced. Berry growth on vines defoliated at the latter date was affected relatively little by leaf removal. On vines partially defoliated in early December, however, berry growth was considerably less than on undefoliated control vines or control vines completely defoliated in January. This may indicate that some substance (s) that influences berry growth, possibly a growth regulator or carbohydrate, is translocated from leaves to fruit clusters at an early stage of berry development. Buttrose (1) found that the growth rate of 'Muscat of Alexandria' berries during the second phase of the growth cycle was not affected by leaves removed during the first growth phase, but, rather, that initiation of this second growth phase was delayed.

The finding that removal of about half of the leaves on a vine did not greatly affect the final maturation of fruits (as measured by °Brix) can be accounted for by at least three factors. First, removal of approximately half the leaves per vine increased the proportion of remaining leaves receiving adequate amounts of light. Kriedemann (7) recently reported that 'Sultana' leaves required 2,500 to 3,000 ft-c for light saturation. In previous work (unpublished) more leaves on foliated vines received less than 500 ft-c of light than did leaves on defoliated vines. Secondly, the reduction in number of leaves reduced the ratio of total leaf area to fruit weight per vine; this may have increased the photosynthetic efficiency in the remaining leaves. Humphries and Thorne (4) and Buttrose (1) have shown that photosynthetic efficiency increases as the size of the sink increases in relation to the source. In the present instance, fruits are the sink and leaves the source. A third factor was the availability of large carbohydrate reserves in the roots, trunk, arms, and canes. Control vines that were completely defoliated at véraison (8°Brix fruit) had enough reserves available to ripen fruit to 14°Brix, compared with control vines with all leaves intact, which matured fruit to 23.2°B (Figure 7). Thus it is possible that as much as 40% of the total sugar supplied to the fruits come from parts of the vine other than the leaves. The extent that carbohydrates are supplied to fruits from woody parts of the vine when all or part of the leaves are intact, cannot be determined from our data. Nevertheless, the possibility has been shown that vines use carbohydrate reserves for fruit maturation when stress conditions occur. A fourth factor was the size of crop. The average crop load on the vines in the above experiments was considerably lower than average for the Merbein area. The relatively small crop probably did not put undue stress on the vines.

Fruit from vines with leaves removed from the apical half of the shoots were lowest in berry weight, °Brix, and sugar per

TABLE 3

Effects of Various Defoliation and Leaf-Darkening Treatments in 'Sultana' Vines on the Number of Nodes per Vine and per Shoot and on the Percentage of Mature Nodes per Vine[a]

Treatment[b]	Total number of nodes per vine	Total number of nodes per shoot	Percent mature nodes per vine
A	1400	15.62	51.21
B-on	....	17.12	53.50
B-off	....	17.09	47.69
B-on + off	1459	....	....
C	1486	16.28	56.53
D	1690	19.44	45.11
E-on	....	15.94	50.64
E-off	....	17.44	45.45
E-on + off	1368	....	....
F	1409	17.60	52.88
G	1397	16.83	40.48
S.E. of mean	79.3	0.637	1.496

[a] Node counts were made in late April and May just prior to leaf-fall.

[b] See Materials and Methods for identification of treatments. ON and OFF refer to fruit sampled from shoots with all leaves on or all leaves off.

berry (Figures 1-3). These results are in accord with findings of Kriedemann (7) and Kriedemann et al. (8), who showed that most recently fully mature 'Sultana' leaves have the highest photosynthetic rate. Older basal leaves on shoots had a photosynthetic rate about one-third less than the more recently mature leaves. Richardson (11) reported that photosynthetic activity of tree leaves rises to a peak at about the time full size is attained. This rate is maintained for varying periods before decreasing toward senescence. May et al. (9) found that removal of leaves from the basal third of all shoots in 'Sultana' vines had relatively little effect on berry weight and sugar content of fruits. This finding emphasizes the importance of maintaining the terminal leaves on shoots throughout the entire growing season.

The higher acidity of berries from defoliated and leaf-darkened vines at the early stages of fruit ripening was undoubtedly due to the slower ripening of these fruits. During the last 6 weeks of fruit maturation there were little differences in the total acidity of fruits from foliated, defoliated, or leaf-darkened vines (Table 2). This suggests that leaves have little direct influence on the total acidity of fruits during the ripening period. Grape berries usually attain maximum acidity shortly before véraison (5), and during the pro-véraison period leaves may affect the acidity of fruits either by supplying the metabolites for organic acid synthesis or by supplying the acids themselves. Hale (2) administered $^{14}CO_2$ directly to grape clusters and found a large percentage of the label in the organic acids, indicating that berries may be an important site for synthesis of these substances. Kliewer and Lider (6) showed that 'Sultana' fruits under the vine canopy were cooler and considerably higher in total acidity than berries receiving direct radiation from the sun. This finding probably explains why fruits on vines with basal leaves removed were lower in acidity than fruits on vines with apical leaves removed (Table 2), since the former fruits were more open to direct exposure to the sun than the latter fruits. The higher acidity of fruits from covered clusters than of fruits from uncovered clusters was most likely due to the lower daytime temperatures experienced by the former fruits.

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