

## The Effect of Reducing Leaf Area on the Growth of Roots, Stems and Berries of Gordo Grape Vines

by

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### Introduction

There are a number of reports of experiments with vines in which the relationship between leaf number and berry growth has been measured (1, 7, 8, 9, 10, 13). In some of these studies (10, 13) shoots were girdled so that berries did not have to compete with roots or main stem for leaf assimilate, whereas in others (1, 7, 8, 9 — information from abstracts) it appears that leaves were differentially removed from otherwise intact plants and berry growth correlated with remaining leaf area. In none of these investigations has the effect of leaf number on the plant as a whole been studied, as attention has been confined to berries only or berries and associated shoot. Thus it is not known whether the plant organs differ in ability to compete for products of leaf assimilation as these become progressively limited.

The experiment described below was an attempt to measure the effect of differing leaf areas on the growth of the whole plant, the parts considered being the root system, parent stem, new shoot and, in particular, berries.

### Material and Methods

One-year-old rooted cuttings of *Vitis vinifera*, var. Muscat Gordo Blanco (syn. Muscat of Alexandria) were planted into 25 cm porous earthenware pots containing John Innes compost in the spring of 1964. Growth during the ensuing season was restricted to one shoot, and it was found that the buds formed on this shoot were fruitful. During the winter of 1965 the new canes were pruned back to the third node, and shoots arising from this node were allowed to grow in spring. All portions of the stem already present at bud burst will be referred to below as trunk, and new growth as shoot. Pots were positioned in the open air, and shoots were attached at intervals during growth to 100 cm — lengths of dowling rod stood vertically in each pot. Plants were supplied with Hoagland's solution weekly during the growing season 1965/66.

Flowering occurred during the first week of November, and on December 6th, when fruit-set had been accomplished, 48 plants, each with a bunch of 30 or more berries, were selected and berry number reduced to 30 by cutting off from the apex of the bunch. At the same time the following four treatments (12 replicates for each) were imposed:

1. Control — untreated
2. 6 leaves retained
3. 3 leaves retained
4. 1 leaf retained

Leaf reduction was made by removing those leaves basal to and opposite the bunch and then cutting off the distal portion of the shoot to leave the requisite number of

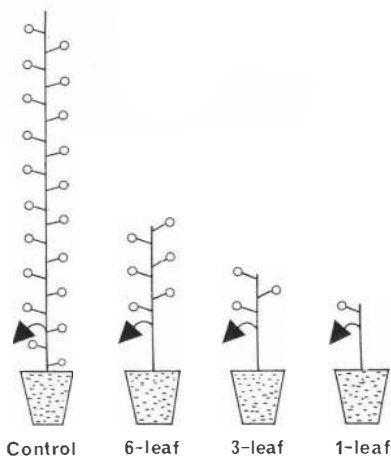


Fig. 1: Diagrammatic representation of treatments.  
Open circles — leaves;  
triangles — bunches.

primary leaves on the shoot as illustrated in Figure 1. The aim during the experiment was to maintain a constant leaf area, and as the primary leaves senesced (judged by loss of fresh green colour) or were wind damaged, a corresponding area of leaf was permitted to remain on lateral shoots which on the treated plants constantly grew out from axillary buds and which otherwise were removed at weekly intervals. Leaves on laterals were smaller than primary leaves, and so by varying the number retained a standard leaf area of approximately 125 cm<sup>2</sup> was maintained at each node by visual comparison. The total leaf areas of two plants selected at random from each treatment were measured on 25th February using a photocell leaf-area-measuring device. The values obtained (Table 2) indicate that a precise control was not obtained, but it is judged that this approach gave a better control than reliance on leaf number alone.

Beginning on the 16th December, 10 days after treatment, and thereafter at fortnightly intervals until 23rd March 1966, the diameters of the most basal 5 berries on each bunch were measured. The diameter recorded was that of a transverse section at a level midway between point of attachment of pedicel and distal end. From these figures mean berry volumes were calculated assuming berries to be perfect spheres (4).

Beginning on 5th February 1966, and thereafter at intervals up to and including 9th March, one berry was removed from the apex of each bunch for all treatments, and on two further occasions for the 3- and 1-leaf treatments (see Fig. 4). After pooling the 12 berries from one treatment for berry fresh weight determination, they were crushed and boiled for 5 minutes with added water. Following suitable dilution titrateable acids (expressed in terms of tartaric acid) were determined by titrating an aliquot to pH 8.4 with 0.1 N KOH. Total sugars were determined on further aliquots, after removing all cellular debris by centrifugation, using the anthrone method as described by Loewus (6). It should be noted that sugar values calculated in this way on a whole berry fresh weight basis are lower than values obtained from refractometer measurements of expressed juice.

All remaining berries were harvested on 14th April, dried to constant weight at 105° C and the average berry dry weight for each plant recorded. On 22nd April a 10 cm portion of the shoot close to the base was taken for fresh weight/dry weight determination, and a 0.5 cm portion immediately above was taken for sugar and starch determinations. Similarly the uppermost 10 cm portion of the trunk was taken for fresh weight/dry weight determination, and a 0.5 cm portion immediately below for sugar and starch determinations. The root system was then washed free of potting soil, removed from the parent stem, and weighed after drying at 105° C.

Sugars in trunk and shoot segments were determined on the 80% alcoholic extract using the anthrone reagent (6). The residue after alcoholic extraction was extracted with chloral hydrate at 80° C, the solubilized starch precipitated with acetone and measured as glucose following acid hydrolysis (3).

**Results**

As pointed out in the previous section, the treatment differential was leaf area rather than leaf number, but for convenience treatments are referred to below in terms of leaf number.

Changes in average berry volume are shown in Figure 2. By 16th December, 10 days after treatment, there already appeared to be a retardation in berry growth of the 1-leaf plants although the difference from control did not reach significance until the next measurement on 30th December. By this time there was evidence of an effect on the growth of the 6- and 3-leaf berries, which differed thereafter from control berries but not from each other. The curve for control berries shows a slight change (not significant) in slope at 7 weeks after flowering (between 30th December and 11th January) which corresponds in time to the lag phase reported by other workers (4). This change in slope was progressively pronounced and prolonged with reduction in leaf number, so that with 1 leaf there was a period of some 6 weeks with little increase in berry size. However none of these changes in slope reached significance. Although the maximum volumes attained were different, the growth

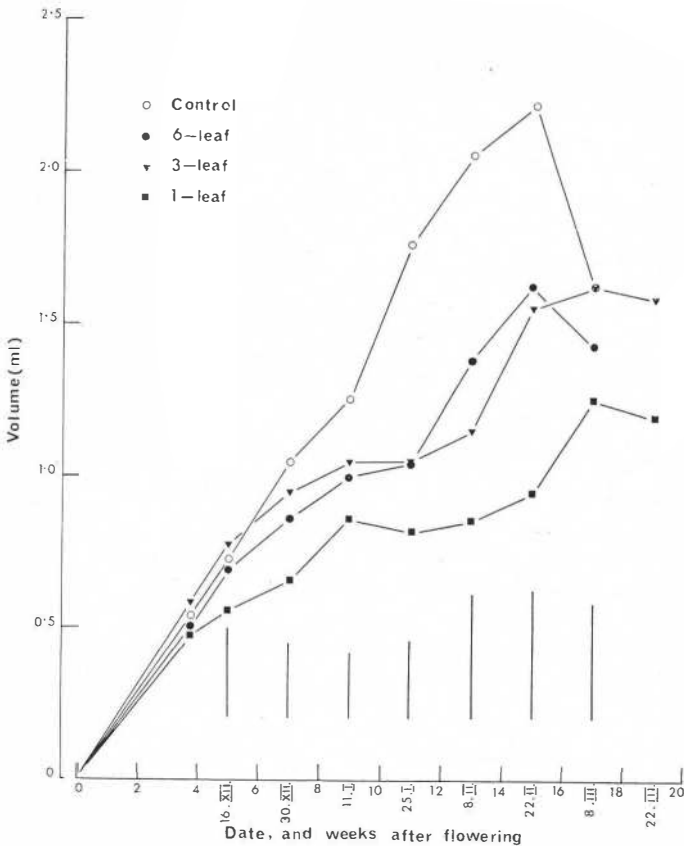


Fig. 2: Changes in mean berry volume over the course of the experiment.

Vertical bars represent least significant differences (5% level) for the respective measuring occasions.

rate during the most rapid period of growth did not differ markedly between treatments. The berries matured from 22nd February onwards, reduction in leaf number being associated with a delay in ripening. The fall in volume seen in Figure 2 coincided with a crinkling of the skin which was observed for control and 6-leaf berries.

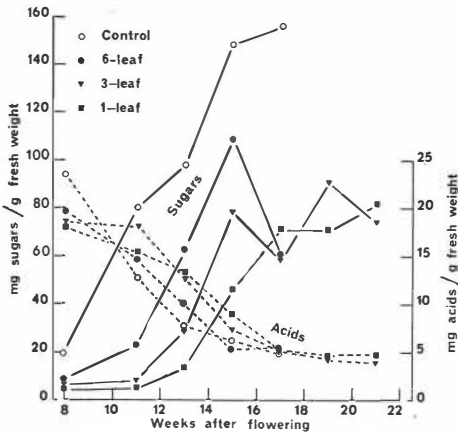


Fig. 3: Changes in mean berry fresh weight over the sampling period. See Fig. 2 for dates.

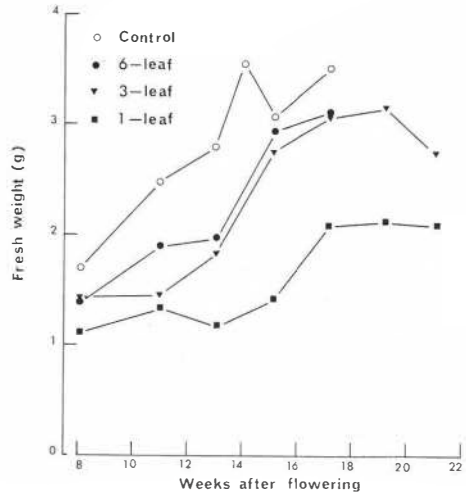


Fig. 4: Changes in total sugars and titratable acids over the sampling period. See Fig. 2 for dates.

Berry fresh weights are shown in Figure 3, and it will be noted that trends are very similar to those of berry volumes.

Leaf number had a marked effect on berry sugars (Fig. 4), the control berries having about 15% total sugars at the last sampling, and the 1-leaf berries about 7%. The values for 6- and 3-leaf berries showed great variation at the later harvests, although much of this could be ascribed to experimental error on 9th March. One notable feature of these results is the progressive delay in sugar accumulation with reduction in leaf number. Thus by 5th January control berries had entered the sugar accumulation phase, whereas the 6-leaf berries started at about 20th January, the 3-leaf at 1st February and the 1-leaf at 9th February. These times correspond approximately with the end of the "lag phase" of Figure 2. Associated with this is a second feature, that once sugar accumulation began the rate of increase did not obviously differ with treatment. This corresponds likewise with volume growth. When expressed on a per berry basis, sugar increases in 6- and 3-leaf berries continued to be similar to that of control berries for the period of rapid increase, but the rate for 1-leaf berries was reduced (6 mg per berry per day compared with 9 mg per berry per day). The rate of fall in acid content over the period observed was fastest for control and progressively slower as leaf number was less, but by 9th March there was little treatment difference (Fig. 4).

Sugar: acid ratios, which are one measure of quality for wine grapes, are presented in Table 1. The values for 6- and 3-leaf treatments on 9th March appear out of sequence, but as noted above sugar values for these treatments showed much

Table 1  
Sugar : acid ratios (w:w) of berries during development

Date	Control	6-leaf	3-leaf	1-leaf
Jan. 1	0.9	0.4	0.4	0.3
Jan. 26	6.3	1.6	0.5	0.4
Feb. 9	13.1	6.2	2.3	1.0
Feb. 23	24.0	19.5	10.8	5.3
March 9	33.0	10.9	11.6	14.4
March 23	n. a.	n. a.	22.8	16.0
April 14	n. a.	n. a.	24.0	17.5

n. a. — not assessed

Table 2  
Mean leaf areas on shoots, and dry weights and carbohydrate contents of plant parts at the final harvest

Treatment	Control (= 20 leaves)	6-leaf	3-leaf	1-leaf	L. S. D. (5%)
Leaf area per plant (cm <sup>2</sup> ) (data from 2 plants)	2470	850	470	125	
Dwt/Berry (g)	0.50	0.43	0.34	0.18	0.23
Shoot Dwt/10 cm (g)	3.46	3.49	2.95	1.97	0.48
Trunk Dwt/10 cm (g)	6.26	6.97	6.46	5.11	1.15
Root Dwt (g)	49.0	30.3	22.2	13.3	7.0
Sugars in shoot (% Dwt)	3.4	3.1	2.5	1.9	
Sugars in trunk (% Dwt)	3.3	2.9	2.3	1.6	
Starch in shoot (% Dwt)	17.4	17.9	13.1	6.3	
Starch in trunk (% Dwt)	19.1	16.6	12.6	4.6	
% Dry matter in shoot	51	49	45	32	3.8
% Dry matter in trunk	55	53	49	43	4.8

variation at the later samplings. It is clear however that leaf reduction at each level affected this ratio.

Values for leaf area on 25th February, and dry weights of the different plant parts at harvest are presented in Table 2. Berry dry weight was reduced with leaf reduction, although due to a large variability only that of 1-leaf berries was significantly below control (and 6-leaf). Dry weight per 10 cm of shoot in the region measured was only reduced in the 3- and 1-leaf treatments, whereas for trunks the effect was only evident in the 1-leaf treatment. Root dry weight was significantly affected at each treatment level. Sugar and starch levels in both shoot and trunk appeared only slightly affected at the 6-leaf treatment, but were progressively lowered at the 3- and 1-leaf treatments. The difference between control and 1-leaf trunk starch contents could account for the corresponding difference in trunk dry weights/10 cm. Percentage dry matter values for both trunk and shoot were reduced at the 3- and 1-leaf treatments, and it was observed that the whole shoot of the 1-leaf plants was reminiscent of the ephemeral portion of the control shoot.

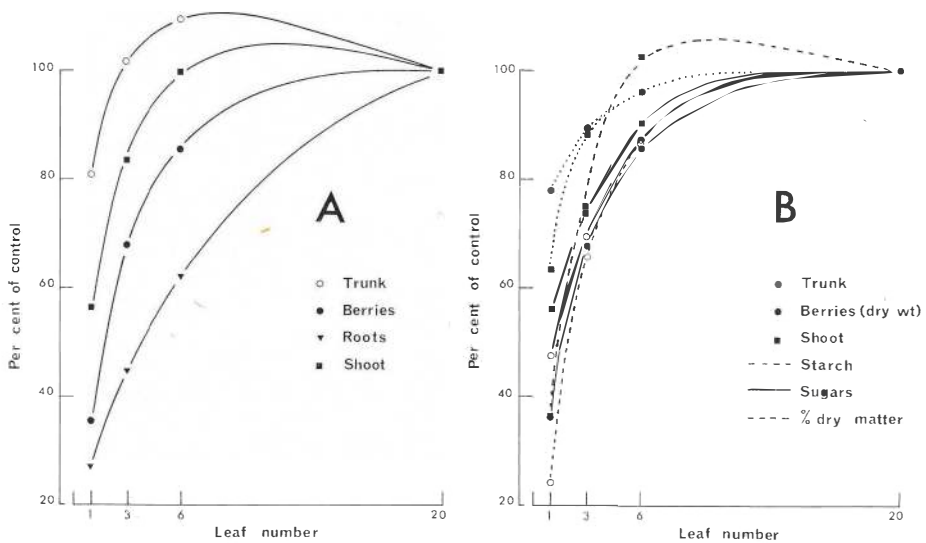


Fig. 5: Dry weights of plant parts, and contents of starch, sugars and % dry matter of treated plants expressed as percentages of the corresponding control values, plotted against leaf number.

Dry weights are plotted in A and the other data in B. The berry dry weight curve in A has been repeated in B for comparison.

### Discussion

To illustrate the extent to which different organs were affected by leaf reduction, values in Table 2 for 6-, 3- and 1-leaf plants have been expressed as a percentage of corresponding control values, and are plotted in Figure 5 against leaf number. From these curves it would appear that in respect of dry weight the trunk was the least affected, followed in order by shoot, berries and roots. The curves for starch and sugar in the trunk and shoot are similar to that for berry dry weight, suggesting that the ability of berries to accumulate dry matter is comparable with the ability of shoot and trunk to accumulate these mobilizable carbohydrates. It is clear from the dry matter curves in Figure 5 that the displacement of water by dry matter occurs in priority to the accumulation of mobilizable carbohydrates. It is possible that this displacement is largely due to accumulation of cellulose and lignin, and so may be a measure of wood formation.

Perhaps the most significant finding was that roots were so markedly affected. Whereas it may be postulated from the curves that development of trunk, shoot and berries would not have been improved at leaf areas in excess of the control, it would be predicted from the curve for roots that their dry weight would have been still greater with additional leaf area. This raises the question of how dependent top growth is upon the size of the root system. Some information on this point has been obtained by calculating total weights at harvest for the various organs, as shown in Table 3, and by plotting root dry weight against total top dry weight to give the curve shown in Figure 6. This result suggests that there was a relationship between roots and tops as long as conditions of stress applied as judged from Figure 5 (treatments 6-, 3- and 1-leaf) but that after relief of such stress root growth increased

Table 3

Calculated total dry weights (g) of plant parts at the final harvest, and increments in dry weights (g) over the experiment assuming values at treatment time to be equal to the final values of 1-leaf treatment.

Plant Part	Totals at final harvest						Total dry weight Leaf number	
	Roots	Trunk <sup>(1)</sup>	Shoot	Leaves <sup>(4)</sup>	Berries	Total		
Control	49	25	23 <sup>(2)</sup>	10	15	122	6	
6-leaf	30	28	14 <sup>(3)</sup>	4	13	89	15	
3-leaf	22	26	6 <sup>(4)</sup>	2	10	66	22	
1-leaf	13	20	2 <sup>(5)</sup>	0.5	5	41	41	
	Increments							
Control	36	5	21	—	15	77	3.9	
6-leaf	17	8	12	—	13	50	8.3	
3-leaf	9	6	4	—	10	29	9.6	

(1) Assume length to be 40 cm, (2) Assume length of 100 cm, and that, because the shoot narrows at the apex, the total weight was 66.6% of the product of length and weight/cm (Table 2), (3) Assume shoot length of 39 cm, (4) Assume shoot length of 18 cm, (5) Assume shoot length of 10 cm, (6) Assume leaf weight of 0.42 g/100 cm<sup>2</sup> (These assumptions were based on data derived from a number of plants corresponding to the control group).

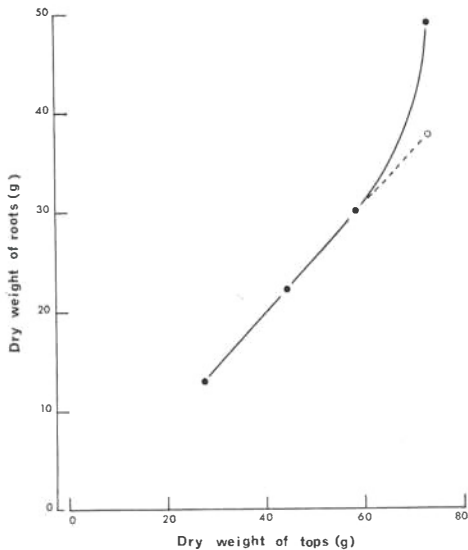


Fig. 6: The relationship between calculated total top (trunk, shoot, berries and leaves) dry weight and root dry weight among the four treatments — solid line.

The straight-line connecting values for 1-, 3- and 6-leaf treatments has been projected to the control top dry weight (73 g) — broken line.

disproportionately. By projecting the straight line portion of the curve in Figure 6 to the value for control top dry weight (73 g), it is judged that 38 g of roots should have been sufficient to support control plants compared with the 49 g found. Thus carbohydrates (products of leaf assimilation) in excess of the requirements for berry, shoot and trunk growth were apparently channelled into new root growth. The shoots in this experiment did not grow much beyond 100 cm, possibly due to wind damage of the apex, but had they grown longer there might have been a diversion of carbohydrate to form additional shoot and a consequent diminution in proportion of dry weight channelled to the roots. In the field, however, Gordo shoots are usually at least as short and it is possible that carbohydrate production in excess of the needs of berries, trunk and shoot is directed into root growth. Under conditions of adequate nutrition and

irrigation root growth in excess of a certain limit may be of no benefit to the plant, unless to provide carbohydrate storage space.

It may be gauged from Figure 5 that approximately 12 leaves (or 1500 cm<sup>2</sup>) were necessary for unhindered development of the organs on these plants. As shoots are normally pruned back to approximately 10 cm no error is involved in basing consideration on results of only this portion of the cane. As an average Gordo cluster in Southern Australia has about 85 berries, or nearly three times the number in the present experiment, it is probable that under field conditions where there are normally two bunches per cane the requisite leaf area per shoot would be considerably in excess of 1500 cm<sup>2</sup>. Further experimentation is called for to assess effects of berry number. On girdled shoots WINKLER (13) found that Muscat clusters (of 40 berries) required from 12–16 leaves (between 1300 and 1800 cm<sup>2</sup>). MOHANAKUMARAN *et al* (7) and ТОДОРОВ and ЗАНКОВ (9), both using Muscat, found 1048 cm<sup>2</sup> of leaf per bunch and 12–24 leaves per bunch, respectively, necessary for normal berry development. Comparison with these results is, however, difficult because either girdling was carried out or cluster sizes and numbers were not stated.

In order to assess efficiencies of the leaves in converting carbon dioxide into dry weight, approximate values for dry weight of whole organs for each treatment were calculated and are tabulated in Table 3, and then an assessment was made of total dry weight increment during the experiment. For this purpose it was assumed, as an extreme case, that for the 1-leaf treatment maximum root, trunk and shoot dry weight had been attained at treatment time, so that the only dry weight gained up to harvest was that of berries. Dry weight increments of roots, trunk and shoot for the three other treatments were then obtained by deducting from their values in the upper part of Table 3 the 1-leaf values, and the results are presented in the lower half of Table 3. The value for total increment per leaf is seen to increase as the leaf number falls, and this trend would still remain even if, as is probable, 1-leaf plants gained weight in parts other than berries. Leaf assimilate not only contributes to dry weight but also to the pool of respiratory substrate, and some assessment of the respiratory load associated with each leaf is given by ratios of total plant dry weight to leaf number in Table 3. The load increases greatly with fall in leaf number. From these calculations it is evident that the efficiency of leaves increases as they become fewer. One explanation for this could be that as the size (more precisely the „intensity” here) of the sink increases the efficiency of photosynthesis increases, as has been demonstrated most recently by HUMPHRIES and THORNE (5) and BURT (2).

If overcropping is thought of as a condition in which carbohydrate stress increases in the plant, then it is probable that the effects of this practice on different plant parts would be comparable with those induced by limiting leaf area. If this is so, increasing severity of overcropping in Gordo would be expected to affect first root development, secondly berry development and available carbohydrate levels in trunk and shoots, and thirdly dry weight of trunk and shoots. It is suggested that crop load could be increased to the point at which there is an effect on maximum berry dry weight attained, without any adverse effect on other plant parts. It is evident from a comparison of studies on overcropping by WEAVER and McCUNE (11), on the one hand, and WEAVER, McCUNE and AMERINE (12), on the other, that effects of overcropping depend very much on variety. It should therefore be borne in mind that the results obtained here with Gordo may not apply to other varieties.

The observations on the course of berry development, as distinct from final dry weight, are difficult to explain. One problem is that if increase in berry size were dependent on carbohydrate supply, other requirements being non-limiting, a slower



rate of growth over the entire growth period could be expected following reduction in leaf area. Whereas this may have occurred before the lag phase, assuming the volume curves to portray a diphasic growth cycle, it does not appear to have taken place in the second growth period. On resumption of growth after the lag phase there is an indication that growth rate and also rate of sugar accumulation were essentially similar in all treatments. "Mature" (= maximum attained) weights differed on account of differing durations of the second growth phase, resulting primarily from effects of leaf removal in delaying the initiation of this phase rather than from effects on the time of its termination. This could mean that for a limited period of second phase growth berries were able to compete successfully with other plant organs for nutrients. A second problem concerns possible effects on the lag phase. From the berry volume curves it appears that it may be possible to prolong the lag phase by reducing leaf area, which suggests that carbohydrates or some other materials exported from the leaf may influence the time at which the second growth phase begins. The second phase in respect of volume increase was preceded in each case by berry sugar increase, as found to occur by COOMBE (4). No explanation can be offered for these results, especially as the reason for the double growth cycle is not understood (4).

### Summary

To measure the effect of leaf number during berry growth on all organs of the grape vine (*Vitis vinifera*) a pot experiment was done using Muscat Gordo Blanco plants maintained in the open. Each plant was allowed to develop one fruitful shoot and 4 treatments (12 plants each) were applied following fruit set: (1) control (2) 6 leaves left (3) 3 leaves left (4) 1 leaf left. Leaves left (by tipping the shoot) were primary leaves at and above the first node above the bunch. When primary leaves senesced or were wind damaged a corresponding area of lateral-shoot leaf (125 cm<sup>2</sup>) was permitted to remain. Leaf area measurement of sample plants gave values of 2470 cm<sup>2</sup>, 850 cm<sup>2</sup>, 470 cm<sup>2</sup> and 125 cm<sup>2</sup> respectively for the 4 treatments. On each shoot there was one bunch limited to 30 berries.

Measurements of berry volume and sugar suggested that there was a diphasic growth curve and that with fall in leaf number there was a longer lag phase and a shorter second growth phase. Growth rate in the second phase was not greatly affected. Acids fell more slowly where leaf number was less, and the sugar: acid ratio was reduced.

From final plant dry weights it was found that the trunk (parent stem) was least affected by leaf reduction, followed in order by shoot, berries and roots. Sugars and starch in trunk and shoot were affected in a way similar to berries. When needs of trunk, shoot and berries were fully met it appeared that excess leaf assimilate was channelled into root growth. The minimal leaf area for unimpeded growth of aerial organs was estimated to be 1500 cm<sup>2</sup> (12 leaves), but in the field where bunches have more berries a greater leaf area would be required.

The data has been interpreted to show that leaf efficiency in terms of carbon fixation, was markedly increased with reduction in leaf number.

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