

PROPORTIONAL REDUCTION IN SHOOT GROWTH OF GRAPEVINES WITH ROOT SYSTEMS MAINTAINED AT CONSTANT RELATIVE VOLUMES BY REPEATED PRUNING

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Summary

Grapevines were established in water culture and shoot length and leaf number were measured after imposing four levels of root-pruning treatment. These levels (control, and 75, 50, and 25% of the control root volume) were maintained for 8 weeks by making weekly checks followed by appropriate pruning. Shoot dry weights were also measured in some plants at fortnightly intervals.

One week after the initial root pruning, shoots pruned to 50 and 25% of the control root volume were already shorter than the control shoots, and shoot-length increments over the final 4-week period bore a close relation to the level of root pruning. Shoot dry weight was affected in a similar way to shoot length. The results are interpreted to indicate that roots are the source of a growth substance required for normal shoot growth.

I. INTRODUCTION

The growth of grapevines was investigated under a range of environmental conditions (Buttrose 1968), and it was found that the root:shoot dry weight ratio was similar after 3 months' growth despite treatment differences of up to threefold in shoot dry weight. This indicated a balance between growth of roots and shoot as found in many plant species. In another experiment with vines (Buttrose 1966), shoots which were pruned to leave one, three, or six leaves did not mature normally in autumn, indicating a shortage of photosynthetic products; but, despite differences in absolute weights due to leaf number, root:shoot weight ratios were again similar in each case. This leads to the proposal that when the demand for photosynthetic products is high relative to the supply, roots and shoots have access to fixed proportions of that supply. In the control treatment of the same experiment unpruned shoots made little extension growth for some 2½ months before harvest and at the same time carried a large leaf area. Under these conditions the demand for photosynthetic products was low relative to supply and it was found that the root:shoot ratio was greater than in the pruned treatments. Thus the root:shoot balance could be altered by manipulation of the shoot.

The question was then raised as to how the size of the root system might influence shoot growth. This question has some practical significance as root pruning or regulation can occur in field plants due to the action of such factors as insects,

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nematodes, and the level of the water-table. With other plants it has been found repeatedly that removal of part of the root system results in an immediate retardation in shoot growth (Humphries 1958). In such experiments (Humphries 1958; Maggs 1964) roots have been pruned on one occasion only with a subsequent harvest. The present paper describes an experiment in which an attempt was made to maintain vine roots at prescribed relative sizes over a prolonged period in order to assess effects on shoot growth.

II. MATERIALS AND METHODS

Dormant hardwood cuttings of grapevine (*Vitis vinifera* L. cv. Muscat Gordo Blanco, syn. Muscat of Alexandria) were collected from a vineyard in the winter of 1966 and stored in plastic bags at 4°C until used. On May 17, 1967, 600 cuttings two nodes long were prepared and the fresh weight of each recorded. They were then planted in vermiculite contained in propagating tubes and placed in a glasshouse to allow root development and bud-burst. At the same time a further sample of cuttings was taken for determination of moisture content. On June 27, 1967, roots were sufficiently long for transfer of the cuttings to water culture. There were 20 replicates of four containers, each container with four plants; the 16 plants of each replicate were chosen for similarity of cane length and diameter. The plants of any one container received the same treatment and the containers were randomized within each replicate. Aerated half-strength Hoagland's No. 1 solution (with added trace elements) was used for the first 3 weeks, after which time full-strength solution was substituted. The Hoagland's solution was renewed every 2 weeks. On July 10 five replicates (20 containers) were harvested and determinations of dry weights of shoot, parent cane, and roots were made for each plant. On July 11 treatments were begun on the remaining plants. There were four treatments: control, and roots pruned to 75, 50, and 25% of control root volume (referred to hereafter as R100, R75, R50, and R25 respectively).

The volume of a root system was measured as the volume of water displaced in a measuring cylinder on submerging all roots basal to the parent cane. Desired volumes were attained by visual assessments, and checks were made by water-displacement measurements. At first pruning was relatively simple, calling for the removal of only a proportion of the adventitious roots arising from the cane; later, when the number of adventitious roots was few, it became necessary to cut off portions of the root growth arising on each adventitious root. Immediately after the initial treatment measurements were made of shoot lengths and leaf numbers. Correction of root volume, removal of lateral shoots, and measurements of shoot length and leaf number were made at weekly intervals until the conclusion of the experiment on September 4, 1967. On July 24, and thereafter every fortnight, one plant from each container was harvested and determinations made of shoot length and leaf number, root volume, and dry weights of leaves, stem, cane, and roots.

III. RESULTS

Root volumes are shown in Figure 1. Until August 14 weekly increments in root volume were greatest for R25 and decreased progressively through R50 and R75 to R100. As a result the weekly pruning over this period was most severe for R25 and least severe for R75. Volumes after pruning were in most cases slightly below the desired value as not all root systems had achieved this volume even before pruning. Root volumes on treatment days could be expressed as the mean of the volume before and after pruning, and a mid-week volume was taken as the mean of the appropriate two values calculated in this way.

Absolute shoot lengths are shown in Figure 2. One week after commencement of treatment, R25 and R50 shoots were shorter than those of R100 (and R75) plants, and thereafter on each occasion shoots of R25 were shorter than those of R50. R75 shoots at no stage differed significantly in length from R100, but the mean value

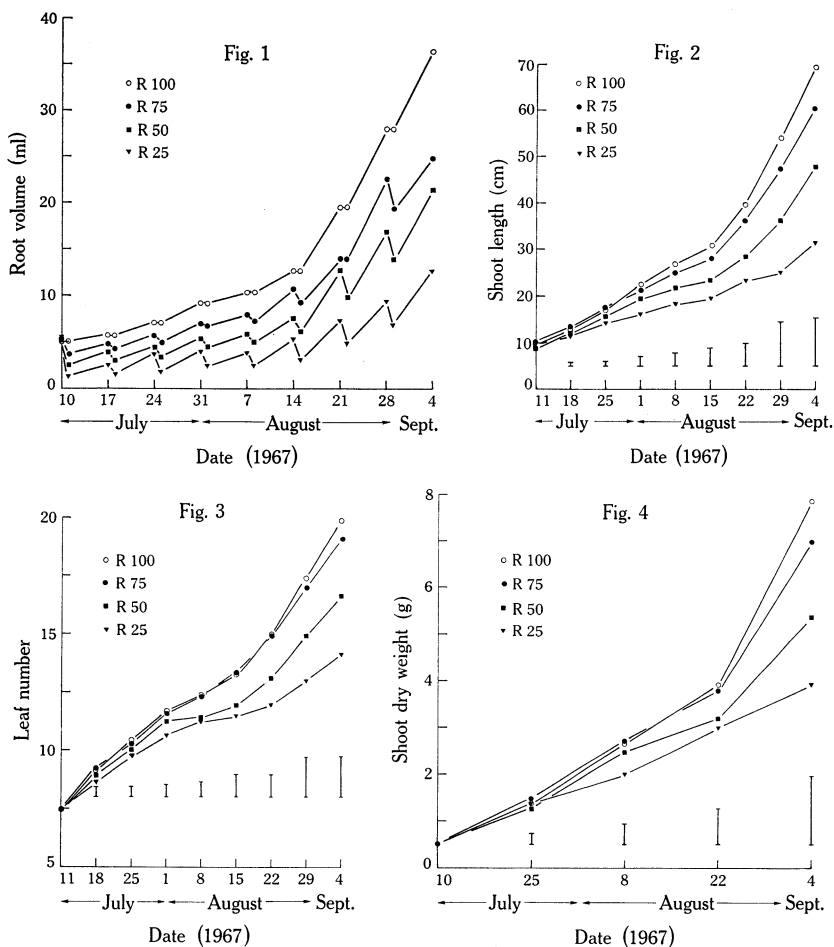


Fig. 1.—Mean root volume per plant for the four treatments during the experiment. Measured volumes prior to pruning are plotted above the appropriate dates, and volumes immediately following pruning are offset by a little more than 1 day.

Figs. 2–4.—Mean shoot lengths (Fig. 2), leaf numbers (Fig. 3), and shoot (stem+leaves) dry weights (Fig. 4) for the four treatments during the experiment. Vertical bars correspond to least significant differences ($P = 0.05$) for each occasion.

obtained for R75 was consistently lower from August 1 onwards. It follows that weekly increments in shoot length were consistently lowest for R25, followed in turn by R50, R75, and R100. In all treatments the rate of shoot extension decreased after July 29 and then increased rapidly after August 12.

Leaf numbers are plotted in Figure 3. Treatment effects were similar to those pertaining to shoot lengths, though it will be noted that the lag phase was more pronounced and the second phase of growth was evident a week earlier, viz. August 5.

Shoot (stem plus leaf) dry weights are plotted in Figure 4. The weight of R25 shoots was reduced from August 8 onwards, but the weight of R50 shoots differed from R100 only at the final harvest. The results on no occasion showed a difference between R75 and R100 dry weights. Total leaf areas per plant showed parallel trends to dry weight, and are not presented separately.

To examine how closely the effects on shoots were related to root volume, mid-week root volumes and weekly increments in shoot length and leaf number were expressed as percentages of R100 values, to give the data in Table 1. Shoot dry

TABLE 1
MID-WEEK ROOT VOLUME AND WEEKLY INCREMENTS IN SHOOT LENGTH AND LEAF NUMBER FOR ALL TREATMENTS, EXPRESSED AS PERCENTAGES OF R100 VALUES

Date	Root Volume				Shoot Length				Leaf Number			
	R100	R75	R50	R25	R100	R75	R50	R25	R100	R75	R50	R25
Aug. 12	100	77	54	33	100	79	44	33	100	125	63	38
Aug. 19	100	73	57	32	100	90	55	39	100	89	67	28
Aug. 26	100	72	56	30	100	75	53	14	100	88	71	42
Sept. 1	100	71	55	30	100	88	78	42	100	84	68	44
Mean	100	73	56	31	100	83	58	32	100	97	67	38

weight increments between August 22 and September 4 were in the proportion 100:83:55:23 for the R100, R75, R50, and R25 treatments respectively. Attention has been confined to the final 4-week period when growth was not complicated by the lag period. There was weekly variation, but considering mean values only, a similarity between those for root volume and shoot length, as well as those for root volume and shoot dry weight, can be seen whereas values for leaf number did not agree so well.

IV. DISCUSSION

This experiment has established that the growth rate of shoots of young grapevines established from cuttings can be regulated by the size of the root system. In seeking reasons for this regulation the following possibilities may be considered:

- (1) supply of water;
- (2) supply of inorganic nutrients;
- (3) pruning damage;
- (4) redistribution of photosynthetic products with roots gaining and shoots losing;
- (5) supply of growth substances by roots.

There was no evidence of wilting among treated plants, even after the initial pruning. Furthermore, towards the end of the experiment, on August 30, measurements

were made of the water deficit (Hewlett and Kramer 1963) of the youngest fully expanded leaf from 10 plants from each treatment, using the leaf-disk method of Weatherley (1950). The results were as follows: R100 6.4%; R75 9.0%; R50 7.5%; R25 5.2%. There is thus no evidence that shoots on treated plants suffered from inadequate water supply. Analyses were not made for inorganic nutrient contents, but plants were observed closely for deficiency symptoms throughout the experiment. No such symptoms were observed, and it was noted that leaves on R25 plants were darker green than on plants of other treatments. There is thus no evidence that treated plants suffered from inadequate inorganic nutrient supply. Effects on the shoot of pruning damage to roots can be excluded on the grounds that the number of roots cut did not differ greatly between treatments, whereas shoot-length increments did differ markedly. The fourth possibility, namely that there was a redistribution of photosynthetic products, was investigated by calculating the dry weight data presented in Table 2. These data show that in the first 2 weeks, before leaf area or

TABLE 2
AMOUNT AND DISTRIBUTION OF DRY-WEIGHT INCREMENTS FOR
TREATMENTS R100 AND R25 DURING THE INITIAL PERIOD OF
THE EXPERIMENT

Period	Plant Part	Dry-weight Increment (mg)	
		R100	R25
July 10-25	Shoot	0.843	0.822
	Root	0.116	0.165
	Shoot+root	0.959	0.987
July 25-Aug. 8	Shoot	1.283	0.674
	Root	0.286	0.223

photosynthetic potential differed appreciably between treatments, root pruning indeed resulted in additional organic nutrient supply to roots and reduced supply to shoots. However, the added supply to roots was some $2\frac{1}{2}$ times greater than the reduction in supply to shoots, suggesting that a simple redistribution of photosynthetic products had not occurred; rather, the suggestion is that photosynthetic efficiency was enhanced. Data from the second 2-week period give still less support to any suggestion that reduced shoot growth is due to competition by roots for organic nutrients. There remains the possibility that shoot effects were due to changes in amounts of growth substances supplied by roots, and some consideration will be given to this suggestion.

Went (1938) postulated a hormone produced by the roots which affected shoot growth, and more recently a number of workers have demonstrated the presence of plant growth substances in bleeding-sap exudate. For example, Kende (1965) found cytokinin activity in sunflower sap and Loeffler and van Overbeek (1964), Nitsch and Nitsch (1965), and Skene and Kerridge (1967) have evidence for the presence of cytokinins in the bleeding sap of grapevines. Substances with gibberellin-like activity have also been found in the bleeding sap of sunflower

(Phillips and Jones 1964), as well as grapevine (Skene 1967). Furthermore, Mullins (1967) found that in non-rooted grapevine cuttings there was a weak growth of extension shoots, and inflorescences failed to develop. Vigorous growth of both shoots and inflorescences occurred when woody cuttings bore a root system before bud-burst, and growth of shoots and inflorescences was promoted when non-rooted cuttings were treated with cytokinins.

It is also commonly held that roots are important to the plant as a site of amino acid synthesis, and indeed Bollard (1957) has shown with a large range of species, including grapevine, that most nitrogen in the tracheal sap is in amino form. There is thus indirect evidence that the size of a root system could influence shoot growth on account of growth substance supply. The question as to whether gross size of root system or the number of root tips is important in this respect has not been investigated in the present experiment.

Shoot growth is the result of both division and extension of cells, and it may be questioned whether root pruning affected one activity rather than the other. The only available measure of cell division is leaf number, and Figure 5 shows that the relationship between shoot length and leaf number was not measurably changed by treatment. This would suggest that both activities of cell growth were affected.

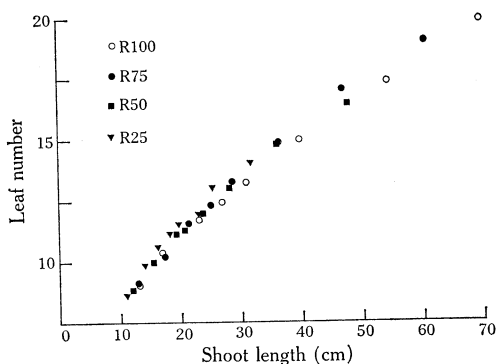


Fig. 5.—Relationship between shoot length and leaf number for the four treatments during the experiment.

There is, however, an indication from Table 1 that root pruning retarded extension growth more than leaf-number increase so that it is possible that the primary effect was on cell extension.

It is a common observation that the shoots of newly planted and young grapevines grow more slowly than those of established, older plants. This is most frequently accounted for on the basis of the greater amount of carbohydrate reserves contained in old plants; it is assumed that much of the new shoot growth is at the expense of reserves. There is, however, no direct evidence to support this assumption. An alternative explanation follows from the results of this experiment. Newly planted grapevines have a small root system available for each shoot, whereas established plants may have a very much larger ratio of root to shoot number. Shoot growth may be regulated by some factor arising in roots, the amount of this factor being related to the size of the root system.

V. ACKNOWLEDGMENTS

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