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Inflorescence initiation in grapes — response to plant growth regulators

by

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Die Frühentwicklung der Infloreszenzen bei der Rebe — Reaktionen auf Wachstumsregulatoren

Z u s a m m e n f a s s u n g : Junge Topfpflanzen der Rebsorte Riesling (*Vitis vinifera* L.) wurden in einem mehrfaktoriellen Versuch über die Wurzeln mit Gibberellin (GA_3), Indolylessigsäure (IAA), 6-Benzylaminopurin (BAP) und Abscisinsäure (ABA) behandelt. Jede Rebe wurde in regelmäßigen Zeitabständen insgesamt 7mal mit 100 ml einer 50 µM Lösung gegossen. In einem Freilandversuch wurden GA_3, IAA, Indolylbuttersäure (IBA) und Naphtylessigsäure (NAA) sowie 2,4-Dichlorphenoxyessigsäure (2,4-D) 3 Wochen nach dem Austrieb in den Stamm von Rieslingreben injiziert. Die Auxine induzierten mehr Blattprimordien, Ranken und Infloreszenzen und verkürzten die Internodienlänge in den Winterknospen der behandelten Reben. Auch die Entwicklungsgeschwindigkeit dieser Organanlagen war beschleunigt. An den Trieben der behandelten Reben war im folgenden Frühjahr die Anzahl der Blüten erhöht. GA_3 wirkte durchweg in entgegengesetztem Sinne wie die Auxine. ABA und BAP verringerten die Ausbildung von Ranken, Infloreszenzen und Blattprimordien in den Knospen, allerdings viel weniger als GA_3; in Kombination mit GA_3 angewandt schwächten sie jedoch dessen nachteilige Auswirkungen auf diese Organe ab. Die Untersuchung der Knospen erbrachte eine Vielfalt von Knospentypen. Ältere Reben wiesen Knospen mit mehr Infloreszenzen und Blattprimordien auf, besonders dann, wenn sie mit auxinartigen Verbindungen behandelt worden waren. Junge Reben hatten — ähnlich wie GA_3-behandelte ältere Reben — weniger Blattanlagen und Infloreszenzen. Wachstumsregulatoren, welche die Knospenfruchtbarkeit förderten, verkürzten auch die Dauer der Primordienentwicklung; es wird vermutet, daß diese beiden Phänomene kausal miteinander verbunden sind.

K e y w o r d s : bud, inflorescence, tendril, leaf, differentiation, growth regulator, auxin, gibberellic acid, cytokinin, abscissic acid.

Introduction

There is considerable evidence that plant growth regulators (PGRs) influence flower-bud initiation in both woody and herbaceous plants (ZEEVART 1978). Gibberellins are generally reported to reduce the initiation of flowers (see JACKSON and SWEET 1972; PHARIS and KING 1985), although they can promote it in conifers, and GA_4 has recently been found to increase flower initiation in cv. Golden Delicious apple (LOONEY *et al.* 1985). SRINIVASAN and MULLINS (1980 a and b) found that GA_3 enhanced the formation of anlagen (uncommitted, potentially reproductive, primordia), helped promote tendril formation, but inhibited inflorescences in grapes. Cytokinin application, on the other hand, tended to promote inflorescence formation and actually caused tendrils to turn into inflorescences. There is less evidence of the role of other PGRs, although JINDAL and DABAS (1982) have increased the formation of fruitful buds by sprays of auxin.

Most applications have been made by spraying the chemical onto the leafy shoots of plants. In the present experiments, various materials were applied to the roots of vines growing in nutrient culture. Evidence using autoradiography indicated that the

applied [14C]gibberellin A_3 (GA_3) and [14C]indole acetic acid (IAA) did move to the leaves and buds from the roots, and responses observed on shoot growth were consistent with other reported responses to these and other growth regulators (PALMA 1985). In other trials, field-grown plants were injected with GA_3 and several auxin-like compounds, and their effects on inflorescences and flowers were measured.

Materials and methods

Pot plant experiment

Single-node cuttings of *Vitis vinifera* L. cv. Riesling were rooted in an outdoor hot bed in late winter using a root temperature of 20 °C. After rooting they were transplanted into 15 cm diameter plastic pots filled with coarse sand and fed with Hoagland's No. 2 solution (HOAGLAND and ARNON 1938). They were grown in a glasshouse with a temperature range of 16—25 °C from 4 October to 4 December 1981 and then in a shadehouse for the remainder of the season. Light intensity was respectively 60 % and 40 % of ambient.

After leaf fall in early winter bud samples were removed from nodes 3, 10, 17, 24 — counting from the first separate node. They were stored in FAA (formalin : acetic acid : 70 % ethanol — 5 : 5 : 90), cut longitudinally with a freezing microtome to 20—25 µm, mounted and examined at 30—40 × magnification. Inflorescences and tendrils in each bud were counted and the means of the four buds were used for subsequent analysis.

Four PGR preparations were used : IAA, abscisic acid (ABA), 6-benzyl-aminopurine (BAP) and GA_3. Each was initially dissolved in a small volume of 10 % methanol at 40 °C and subsequently made up to the required volume with distilled water.

The experiment was a complete, randomised block 2 × 2 × 2 × 2 factorial, where each growth regulator, if present, was at 50 µM concentration. 100 ml of each of the 16 treatment solutions were applied on 7 occasions by watering the sand just after a regular watering with Hoagland's solution. 6 single-vine replicates were used for each treatment. PGRs were applied every 2 weeks from 4 October 1981 to 1 January 1982.

Field plant experiment

Growth regulators were injected by a method reported earlier by JACKSON and COOMBE (1967). Two 2-mm half, rings 2 cm apart, were made around the trunk of 4-year-old Riesling vines growing in Belfast, Canterbury, New Zealand (960 degree (C) days, 630 mm p.a. precipitation). The bark was removed between the cuts. A wad of cotton wool sufficient to absorb 30 ml of aqueous solution was placed around the cuts and covered with black polythene, the bottom was sealed with adhesive plastic tape and 30 ml of the appropriate solution poured into the cylinder so formed. The top was then sealed with tape. Treatments were applied on 1 November 1982. The cotton wool was examined every 15 d but as it was still wet at the end of the experiment, only 1 application was made.

Samples of buds from leaf axils were removed with a sharp knife from one randomly-selected shoot on each vine every 14 d from 22 November 1982 to 14 February 1983. Buds on each shoot were selected from position 3, 4, 6, 7, 9 and 10, counting from the basal node, and buds 12 and 13 were included as the shoot grew. Buds were stored in FAA until dissection and examination.

In the following spring (23 September 1983), 4 canes per vine were removed and sectioned into single-node cuttings, which were placed vertically in plastic trays in a

greenhouse maintained between 18 and 25 °C, the bases of cuttings were in tap water. 8 weeks later, the inflorescences and flowers on each shoot that emerged from the bud were counted.

Treatments listed in Table 4 were applied to the vines, the concentration of each was 50 µM, except 2,4-D at 2.5 µM. There were 6 vines for each of the 6 treatments arranged in a randomised complete block design.

Results

Experiment 1 — Young pot-grown vines

1. Effects on inflorescence and tendril formation

The overall main effects of growth regulators on inflorescences are shown in Table 1. Application of IAA increased (although not significantly), GA_3 reduced, while BAP and ABA showed little effect on inflorescence number. Effects of tendril formation (not shown) were not significant although IAA increased the number of buds bearing tendrils from 7.3 to 13.0 % ($P \leq 0.08$).

Table 1

The effects of IAA, GA_3, BAP and ABA on the percentage of buds bearing inflorescences (above) or inflorescences and/or tendrils (below)

Der Einfluß von IAA, GA_3, BAP und ABA auf den prozentualen Anteil der Knospen mit Infloreszenzen (oben) oder mit Infloreszenzen und/oder Ranken (unten)

Percentages	−IAA	+IAA	$-GA_3$	$+GA_3$	−BAP	+BAP	−ABA	+ABA
% of buds bearing inflorescences	17.7	23.9	33.9	6.8	22.4	18.2	21.4	19.3
P value	NS		≦ 0.001		NS		NS	
% of buds bearing inflorescences and/or tendrils	25.0	35.9	43.8	17.7	31.6	29.2	33.9	27.6
P value	≦ 0.02		≦ 0.001		NS		NS	

NS = Non-significant.

Buds bearing tendrils and/or inflorescences were significantly increased by IAA and reduced by GA_3. Although not significant as main effects, BAP and ABA did significantly alter the vine's response to GA_3; these are shown in interactions (Table 2). Gibberellin A_3 reduces the percentage of buds bearing inflorescences from 50 to 0 %. In the presence of BAP and/or ABA, two interesting things happen. Firstly, without GA_3 or BAP, ABA reduces inflorescence number; without GA_3 or ABA, BAP has the same effect. If GA_3 is present BAP and/or ABA increase the number of buds bearing inflorescences, i.e., they counteract the deleterious effects of GA_3. A similar response is obtained for buds containing inflorescences and tendrils.

Table 2

Interactions between GA_3, BAP and ABA on the percentage of buds bearing inflorescences (above) or inflorescences and/or tendrils (below)

Auswirkung der Interaktionen zwischen GA_3, BAP und ABA auf den prozentualen Anteil der Knospen mit Infloreszenzen (oben) oder mit Infloreszenzen und/oder Ranken (unten)

Percentages		−BAP		+BAP	
		−ABA	+ABA	−ABA	+ABA
% of buds bearing inflorescences	$-GA_3$	50.0	27.1	27.1	31.3
	$+GA_3$	0.0	12.5	8.3	6.3
P value			≦ 0.014		
% of buds bearing inflorescences and/or tendrils	$-GA_3$	62.5	29.2	41.7	39.6
	$+GA_3$	10.4	25.0	18.8	16.7
P value			≦ 0.008		

2. The number of leaf primordia per bud

It can be seen (Table 3) that GA_3 significantly reduced the leaf primordia number. Interactions (not presented) were significant for GA_3 × ABA × BAP and the tendencies were parallel to those shown in Table 2.

In an analysis of those buds which contained inflorescences and/or tendrils and those which were barren (data not shown) it was found that, for all treatments, there were more primordia in the fertile buds — by, on average, 28 %.

Table 3

Effects of IAA, GA_3, BAP and ABA on the average number of leaf primordia (above) and the average length (mm) of internodes per bud (below)

Einfluß von IAA, GA_3, BAP und ABA auf die durchschnittliche Anzahl der Blattanlagen (oben) und die Durchschnittslänge (mm) der Internodien je Knospe (unten)

	−IAA	+IAA	$-GA_3$	$+GA_3$	−BAP	+BAP	−ABA	+ABA
Average number	4.60	4.67	5.03	4.22	4.69	4.55	4.62	4.63
P value	NS		≦ 0.001		NS		NS	
Average length	0.26	0.22	0.17	0.30	0.24	0.24	0.24	0.24
P value	≦ 0.001		≦ 0.001		NS		NS	

NS = Non-significant.

3. The length of internodes within buds

Table 3 also shows that, in buds treated with IAA, internodes were significantly shorter, and with GA_3, significantly longer. Two two-way interactions were significant. GA_3 × IAA and GA_3 × ABA; both show that the GA_3 effect of increasing internode length was reduced if IAA or ABA was added. A three-way interaction also occurred viz. GA_3 × ABA × BAP, once again the effect was for ABA and/or BAP to reduce the GA_3 effect of internode elongation (for these and other data not presented, see PALMA 1985).

Experiment 2 — Field-grown vines

1. The number of inflorescences per bud

Fig. 1 shows the mean number of inflorescences for all buds on the shoot, sampled at different dates. On the first sampling (22/11) IAA gave a slight increase but on most subsequent occasions 2,4-D-treated shoots had more inflorescences. Auxin-treatments increased inflorescence numbers, GA_3 reduced them.

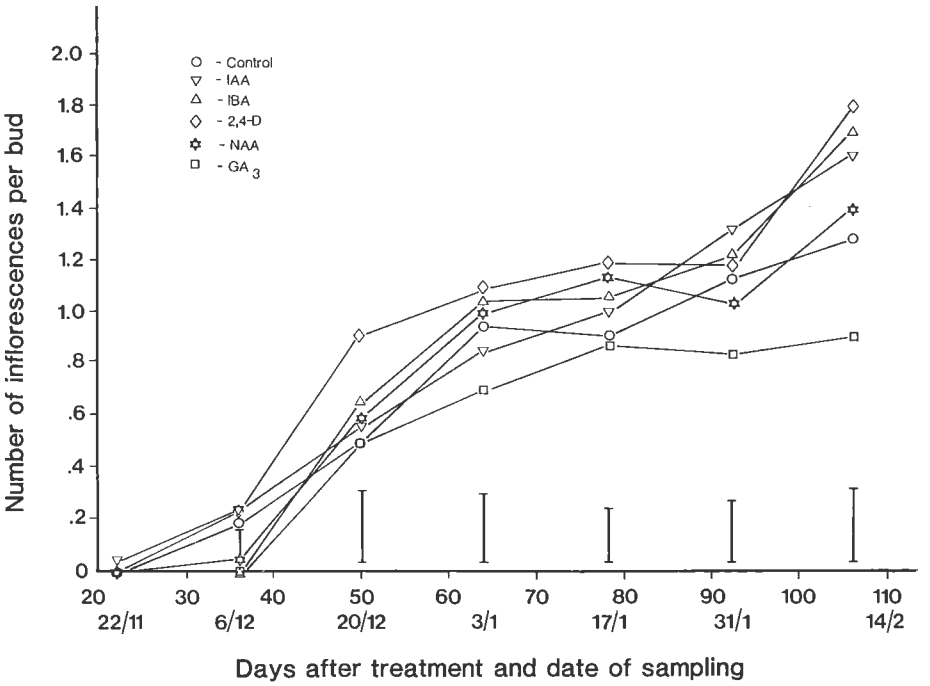


Fig. 1: The effects of growth regulators on the average number of inflorescences per bud estimated at different dates after treatment. Each figure is the mean of 6 or more buds per shoot on each of 6 vines. The vertical lines represent LSD values ($P \leq 0.05$).

Der Einfluß von Wachstumsregulatoren auf die durchschnittliche Anzahl der Infloreszenzen je Knopse zu verschiedenen Zeiten nach der Behandlung. Die einzelnen Kurvenpunkte stellen Mittelwerte aus 6 oder mehr Knospen je Trieb von jeweils 6 Reben dar. Die senkrechten Strecken geben die Grenzdifferenzen für $P \leq 0{,}05$ an.

2. The number of leaf primordia per bud

The responses of leaf primordia (data not shown) paralleled those of inflorescences presented in Fig. 1. There was an early increase due to IAA which, in this case, continued till the second sampling (6/12), subsequently 2,4-D had the major effect in increasing numbers. GA_3 consistently reduced leaf primordia.

Table 4 summarises the final leaf primordia number for all bud positions sampled. All auxin treatments, but especially 2,4-D and NAA, increased leaf primordia number, GA_3 reduced it.

Table 4

The effects of growth regulators on the average number of leaf primordia, inflorescences and flowers per bud, plus the percentage of fruitful buds per shoot evaluated after bud burst

Der Einfluß von Wachstumsregulatoren auf die durchschnittliche Anzahl der Blattanlagen, Infloreszenzen und Blüten je Knospe sowie den prozentualen Anteil generativer Knospen je Trieb (nach dem Austrieb ermittelt)

Treatment	Average number			Percentage Fruitful buds per shoot
	Leaf primordia per bud	Inflores-cences per bud	Flowers per bud	
Control	6.15 c	1.60 A b	234 B c	88.8 a
IAA	6.50 b	1.88 A a	285 AB b	90.4 a
IBA	6.66 b	1.89 A a	324 AB ab	90.0 a
2,4—D	6.71 a	1.95 A a	371 A a	92.1 a
NAA	6.71 a	1.98 A a	369 A a	90.2 a
GA_3	5.95 d	1.20 B c	128 C d	75.9 b

Treatments with no common small letters are significantly different at the 5 % level, while treatments with no common capital letters are significant at the 1 % level.

3. Relationship between leaf and inflorescence primordia

In young plants, those buds which contained inflorescences and/or tendrils had more leaf primordia (see above) and so too did field-grown vines. On 6/12 buds containing flowers generally had twice as many leaf primordia as those without flowers; for later sampling dates these differences were reduced, but the trend was similar (for original data see PALMA 1985).

4. The number of inflorescences and flowers

Examination of the inflorescences on shoots developing the following season (data not presented) show trends very similar to the buds examined in the first season (Fig. 1). This examination also gave us the opportunity to count the number of flowers per bud rather than just record inflorescence number. Flower numbers are shown in Fig. 2. All auxins, but especially 2,4-D and NAA tended to increase flower numbers, GA_3 reduced them. Note that because the higher order buds (above position 9) were not present on all canes, analyses were not done on these data.

A summary of the mean data for all buds on the shoot is given in Table 4.

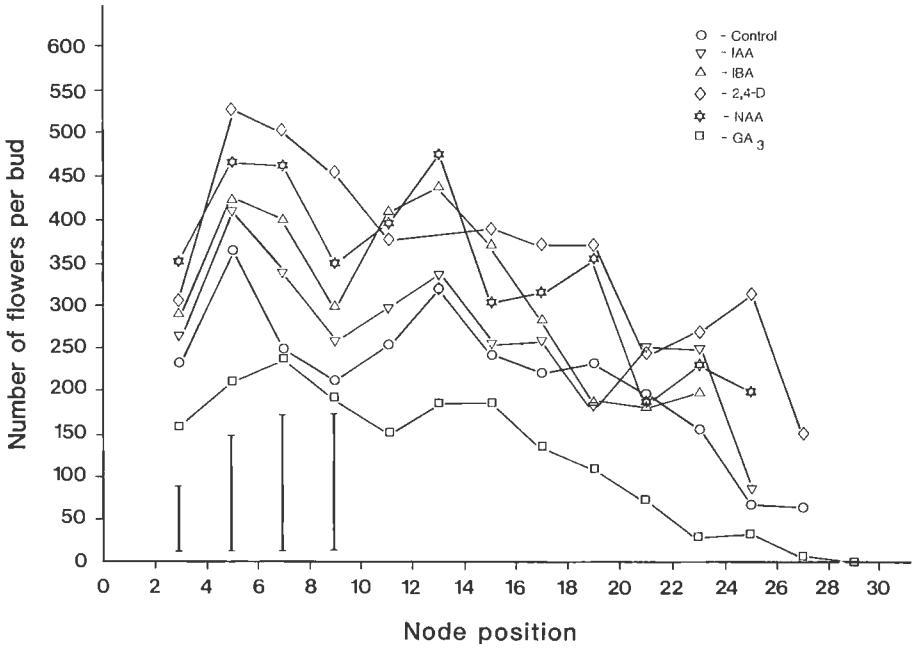
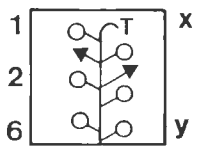


Fig. 2: The effects of growth regulators on the average number of flowers per bud for the different node positions on the main shoots. Figures are the means of 4 canes on each of 6 vines. The vertical lines represent LSD values ($P \leq 0.05$).

Der Einfluß von Wachstumsregulatoren auf die mittlere Anzahl der Blüten je Knospe in Beziehung zur Knospenposition an den Haupttrieben. Die Kurvenpunkte stellen Mittelwerte von 4 Tragruten an jeweils 6 Reben dar. Die senkrechten Strecken geben die Grenzdifferenzen für $P \leq 0{,}05$ an.

Bud forms observed in Experiments 1 and 2

Examination of cross-sections through many buds during the course of this work indicated that, by the dormant period, many different bud forms occurred in Riesling grapes. These are illustrated in Fig. 3 which shows the various types, categorised according to numbers of leaf primordia, inflorescences and tendrils and the likely pathways of development. The representation of a bud containing 6 primordial leaves, 2 inflorescences and 1 tendril is as follows:



It is possible to distinguish between different vines or treatments by the distribution of buds that occur. For example, from a sample of 77 untreated young plants grown indoors (Experiment 1) the number of buds found in each category are shown at position x in Fig. 3. From 58 control plants grown outdoors (Experiment 2) distribution of buds is shown in position y.

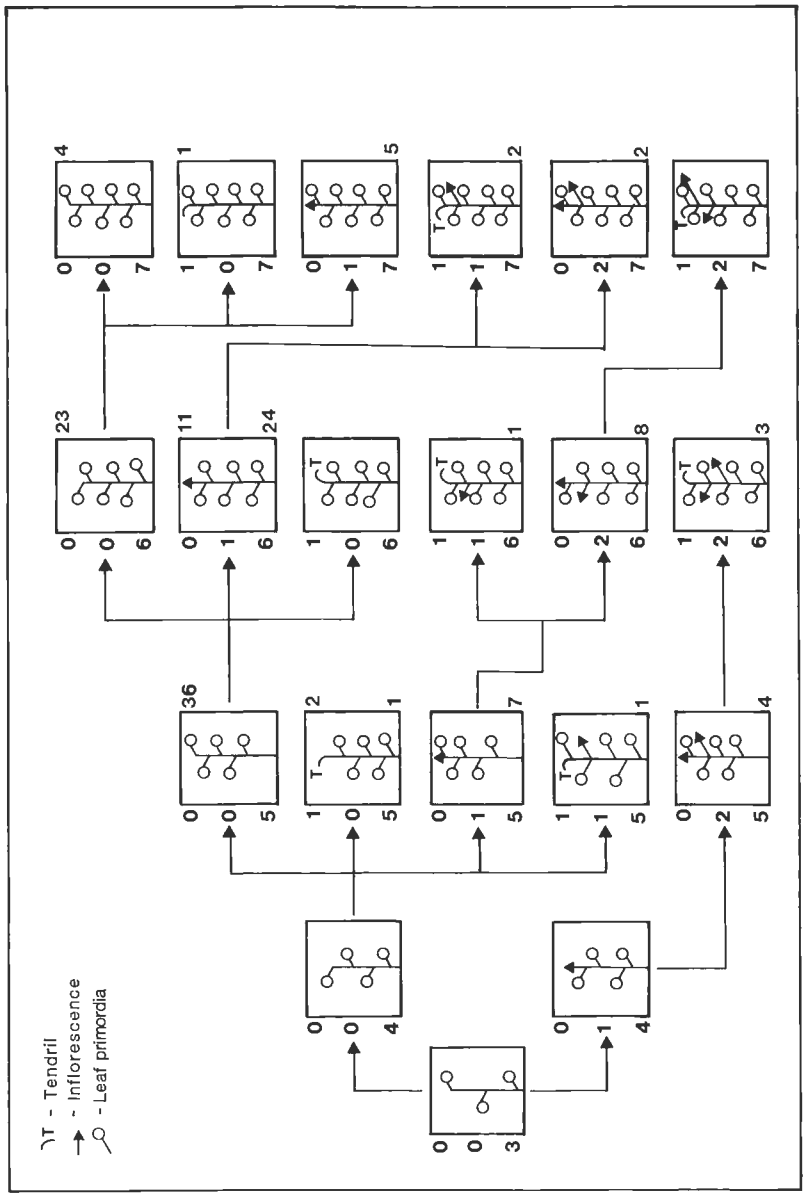


Fig. 3: Bud forms found in Riesling vines. For details see text.
Bei Rieslingreben gefundene Knospentypen. Einzelheiten s. Text.

In mature plants, 7 examined buds formed their first inflorescence after the 4 leaf primordia, 17 after the 5th leaf primordia, 28 after the 6th and 5 after the 7th. In young plants many unfruitful buds occurred and none formed their first inflorescence before the 6th leaf primordia.

Fig. 4 shows the number of buds found after treatment of mature plants with growth regulators; this is data from Experiment 2. Numbers of buds found in each category are shown after the name of the regulator found in each box.

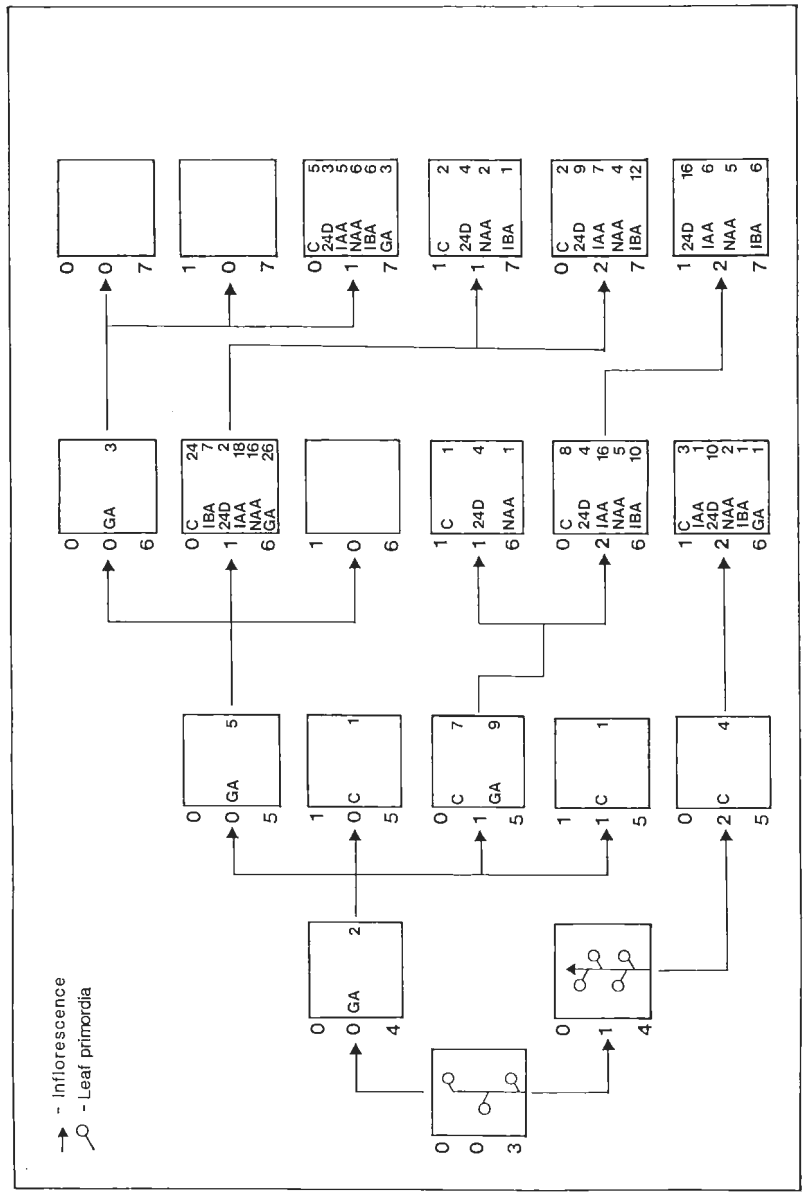


Fig. 4: Bud forms found in Riesling vines treated with plant-growth regulators. For details see text.
Knospentypen, die bei Rieslingreben nach Behandlung mit Wachstumsregulatoren gefunden wurden. Einzelheiten s. Text.

The more fruitful buds form their first inflorescence after fewer leaf primordia and such buds are seen towards the lower part of the diagrams. By far the majority of buds which have produced their first inflorescences after 4 or 5 primordia and finish with 2, have received an auxin treatment - viz., 2,4-D: 30, IAA: 23, NAA: 12, IBA: 17, compared with control: 11.

Discussion

The response of grapevine buds to growth regulators has been considerable. The most dramatic effect was from GA_3 which reduced both inflorescence and leaf primordia number, and increased internode length in the bud. IAA, on the other hand, appeared to have opposite effects; it increased the production of inflorescences and/or tendrils and reduced internode length in the bud. It interacted with GA_3 in many of these effects. While BAP and ABA caused no overall significant responses when applied alone (Table 1), they interacted with GA_3 to reduce its effects (Table 2). Interactions do, in fact, suggest that without GA_3, BAP and ABA r e d u c e d inflorescences, tendrils and leaf primordia.

Experiments with fully-grown outdoor vines confirmed the effects of auxins and GA_3 on leaf primordia, inflorescences, and tendrils and also showed that auxins increased flower numbers, while GA_3 reduced them. Several auxin-like regulators can induce these effects which can be picked up in examined buds between 22 and 36 d after treatment. The fact that two different application methods on both young and old plants produced similar results suggests that the results are real ones and possibly mirror responses extant within the plant.

The response to auxin is interesting since there is, to the authors' knowledge, only one reported instance of auxin influencing inflorescence or flower production. JINDAL and DABAS (1982) found an increased percentage of reproductive buds after spraying Thompson Seedless grape vines in spring with IBA and 4-chlorophenoxyacetic acid (4-CPA). This work and our own contrasts with that of SRINIVASAN and MULLINS (1980 a and b) which indicates a key role of GA_3 and cytokinins in inflorescence formation. LUCKWILL (1970) also suggests that, in apples, the gibberellin/cytokinin balance has a key function.

Our work does not necessarily support the above conclusions. The cytokinin BAP, as indicated, does counteract the deleterious effects of GA_3, but alone it may (like GA_3) reduce production of inflorescences (Table 2). The inhibitor ABA had similar effects to BAP. An important role for auxin was suggested. It increased the production of tendrils/inflorescences (Table 1) and reduced internode length in the bud (Table 3), mainly by counteracting the increase due to GA_3.

SRINIVASAN and MULLINS worked primarily with inflorescences and tendrils on growing shoots or in tissue culture. Under their experimental situation they examined the formation of anlagen (uncommitted primordia) and the conversion of tendrils to inflorescences. The difference between formation of these organs on a growing shoot for expression in the current season, and the formation of dormant buds for the next season is considerable and, in fact, it is not surprising that differences do occur.

Examination of bud forms (Figs. 3 and 4) suggest that the bud does not have a fixed formula for leaves, inflorescence or tendril numbers at dormancy. It is adaptable and may be influenced by the age of plant and other factors. It is also variable between cultivars and, possibly disctricts, for example in Merlot the first inflorescence was noted when 3 scales and 4 leaf primordia were present (CAROLUS 1971). In Shiraz it was seen after leaf 5 (SRINIVASAN and MULLINS 1976). For Concord and Riesling it appeared after nodes 6 and 7 respectively — presumably leaves 3 and 4 (PRATT 1979).

In young plants fewer inflorescences form and, when they do, they are seen only after 6 leaf primordia appear (Fig. 3). A similar situation occurred with outdoor, mature plants treated with GA_3 (Fig. 4), suggesting perhaps that young plants have higher endogenous gibberellins.

Auxins tend to increase the speed of leaf primordia and inflorescence production. This is especially marked with 2,4—D and IAA. This association of rapid primordia

production (short plastochrone) with bud fruitfulness has been found in other plants. For example, FULFORD (1965, 1966 a and b, 1970) noted a positive relationship between short plastochrone and the ability of apple buds to initiate flowers. He suggested that plastochrone is regulated by hormones produced in adjacent organs — a viewpoint which is not inconsistent with the results in this paper.

It seems likely, therefore, that the formation of anlagen and their conversion to either tendrils or inflorescences is under hormonal control. Within the developing bud the evidence suggests that auxins, gibberellins, cytokinins or inhibitors are involved in the processes of primordial shoot elongation, leaf formation and the presence or absence of inflorescences or tendrils. Gibberellins elongate the primordial shoot by increasing internode elongation, but tend to depress leaves, inflorescences and tendrils; cytokinins and abscisic acid may balance GA and overcome these depressive effects. Auxins promote tendril, inflorescence and flower formation and counter the internode elongation effects of GA_3.

Summary

Young pot-grown vines of Riesling grapes (*Vitis vinifera* L.) were treated, via roots, with gibberellin A_3 (GA_3), indole acetic acid (IAA), 6-benzyl-amino purine (BAP) and abscisic acid (ABA) in a factorial experiment. Seven 100 ml applications at 50 µM were applied at regular intervals. In a second experiment GA_3, IAA, indole butyric acid (IBA), naphthalene acetic acid (NAA), and 2,4-dichlorophenoxy acetic acid (2,4 - D) were injected into the trunks of field-grown Riesling vines 3 weeks after bud burst. Auxins induced more leaf primordia, tendrils and inflorescences and reduced internode length in the buds of treated vines examined the following winter. The rate of formation (plastochrone) was also increased. Flowers appearing on shoots the following spring were more numerous on treated vines. GA_3 had opposite effects to auxins on all the above. ABA and BAP reduced the production of tendrils, inflorescences and leaf primordia in the bud — although much less than GA_3 — however, when applied with GA_3, they reduced its deleterious effects on these organs. Examination of buds revealed a variety of bud forms. Buds which had more inflorescences and primordial leaves were from mature vines, especially if treated with auxin-like compounds. Young vines had fewer leaf primordia and fewer inflorescences, a situation also found in GA_3-treated older plants. Treatments or conditions which favoured more fruitful buds also tended to reduce the plastochrone and it is suggested that the two phenomena are causally related.

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