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Volcani Institute of Agricultural Research, Rehovot, Israel

The Determination of Induction and Differentiation in Grape Vines[1]

by

S. Lavee*), U. Regev and R. M. Samish

Introduction

The grape vine bud is a mixed bud containing both vegetative and fruit primordia. No morphological signs are known for distinguishing between differentiated and non-differentiated buds (26). Differentiation in grape vines occurs in the spring in the newly formed buds of the developing shoot (14). The proportion of buds in which differentiation to flower primordia occurs differs among varieties. In the Sultana grape vine 30—40% of the buds differentiate (4) while in Alphonse Lavallee 100% is rechaed (17).

In this work we tried to determine the time of "physiological differentiation" as distinguished from "apparent differentiation" when primordia are detectable by means of bud dissection, referred to here as „differentiation".

Differentiation of buds was found to be affected by their position along the shoot (4, 27). For differentiation experiments it was therefore important to choose those buds the location of which provided maximum differentiation potential.

Various m thods have been described for the determination of differentiation. Many investigators, both with grapes (2, 4, 26, 33) and with other fruits (5, 6, 9, 29), utilized the morphological appearance of flower primordia in the buds for differentiation detection. However, the time of induction could not be determined by optimal means. Hochberg (17) tried, by decapitation of the shoots at various dates in spring, to force the newly formed buds to sprout and thereby to determine the differentiation in the same season.

The theories concerning the biochemical mechanism of flower bud differentiation postulate (8, 18, 19, 21, 23, 25) that the active material is produced in the leaves. This was confirmed by Harley *et al.* (15) and Knott (20), showing that the presence of leaves was obligatory in the process of differentiation.

The transfer of the impulse for differentiation from the leaves to the buds enables a determination of the time of induction by means of defoliation (12, 13, 16, 30). Therefore, with the grape vine we employed defoliation at successive constant intervals to determine the time of induction. In addition we sought to determine the time interval between induction and visible differentiation which would represent the time required for development of primordia.

The relation between leaves and differentiation had been described as an accumulation of metabolites. Gardner *et al.* (14) and others (1, 6, 10, 16, 24) showed the need of accumulation of carbohydrates as a condition for differentiation. On the other hand, the accumulation of soluble carbohydrates was shown to inhibit differentiation (27.) Other workers have emphasized the significance of auxin transport

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*) Present address: Dept. of Biology, Yale Univ., New Haven, Conn. U. S. A.

(8). All these factors must be considered when girdling techniques are used to study the flow of the induction impulse from one branch to the other. Such a movement of the impulse was demonstrated by REECE and his co-workers (28, 30) in the mango and was also generally described by CHANDLER (10) and LANG (21), who suggested that the impulse is not polar-directed but can move in both directions in the plant. In a previous work with olive, however, we could find no effect of girdling, thus there was no transfer of the induction impulse to the defoliated branch from the neighboring normal shoots (22). In the present work we tried to determine the transport of the initiation impulse from one branch to another in the grape vine by performing defoliation and strangling experiments.

Materials and Methods

The plant material: Alphonse Lavallee and Sultana grape vine varieties were chosen for the determination of the time physiological induction and distinguishable differentiation in grape vine buds occures.

Eight-year-old ungrafted Sultana and Alphonse vines grafted on 8 B were taken. In a vineyard on alluvial loam at Miqwe Ysrael located in the coastal plain, each variety was growing in a separate plot. With Sultana the relative amount of differentiating buds increases gradually from the base to a maximum in buds 5—11 (33). With Alphonse full differentiation is found even in basal buds (17). Therefore, we chose for our experiments the 7th fully developed bud from the base in the Sultana and the 2nd and 4th buds in Alphonse (not counting the basal buds at internodes shorter than 1 cm).

The experiments were performed in spring 1960. The sprouting was not uniform in both varieties. In the Sultana it started from a few buds on March 16th and continued for ten days. For the experiments we used shoots from buds which opened in the middle of the sprouting season, namely March 21st (± 3 days). With Alphonse sprouting started on March 28th and continued for 8—10 days. We tried to choose the shoots of buds which opened on April 2nd (± 2 days). For each variety and treatment we used 12 replicates ditributed at random.

Treatments: Defoliation and strangling methods as described for other fruit species (1, 3, 22, 24, 30) were chosen. Four treatments were given to canes of each variety: (1) defoliation, (2) defoliation + strangling, (3) strangling, and (4) untreated control.

Defoliation was performed by removing all leaves above the bud to be examined (7th, Sultana; 2nd, Alphonse), including the leaf subtending the bud. Strangling was carried out by tying raffia around the cane in the middle of the internode below the examined bud. The raffia was fastened tightly but injury to the xylem was avoided. An early experiment of girdling by ring barking failed because a high percentage of the canes broke.

The treatments were repeated (each time on different canes) for 6 successive dates at intervals of 9—10 days from April 20th — June 4th.

Field measurements: At each date of treatment we determined: 1. lenght of the shoot above the bud to be examined; 2. number of leaves from the bud to the apex (counting only leaves with an area over 1 cm^2); and 3. total leaf area of the counted leaves. Measurements of length and number of leaves were made at each date on 48 replicates, determination of leaf area was made on 12. Leaf area was determined by a method based on a comparison between area and weight (7). Comparison of this method with planimetric measurements in grape vines revealed no

significant difference between the two methods, while the one used was quicker and easier to handle.

Preparation and analysis of buds: Immediately after collection the buds were immersed in 70% ethanol for later examination. For differentiation determinations the buds were collected every 9—10 days from April 20th to June 4th. For determination of the induction time all buds were collected on June 13th. Determination of the percent of differentiation in the buds was made during September 1960. The buds were dissected under a binocular (enlargement 20x, 60x) and differentiation determined according to WINKLER and SHEMSETTIN (33) and others (2, 4, 6). The appearance of a wide round body near the apex with 2—3 cuts in it indicates the beginning of formation of the bunch primordia. On June 13th, when the samples for determination of induction time were taken, the primordia had the complete bunch form.

Statistical methods: In all cases where percents of differentiation were compared, a t-test was used after a transformation of the percent to an angle, the sinus of which was the square root of the equivalent percentage (31). The t-test was applicable because in these experiments there was a logical comparison only of pairs of treatments at a time. The percentage of differentiation at each date and treatment was a mean of 12 measurements. Comparison of the standard deviations of the various measurements was also subjected to the t-test. The critical t was in all cases for a significance of $P = 0.05$.

For the strangling treatment we tried to fit a linear regression of the percent of differentiation on a basis of leaf area and also shoot length. The method of least square regression was used (11) with the assumption that the regression line would be linear.

Experimental Results

The percent of differentiation in the 7th bud of Sultana and the 2nd of Alphonse Lavallee, as affected by the defoliation treatments, is shown in Table 1.

Table 1

The effect of defoliation and strangling at successive dates on the percent of differentiation in the 2nd bud of Alphonse Lavallee and the 7th bud of Sultana. (Analysis June 1960, differentiation in per cent)

Date of treatment	Alphonse Lavallee (2nd bud)				Sultana (7th bud)			
	Defoliation	Defoliation + strangling	Strangling	Control	Defoliation	Defoliation + strangling	Strangling	Control
20/IV/60	0	0	67		0	0	33	
30/IV	33	50	75		0	0	42	
9/V	75	67	83		17	8	33	
18/V	92	83	100		33	25	50	
27/V	100	100	100		42	33	42	
4/VI	92	100	100		42	33	42	
13/VI	—	—	—	96*	—	—	—	42*
Expt. t	0.56		—		3.02		0.25	
Critical t	2.57		—		2.36		2.57	

* Results of 36 shoots, all other data derived from 12 shoots.

The untreated Alphonse Lavallee shoots showed a differentiation level nearing 100% (already in the second bud) while that of Sultana (even in the 7th bud) reached only 42%.

In both varieties early defoliation prevented or reduced differentiation. The later treatments were ineffective, with results similar to the respective control. The time of induction for the differentiation could be determined as a period between the last defoliation date preventing differentiation and the first one showing it. Strangling the shoot below the examined bud had no effect on the time of induction. It did,

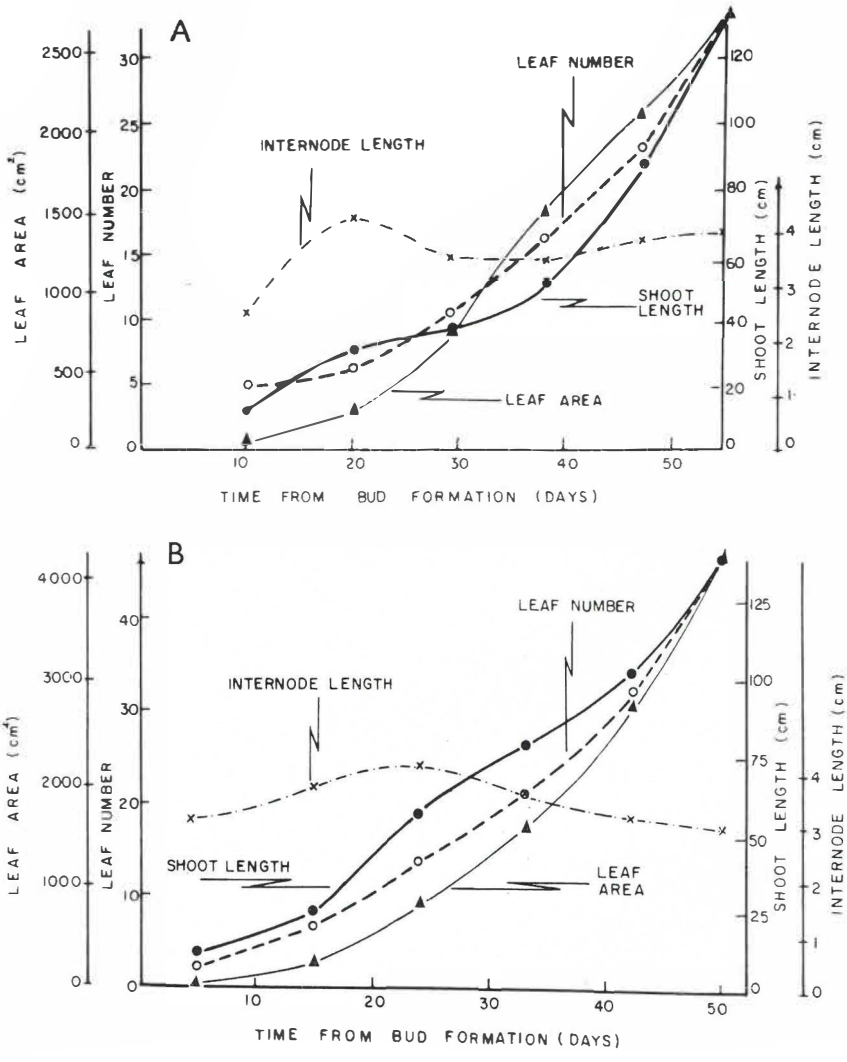

Fig. 1: Length of shoot, number of leaves and their area above the seventh bud of Sultana canes (A), and above the second bud of Alphonse Lavallee (B) at the various treatment dates.

Each point is the mean of 48 measurements expressed on the basis of days from the appearence of the examined bud.

however, cause a reduction in the percent of differentiation which was even significant with defoliated Sultana shoots. With Alphonse early strangling reduced the differentiation of undefoliated shoots. Thus it was suggested that induction was not induced by the leaves below the examined bud and the effect of the strangling was mainly a nutritional disturbance.

The quantitative analysis of the cane development at the various dates of treatment made by measuring the length, leaf area and leaf number of the shoots from the examined bud to the apex at each date of treatment, is shown in Fig. 1.

The growth at time of defoliation treatments was very intensive. The inclination of the curves, expressing growth rate, increased throughout the experiment (last recording June 4th). The curve for leaf number is hyperbolic in both varieties. On the other hand, the shoot length curves in Sultana show a slow rate up to 45 cm while thereafter the rate increases sharply and stays strong and linear to the end of the experiment. In Alphonse this curve is close to linear from the first (10 cm length) to the last measurements (140 cm length). The curve for leaf area is hyperbolic for Alphonse and sigmoid for Sultana. The length of the internodes at the various dates of the treatments is expressed as the ratio between length of the shoot and its number of leaves. In both varieties the resulting curve is around a horizontal axis reaching a maximum during the first 10 days of May.

From the curves describing shoot development we tried to determine the most suitable calculation base for the differentiation curves. The standard deviation, as percent of mean on each date, was calculated for each of the three curves (Table 2).

The standard deviation of leaf area was relatively larger than that of other measurements. This difference, which was statistically significant, might be due partly to the fact that these deviations were calculated from only 12 measurements

Table 2

Standard deviation of length of shoot, number of leaves, and leaf area in Alphonse Lavallee and Sultana expressed as per cent from the mean on each treatment date.

Date	Shoot length (cm)		Number of leaves		Leaf area (cm^2)	
	Sultana	Alphonse Lavallee	Sultana	Alphonse Lavallee	Sultana	Alphonse Lavallee
20/4/60	7.7	4.0	4.7	4.2	12.3	11.3
30/4	5.7	4.1	2.9	3.4	10.4	10.5
9/5	4.6	2.6	3.6	2.7	9.9	7.8
18/5	4.7	3.5	4.2	4.0	10.6	9.7
27/5	2.6	1.8	3.2	3.9	8.5	4.8
4/6	3.2	2.0	2.9	2.9	4.4	6.1
Number of measurements on each date	48	48	48	48	12	12
critical t $t_1 = 2.2$ $t_2 = 2.12$		$t_1 = 1.1$		$t_2 = 4.9$		Sultana
		$t_2 = 5.2$				
	Alphonse Lavallee	$t_1 = 1.4$		$t_2 = 4.1$		
		$t_2 = 4.4$				

each, while the others were based on 48. No significant difference was found between the deviations of leaf number and shoot length (t_1). It should be noted that the standard deviations decreased with time, which indicated an increase in reliability of the measurements in the more developed canes. With both varieties similar results were obtained.

Due to the similarity of the various growth curves and their standard deviation, we decided to examine the correlations between differentiation and each of the different criteria, namely, time in days, leaf number, leaf area and shoot length. The time of bud formation was calculated from an interpolation of the various curves of development, allowing a possible deviation of $\pm$ 4 days. The correlations between differentiation and the four criteria as induced by defoliation and strangling. are shown in Fig. 2.

The differentiation curves of both varieties according to all four bases show, in the defoliation treatments (with and without strangling), a rapid increase in the percentage of differentiation, which levels off at the later dates of treatment. A point of inflection in these curves could be suggested. The differentiation curves of the strangling treatment (without defoliation) of Sultana fluctuate around a horizontal line the tolerance interval of which includes the control. With Alphonse this is not the case, as the control was 100% differentiated.

In Sultana the differentiation curves of both defoliation treatments are similar. However, in Alphonse they have a slightly different tendency. While the differentiation curve of the defoliation treatment is similar to that of the Sultana, the one for defoliation + strangling shows a slight lag period in the middle. Since, as suggested earlier, the strangling effect was not directly connected to induction, we will consider here the defoliation treatment only.

The calculated point of inflection of the curves might serve as a criterion for the end of the induction period for differentiation. When calculated on the basis of bud age, the point of inflection is 40—45 days in the Sultana and 30—35 days in Alphonse after the formation of the examined bud. Thus Alphonse concluded its induction period in 10 days less than did Sultana.

It was of interest, though, that about the same number of leaves, 18—21, were needed in both varieties in order to reach the inflection point of the curve. On the basis of shoot length, induction terminated in Sultana with 10 cm less (60—65 cm) than in Alphonse (70—75 cm). These results point to a greater vigour and more rapid growth of the Alphonse. When differentiation was calculated on the basis of leaf area a significant difference was found between the varieties. While in Sultana the point of inflection of the curve is at a leaf area of 1800—1900 cm^2, Alphonse reached this point with a leaf area of only 1100—1200 m^2. Thus in Alphonse less than ⅔ of the leaf area of Sultana was needed to achieve the completion of the induction period.

The effect of the strangling (without defoliation) at early dates showed a decrease in differentiation (Fig. 2). However, by examining the difference of the curve from a horizontal line with the least square regression method, we found that for Sultana it was not significantly different from a straight line: on a time basis, $t = 5.6$; on leaf area basis, $t = 3.2$, while the critical t was 2.75. In Alphonse, on the other hand, the lines were significantly different from the control line, as on time basis, $t = 1.17$, and on leaf area basis, $t = 1.18$. In the strangling of Alphonse, therefore, the hypothesis of a horizontal line for differentiation was not substantiated. However, it should be noted that natural differentiation was about 100%, precluding the possibility of increase. At early stages the strangling was a severe treatment which damaged the xylem, as on the first date of treatment six of the shoots declined and

the other six reached the end of experiment in a poor condition despite the presence of the leaves.

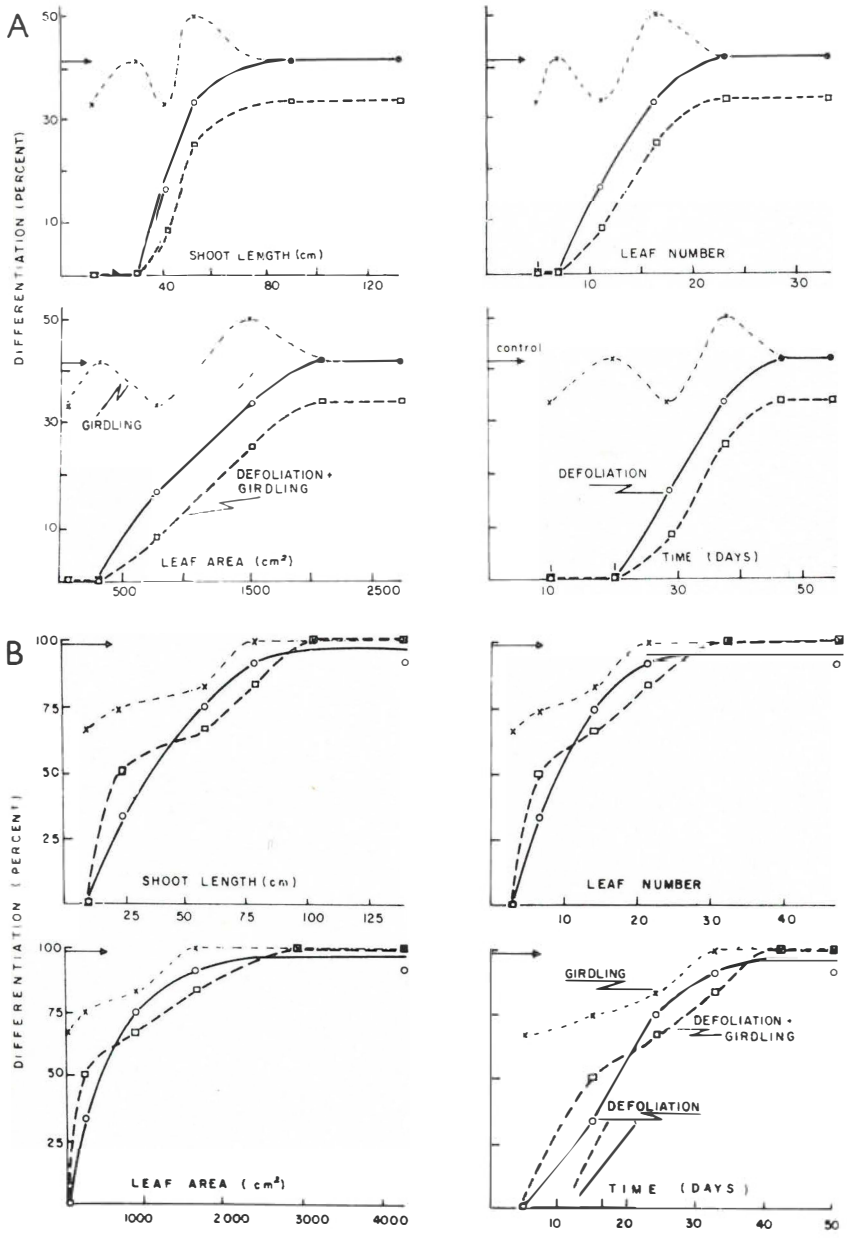

Fig. 2: The effect of defoliation at various dates on the differentiation of the 7th bud of Sultana canes (A) and the 2nd bud of Alphonse Lavallee canes (B) expressed on four different bases.

All measurements from above the examined bud; strangling = girdling.

Table 3

The stages of development of shoots at start and mid value of induction in Alphonse Lavallee and Sultana vines according to the defoliation treatment (all measurements above the examined bud).

Measurements	Sultana 7th bud		Alphonse Lavallee 2nd bud	
	Start of induction	Mid value of induction	Start of induction	Mid value of induction
Leaf number	7	12	3	9
Shoot length (cm)	30	43	9	35
Leaf area (cm)	310	925	28	440
Date	30/4/60	11/5/60	20/4/60	4/5/60
Time from bud formation (days)	20	31	5	19
* Time from mid bloom (days)	—9	—2	—19	—5

* May 9, 1960, was chosen as mid bloom. Flowering started in both varieties on May 2nd and continued for two weeks.

As the point of inflection in the differentiation curves was not a definite one, we tried to find more objective criteria for induction determination. The start of induction, determined as the last defoliation date on which no induction was found, and 50% differentiation, determined as the date on which half the maximum induction of the tested variety occurred, were chosen. For Alphonse, 47%, and for Sultana, 20.8% of differentiation were determined as the half values. The development of the vines at these start and mid values of induction is shown in Table 3.

The start of induction in Alphonse preceded that of Sultana both on a basis of time from the examined bud formation, and shoot development. These results correspond with those obtained for the end of induction, except for the number of leaves needed, which was — at the end stage — equal for both varieties.

In Alphonse the time interval needed for differentiation of a higher bud was determined. The rates of differentiation according to all calculation bases, when measured from the second bud, were lower in the 4th than in the 2nd bud up to the end of induction when both buds reached the full percent of differentiation (96

Table 4

The lag of development of shoot between the second and fourth buds of Alphonse Lavallee at mid value and end of induction.*)

Induction	Bud position	Time from bud formation (days)	Leaf area (cm^2)	Leaf number	Shoot length (cm)
Mid value	2nd	19	440	9	35
	4th	21	560	11	42
	Difference	2	120	2	7
End value (point of inflection)	2nd	32	1190	19	77
	4th	37	1470	23	94
	Difference	5	280	4	17

* All measurements from second bud to apex.

100%). The difference represents the lag in time and development of shoots between the differentiation of the two buds. A comparison of these differences at the mid value and end of induction of the two buds is shown in Table 4.

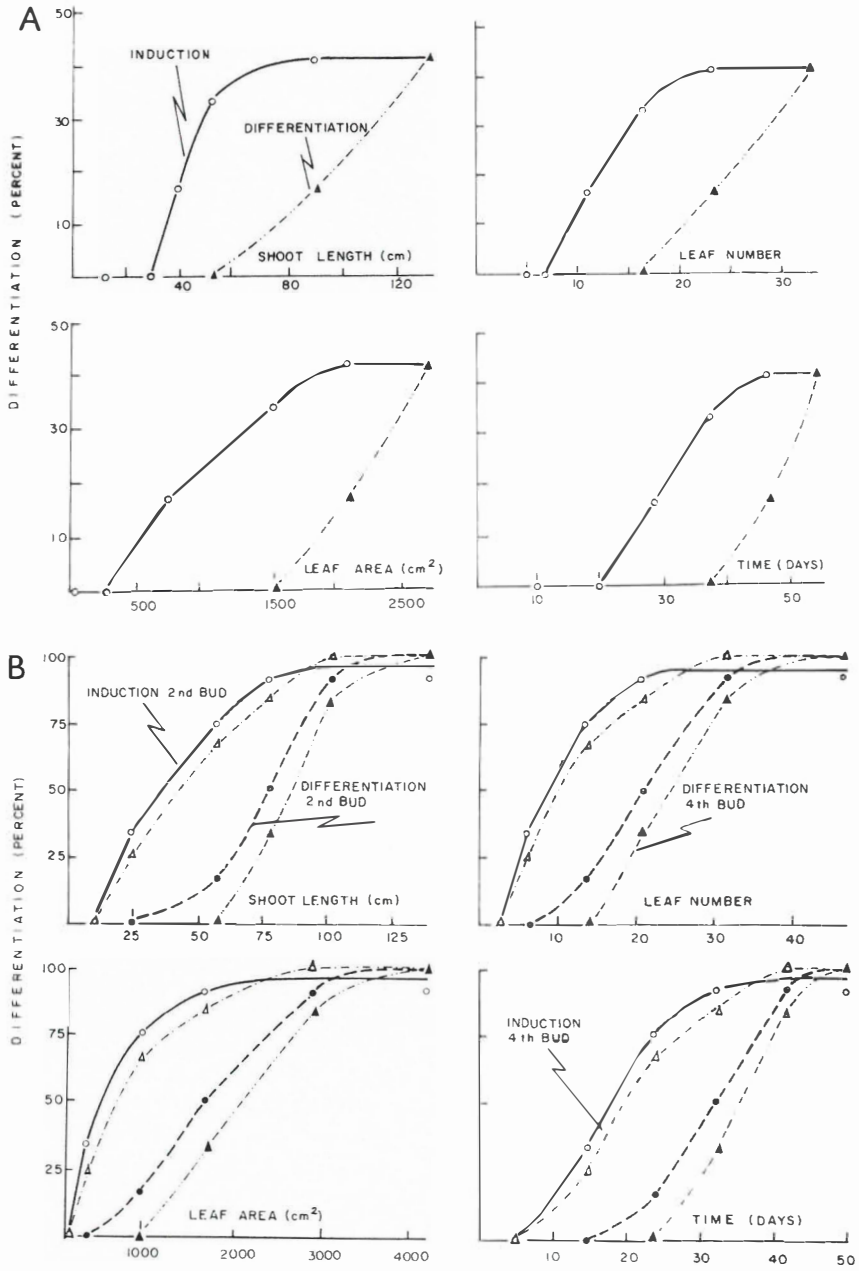

Fig. 3: A comparison between induction and differentiation in Sultana (7th bud) and Alphonse Lavallee (2nd and 4th buds) on 4 bases calculation.

After induction in the 2nd bud another 2—5 days, accompanied by an addition in leaf area (120—280 cm^2), leaf number (2—4) and shoot length (7—17), were needed for induction in the 4th bud.

Time of differentiation was determined as the date on which primordia were first observable during bud dissection under a binocular. These determinations were made in buds removed from normal shoots at each date of defoliation for induction time determination. A comparison between induction and differentiation in the examined buds of both varieties was made on the four calculation bases (Fig. 3).

The lag in time and development between induction and differentiation shown along the curves was significant for the whole experimental period in both varieties (calculated t for Alphonse was 5.7, and for Sultana, 3.4; critical t for both varieties was 3.18). The difference in time and development of shoots, between induction and differentiation, could be considered as the period needed for the primordia to develop. This period was calculated on the four bases of development for both varieties at the mid values of induction and differentiation (Table 5).

The rapidity of growth of Alphonse during the period between induction and differentiation was much higher than that of Sultana, similar to what was shown earlier for the induction period itself. However, the number of leaves and their area, formed between induction and detection of the primordia with the binocular, was similar in both varieties (a difference less than 8%). It may be concluded that differentiation, defined as development of the primordia, is a growth process no longer dependent on the induction.

A comparison between differentiation in the 2nd and 4th buds of Alphonse showed that their principal behavior was very similar except for a consistent delay in the latter, which was due, in both cases, to measuring from the second bud upwards. Therefore, this delay, which paralleled that of induction time, represents the period of time and development needed for the higher bud formation.

Discussion

The time of differentiation of grape vine buds has usually been determined as the time when the primordia could be detected by dissecting the buds under a

Table 5

The difference in time and development of shoots between induction and differentiation in Sultana (7th bud) and Alphonse Lavallee (2nd bud) at mid values.

Object	Leaf area (cm^2)	Leaf number	Shoot length (cm)	Date (days)
		Sultana		
Induction	925	12	43	May 11
Differentiation	2220	25	99	May 29
Difference	1295	13	56	18
		Alphonse Lavallee		
Induction	440	9	35	May 4
Differentiation	1650	21	78	May 18
Difference	1210	12	43	14

binocular (4,33). Another method is based on severe decapitation of the shoots, thereby forcing the buds to burst in the same season (17). Both methods give a good indication of the time and amount of differentiation but do not determine the time of induction. In the first method the appearance of the primordia itself is determined, and in the second the leaves left above the examined bud continue to induce differentiation also after the decapitation. In this work we could show that by means of defoliation it was possible to determine the induction time in grape vine buds similar to what was shown for other fruit species (1, 12, 30, 32).

The factors initiating differentiation, produced in the leaves, seem to behave differently in various species. CHANDLER (10) and other (21, 34) showed that the impulse can move down in one branch and up into another. With grape vines we could not confirm this. It seems that here the induction impulse comes only from the leaves located at and above the examined bud, as differentiation stopped both in strangled and unstrangled early defoliated canes. The strangling, replacing classical girdling due to the softness and breaklage of young canes, had no direct effect on induction and differentiation. The reduction in the amount of differentiation on the strangled canes seems to be due to nutritional disturbances mainly in defoliated canes, where severe deficiency in both mineral and organic nutrients must have occurred. Similar results were obtained with olives (22), where girdling also had no effect on the time of induction but reduced slightly the amount of differentiation. No antagonism between growth and differentiation could be found in the grape vine. Furthermore, it was shown that both induction and differentiation in the buds took place at the time of most intensive growth and were correlated with it. This might suggest that the hormone-governed processes leading to induction in the grape vine are on a different level than in many other fruit species, or that the equilibrium between growth and flower hormones at which induction occurs (23) takes place under specific conditions. It should be noted though that this does not eliminate the possible correlation between the general vigour of a variety and its fruitfulness, as in this work time of induction and differentiation were determined only in relation to the growth curve within the same variety.

The greater fruitfulness of Alphonse in comparison to Sultana is known (17). In this work it could be shown that in order to complete the possible induction about the same length of shoot and number of leaves were needed in both varieties. Still the Alphonse reached this stage in a shorter time than, and with about ⅔ the leaf area of Sultana. Furthermore, the percent of differentiation in Alphonse was about double that in Sultana. A similar value regarding leaf area was obtained also at the mid value stage. Thus it could be concluded that the efficiency of the leaves per unit leaf area, in producing factor for differentiation, was significantly higher in the Alphonse variety. Leaf number and shoot length seem to be preferred criteria for determination of the induction period as they were less variety dependent than were time from bud formation, and leaf area.

The interval between induction and differentiation expresses initial primordial development, i. e., from time of induction to microscopic detection. Regardless of the different efficiency of the leaves of the two varieties in inducing induction, the leaf area needed for the development of the primordia was rather similar in both varieties. On a time basis, however, the primordia development period was shorter in Alphonse than in Sultana. This could be explained by the more rapid rate of development of this variety, as shown earlier. Therefore, it seemed that the development of the primordia is a growth process dependent on the vigour of the variety and not on the process connected with the induction and its efficiency.

The time difference in differentiation of the second and fourth buds of Alphonse was about four days, or two days per bud. This result corresponds nicely with BARNARD's report (4) of a difference of 30 days between differentiation in the first and 16th buds of Sultana. Therefore, despite the differences between the varieties in efficiency, fruitfulness and growth, the rate of advancing differentiation along the cane was of a similar order in both varieties.

Summary

The induction and differentiation of 8-year-old Alphonse Lavallee and Sultana grape vines were studied.

1. Defoliation methods enabled us to determine the induction time in grape vines as in other fruit species.
2. Induction and differentiation in the tested varieties were not connected with temporary growth cessation; on the contrary, process took place during the most intensive growth.
3. A correlation was found between the number of leaves and induction period. 18—21 leaves above the examined buds were needed in both varieties to complete the induction.
4. The leaf area needed for induction in a bud of Sultana was 1½ times larger than that needed for Alphonse. The efficiency of the leaves of Alphonse to induce differentiation was thus greater.
5. The primordia development from induction to detection under the microscope (differentiation) was connected with a constant vegetative development. The time needed for this development was determined by the growth rate of the variety (18 days in Sultana, 14 days in Alphonse).
6. The translocation of materials inducing differentiation from the base of the shoot upwards has not been proved in our work.
7. In Alphonse a lag period of two days was found for the differentiation of each bud along the cane.

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Dr. S. Lavee
The Volcani Institute of
Agricultural Research
P. O. B. 15
Rehovot
Israel