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Shoot growth and anthesis in Vitis[1])

by

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La croissance des rameaux et l'anthèse de la vigne

Résumé. — La majorité des rameaux verts de la vigne montre un nombre assez constant d'entrenoeuds au moment de l'anthèse. *Vitis vinifera* L. (16—19) présente un plus grand nombre d'entrenoeuds que *V. labruscana* BAILEY (12—14). On retrouve dans diverses conditions (années, variétés, pays, climats, pratiques culturales) cette synchronisation de la vitesse du développement des noeuds de l'apex végétatif avec celle des fleurs sur les inflorescences. La vigueur de la vigne elle-même est le facteur responsable des plus grandes variations dans le nombre d'entrenoeuds au moment de l'anthèse.

Introduction

Grapevine shoot development has been divided into 4 morphological and chronological phases: (a) formation of nodes in the buds which become the dormant compound bud at the end of the first growing season; (b) formation of new nodes and elongation of all internodes from bud swell (BAGGIOLINI 1952) to anthesis in the spring of the next growing season; (c) further shoot growth, especially elongation of younger internodes, from flowering to midsummer; (d) slow growth and maturation of the shoot into a cane, from mid-summer to leaf abscission (BUGNON and BESSIS 1968, BERNARD 1974, 1975). Inflorescences form during phase (a) and flowers during phase (b) (CAROLUS 1970, 1971, SCHOLEFIELD and WARD 1975); fruit set and berry development occur during phases (c) and (d).

We had noted that at phase (b) grape shoots appeared to have a constant number of internodes. The preliminary data in Fig. 1 suggest that *Vitis vinifera* L. cv. Muscat Gordo Blanco in South Australia flowered when the shoots had an average of 17 visible internodes despite large differences in time of flowering and shoot length. We therefore investigated the morphological relationships of shoot growth and anthesis during phase (b) in several cultivars of *V. vinifera* and *V. labruscana* BAILEY growing in Australia and New York, U.S.A. Some observations were also made in Switzerland.

Materials and methods

There are at least two categories of shoots on most grapevines: the major and most obvious group is longer and has more nodes at the end of phase (d) in compar-

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ison with the shorter shoots of the smaller group (up to 30% of all shoots on a vine). Both groups may emerge from primary buds and may bear inflorescences. Our studies were confined to the larger group because they seemed more expressive of the growth potential of shoots of cultivated grapevines.

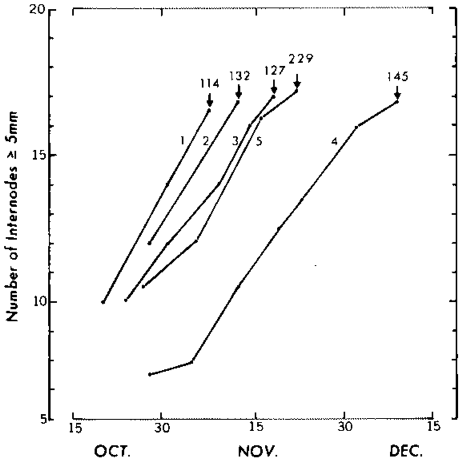

Fig. 1: Mean number of internodes per shoot of *V. vinifera* cv. Muscat Gordo Blanco in 3 vineyards in South Australia (1, 2 = Waikerie 1963, 1964; 3, 4 = Nuriootpa 1963, 1964; 5 = Waite 1964). Values are based on measurements of 20 to 30 shoots. The date of anthesis (↓) and the average length of the shoot (cm) on that date are indicated.

Nombre moyen d'entrenoeuds des rameaux chez *V. vinifera* cv. Muscat Gordo Blanco dans 3 vignobles en Australie du Sud (1, 2 = Waikerie 1963, 1964; 3, 4 = Nuriootpa 1963, 1964; 5 = Waite 1964). Valeurs basées sur l'observation de 20—30 rameaux verts. Sont indiquées la date de l'anthèse (↓) et la longueur moyenne des rameaux (cm) à cette date.

The 8 cultivars were examined at 3 different climatic sites (Tables 1 and 2). Vines in South Australia were spur-pruned and trained to a Claremont trellis (COOMBE 1974), and those in New York were cane-pruned and trained to Hudson River Umbrella (SHAULIS *et al.* 1972). White Riesling vines in 1975 in New York showed so much winter injury (SHAULIS *et al.* 1968) that it was difficult to select shoots that continued to grow throughout the flowering period.

About 25 actively growing, well exposed shoots per cultivar were randomly selected before flowering began at each site in South Australia and New York. Shoot measurements were made at 1-2-day intervals during the course of flowering. The number and lengths of internodes were determined along each shoot from the most basal internode ≥ 10 mm long to the most apical internode ≥ 5 mm. At the same time the percentage of flowers at anthesis (i. e., with caps (calyptras) abscised) on all clusters on each shoot was estimated. These data were plotted against time and the date of 70% anthesis was determined. This stage was selected because the rate of change was then rapid and hence the interpolated date had small variability

(Table 2). This date was applied to graphs of internode number and shoot length against time to determine values at 70% anthesis.

Table 1

Climatic data from weather stations near sites at which grape shoots were measured[1])

Données climatiques des stations météorologiques près des sites expérimentaux[1])

Site	Temperature (°C) Avg. daily		Temperature (°C) Absolute		Avg. relative humidity (%)		Avg. annual precipitation	
	Max.	Min.	Max.	Min.	A.M.	P. M.	Sum of monthly avg. (mm)	Avg. number of days with $\geq$ 0,3 mm
Waite Institute, Adelaide, South Australia	20.9	11.9	44.3	0.3	61	48	629	135
Albany, New York U.S.A.	13.9	4.4	40.0	—32.2	78	62	879	137
Zürich Switzerland	14.0	5.3	37.7	—23.2	86	60	1089	158

[1]) Sources: ANONYMOUS 1968, 1972; ANONYMOUS 1975). Averages are based on observations for 51, 57, and 30 years respectively.

Apical buds covered by the lowest pair of stipules and containing internodes < 5 mm were taken from 7—10 similar shoots at some sites during the flowering period. Under a stereoscopic microscope all emerged leaf primordia were counted to determine the number of internodes then initiated. The total length of the bud, negligible in relation to the entire shoot length, was not included in the shoot length.

Table 2

Shoot lengths and internode numbers of *Vitis* species at 70% anthesis

Longueur et nombre d'entrenoeuds des rameaux verts des vignes quand l'anthèse est réalisée a 70%

Site	Species	Cultivar	Year	Date	Shoot length (cm)	Number of internodes: Visible	Number of internodes: In shoot tip[2])	Number of shoots measured
Adelaide, South Australia	*V. vinifera*	Grenache	1974	Nov. 27.6 ± 0.6	104 ± 3	19.2 ± 0.3	7.5 ± 0.2	23
			1975	Nov. 17.6 ± 0.2	108 ± 3	18.7 ± 0.3	—	25
		Shiraz	1974	Nov. 25.8 ± 0.5	132 ± 5	18.1 ± 0.2	8.8 ± 0.2	23
			1975	Nov. 17.6 ± 0.2	143 ± 4	18.9 ± 0.2	—	25
		Cabernet Sauvignon	1974	Nov. 23.2 ± 0.4	90 ± 4	16.6 ± 0.2	7.5 ± 0.2	24
			1975	Nov. 16.7 ± 0.3	108 ± 3	17.5 ± 0.3	—	26
		White Riesling	1975	Nov. 14.8 ± 0.2	72 ± 3	16.4 ± 0.1	—	26
Geneva, New York	*V. vinifera*	White Riesling	1975	June 21.0 ± 0.3	67 ± 6	15.9 ± 0.7	9.5 ± 0.3	22
			1976	June 23.2 ± 0.2	80 ± 4	18.0 ± 0.2	10.8 ± 0.2	24
	V. labruscana	Concord	1975	June 15.7 ± 0.1	87 ± 5	11.5 ± 0.2	7.6 ± 0.3	20
			1976	June 17.8 ± 0.1	104 ± 4	13.5 ± 0.2	8.0 ± 0.3	22
Wädenswil, Switzerland	*V. vinifera*	Chasselas	1976	—	83 ± 4	16.2 ± 0.5	—	—
		Pinot noir	1976	—	94 ± 3	14.5 ± 0.5	—	—
	V. labruscana	—	1976	—	—	12.0	—	—

[1]) Visible internodes include those $\geqslant$ 10 mm long at the base of the shoot to those $\geqslant$ 5 mm long at the tip.

[2]) Internodes $<$ 5 mm include all those leaf primordia in the apical bud covered by the stipules of the lowest folded leaf.

This measurement was made only once during flowering, with the assumption that these values did not significantly change during the flowering period.

Shoot measurements at Wädenswil, Switzerland, were made on 24th June 1976 using a less exact method. 60 shoots each of Pinot Noir (clone 2/10) and Chasselas (syn. Weißer Gutedel) growing on 5 C rootstock on a "Zweietagen" system (EGGENBERGER *et al.* 1975) at the Federal Grape Station were assessed for internode number, shoot length, and percentage of anthesis. These figures were grouped into 5 or 6 classes based on stage of flowering, the averages and standard errors of the means of each calculated, and the values at 70% anthesis interpolated. On one vine of *V. labruscana* cv. unknown 7 shoots were assessed in the same manner.

To gain information on one possible source of variation in the internode number at flowering, shoots from vines showing different rates of shoot elongation were compared in 1975. Three 10-year-old Muscat Gordo Blanco vines at Adelaide were selected for their widely different shoot vigour brought about mainly by root restriction: the weak vine grew in a glazed pipe (length 53 cm, internal diameter 31 cm); the other 2 vines grew in a vineyard, the more vigorous vine being in an outside row. On each vine internodes of 3 shoots were measured on 4 dates, twice before and twice after 70% anthesis.

To determine the number of nodes formed during period (a), 21 primary buds from the lower 5 nodes of White Riesling canes in New York were dissected at bud swell in 1975, and the number of internodes assessed.

Results

The South Australian sites differed from the New York and Swiss sites in having hotter, drier summers and winter temperatures above freezing (Table 1). Irrigation was used in Australia to bring the annual precipitation up to about 760 mm (COOMBE 1974).

A striking feature of the shoot measurements is the low variability of the number of internodes per shoot at 70% anthesis (Table 2). The standard errors of the means are only 1.0 to 1.7% for all South Australian and New York data, except for the greater variability (4.4% of the means) of White Riesling in 1975 in New York. In contrast, the shoot lengths between sites and cultivars varied widely. The standard errors of the means of shoot lengths were 3 to 6% of the means, except for the greater variability (9%) of White Riesling in 1975 in New York.

It is clear that the mean numbers of internodes at 70% anthesis were consistently higher for *V. vinifera* (16—19) than for *V. labruscana* (12—14). The average internode number for *V. labruscana* was similar in Switzerland and New York. The values for *V. vinifera* were generally lower and more variable in New York and Switzerland than those for the same species in South Australia (Table 2).

The internode lengths of the 3 shoots from each of the Muscat vines of different vigour were similar and only one from each vine is shown in Fig. 2. The shoot lengths on 19th December indicate the large vigour differences in the 3 vines: 54, 141 and 243 cm. The number of internodes at 70% anthesis were 16.5, 18 and 22, respectively. Thus, although the variation within each vigour group was small, the differences between the groups were relatively large, in fact larger than the differences between *V. vinifera* cultivars growing in 3 countries (Table 1). It must be pointed out, however, that these differences in vigour were extreme. The differences in vigour were evident early in the growth of the shoot: the length of the internode above the basal

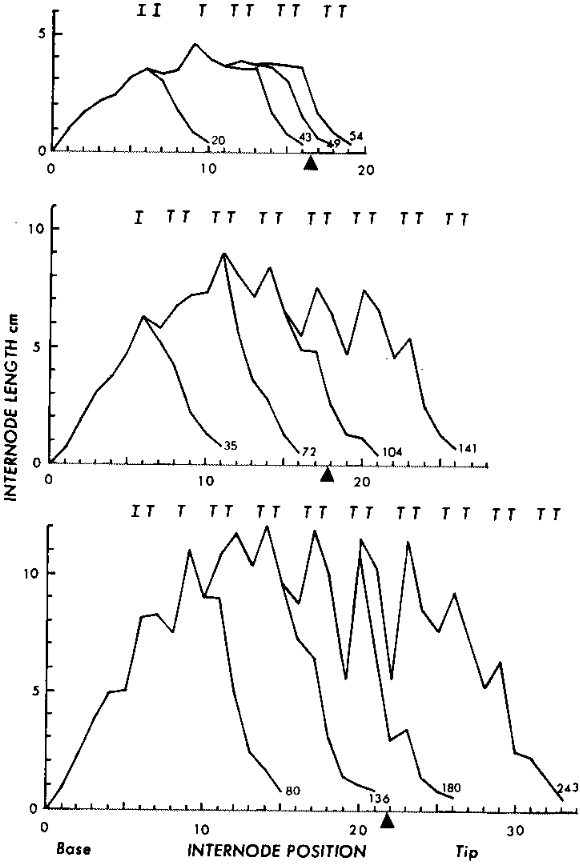

Fig. 2: Lengths of internodes on 4 dates (11th, 19th November; 1st, 19th December 1975) of a typical shoot on each of 3 vines of different vine vigour of *V. vinifera* cv. Muscat Gordo Blanco. The positions of inflorescences (I) and tendrils (T), the total shoot length (cm) on each date, and the internode number at 70 % anthesis (▲) are indicated. Top: weak vine; middle: normal vine; bottom: vigorous vine.

Longueurs des entrenoeuds d'un rameau sur 3 vignes de vigueurs différentes à 4 dates (11 et 19 novembre; 1er et 19 décembre 1975) chez *V. vinifera* cv. Muscat Gordo Blanco. Position de l'inflorescence = I; vrille = T; nombre d'entrenoeuds à 70 % anthèse = ▲; longueur totale du rameau à chaque date en cm. En haut: vigne faible; milieu: vigne normale; en bas: vigne vigoureuse.

inflorescence, which had attained its full size several weeks before flowering, appeared to forecast the total growth of the shoot by the time of anthesis because it was proportional to both mean internode length and node number.

The numbers of internodes within the swelling buds of White Riesling in New York, 1975, ranged from 6.2 to 8.3, depending on nodal position.

Discussion

The well developed shoots on a grapevine have a relatively constant number of visible internodes when anthesis occurs, even under widely different growing conditions. This number is greater in *V. vinifera* cultivars than in *V. labruscana:* we found means of 16—19 externally visible internodes at anthesis, in agreement with the values found by Bojinova-Boneva (1976) in Bulgaria for *V. vinifera* cultivars, and 12—14 for *V. labruscana* cultivars. With *V. vinifera*, vigour of the individual vine (Fig. 2) influenced internode number at flowering more than did cultivar, district and cultural conditions (Table 2).

The development of the shoot involves both node formation at the apical meristem and elongation of the internodes. The nodes formed up to the stage of anthesis comprise 2 categories: a) The basal nodes, about 8 in number, were present before bud break and were initiated within the primary bud during the first growing season (Barnard and Thomas 1933, May 1964). The number of nodes varies with position of the bud along a cane (Bugnon and Bessis 1968, Carolus 1970, Buttrose 1974) or cultivar (Bouard and Pouget 1971). It is similar in *V. vinifera* and *V. labruscana* (Pratt 1959). Some of these nodes bear inflorescences. The elongation of these internodes is completed before anthesis (Fig. 2), as shown by Jacquinet and Simon (1971). There is often a short internode (Carles *et al.* 1964, Jacquinet and Simon 1971) or a disruption of the 1-1-0 pattern of *V. vinifera* inflorescences and tendrils between this group of nodes and those which follow, as seen in Fig. 2 (Jacquinet 1974). b) Nodes initiated between bud break and anthesis include about 4 *(V. labruscana)* or 10 *(V. vinifera)* visible nodes and about another 8 at the shoot tip.

These results suggest that there is synchrony in the rates of development of new nodes and of flowers during period (b). It is possible that this synchrony is exercised by a dependence of the development of one organ on the development of the other. This could be tested by excision experiments. Another explanation is that the development of both may be influenced directly by the same factor; it would appear that this factor would not involve the elongation of internodes except under extreme circumstances (Fig. 2). Of hormonal candidates, the most probable are cytokinins produced by the roots (Buttrose and Mullins 1968, Mullins 1968, Pool 1975, Pool and Powell 1975), and distributed by partitioning of the xylem sap between the vegetative and the floral meristems.

However, shoot growth can be greatly modified by environmental factors. Shoot length and, to a less extent, the number of visible internodes tended to be less in New York and Switzerland, where below-freezing winter temperatures occur, than in Australia, which has warmer winters. Low winter temperatures tend to injure *V. vinifera* more than *V. labruscana* by freezing of buds or canes, or both (Shaulis *et al.* 1968). Cold injury to phloem and cambium in trunks and canes may limit or interrupt translocation during spring and affect the synchronous development of nodes and flowers. It also greatly affects shoot elongation (Pratt, unpublished data), but this effect is minimized in the present data by the progressive selection of growing shoots of White Riesling in New York. Growing season temperatures, which are lower in New York and Switzerland than in Australia, are known to influence the rate of internode elongation (BUGNON and BESSIS 1968, JACQUINET and SIMON 1971). Cultural practices, especially pruning and training, differed between sites, and may also account for some variation.

Summary

In the majority of shoots on a grapevine the number of internodes is fairly constant at anthesis. The number of visible internodes was higher in *Vitis vinifera* L. (16—19) than in *V. labruscana* BAILEY (12—14). This synchrony in the rates of development of nodes at the shoot tip and of the flowers on the inflorescences was found in a wide array of conditions (time, cultivars, countries, climates, cultural practices). The factor found to cause greatest variation between vines was vine vigour.

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