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Influence of berry growth and growth regulators on the development of grape peduncles in *Vitis vinifera* L.

by

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Der Einfluß des Beerenwachstums und von Wachstumsregulatoren auf die Entwicklung der Traubenstiele bei *Vitis vinifera* L.

Zusammenfassung: Das Entfernen der Beeren vom Stielgerüst der Sorte Roter Gutedel nach dem Fruchtansatz (≧ 3 mm Durchmesser) hatte nur einen geringen Einfluß auf die weitere Entwicklung des Traubenstiels. Wurden jedoch jüngere Beeren oder Blüten vor diesem Stadium entfernt, bildeten sich an der Basis der Stiele Trennzonen; die behandelten Traubenstiele starben anschließend ab und wurden abgeworfen. Wurden die Traubenstiele nach dem Entfernen der Blüten bzw. der Fruchtknoten mit α-Naphthylessigsäure (NAA) behandelt, so unterblieben Absterben und Abszission der Traubenstiele. Davon ausgehend wird angenommen, daß die in den Blüten gebildeten Auxine die Entwicklung des Traubenstiels fördern. Behandlung mit Chlorcholinchlorid (CCC), 6-Benzyladenin (BA), Indol-3-essigsäure (IAA) oder Indol-3-buttersäure (IBA) verhinderte die induzierte Abszission nicht. Die fehlende Wirkung der beiden Auxine IAA und IBA ist möglicherweise auf deren chemische Instabilität zurückzuführen.

Die Behandlung mit Gibberellinsäure (GA) verhinderte ebenso wie NAA die induzierte Abszission des Traubenstiels. Zusätzlich förderte sie die Bildung des Metaxylems. Gibberelline, die während der Blüte und des Fruchtansatzes in den Fruchtknoten gebildet werden, scheinen ebenfalls die Entwicklung des Traubenstiels zu beeinflussen. Das Auftreten der Stiellähme, welches in Verbindung mit einem Gibberellinmangel während des Fruchtansatzes steht, unterstützt diese Vorstellung.

Key words: berry, growth, growth regulator, bunch, flower biology, stiellaehme.

Introduction

Work on grape peduncle necrosis (stiellaehme) (11, 14, 15) has shown that flower and berry growth influence peduncle development in different ways. The removal of the flowers from inflorescences caused an immediate cessation of length increase and the formation of abscission layers at the base of the rachis within 14—20 d and/or death of the peduncle. Once berries have set, however, berry removal does not have these effects: the peduncles remain green and turgid until the end of the growing season; an additional feature is that symptoms of grape peduncle necrosis do not develop (11, 15, 16).

These results suggest an important change in growth behaviour of the peduncle that develops at the time of berry setting. After this stage, the peduncle becomes self-sufficient in the sense that its development is uninfluenced by berry removal. It is possible that the berry influences the development of vascular tissue and the establishment of assimilate transport pathways so that, once established, berries are no longer required for their maintenance. In contrast, developing flowers do not influence the peduncle in this way and their presence is necessary at the ends of the peduncle branches for continuous health of the peduncle.

The mediator of this latter effect could be hormones produced by the flower acting in some way to maintain peduncle growth. This hypothesis can be tested by excision of flowers and substitution by treatment with growth regulators. Such experiments are described in this paper using measurements of growth and development and examination of microscopic sections.

Materials and methods

Treatments were applied to inflorescences and clusters of cv. Roter Gutedel (syn. Red Chasselas) growing on the Research Station at Wädenswil. Flowers and berries were removed, at the stages specified, by snipping off with scissors; growth regulators were applied by dipping the inflorescence or cluster in a 100 ppm solution of the substance for 10 s; for combined treatments the dipping was done within 1 h after flower/berry removal. The following growth regulators were used: indole-3-acetic acid (IAA), 3-indolebutyric acid (IBA), α-naphthalene acetic acid (NAA), benzyladenine (BA), gibberellic acid (GA), and 2-chloroethyltrimethyl ammonium chloride (CCC). Generally, 5 or 10 clusters were used for each treatment.

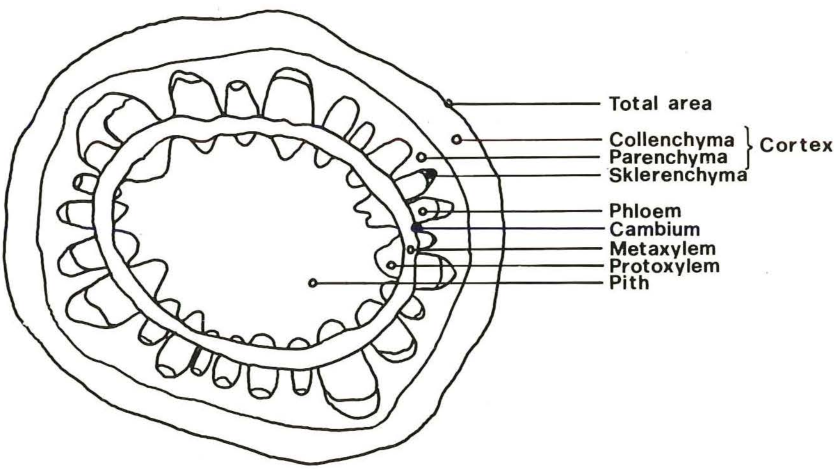

Fig. 1: Measurement of cross sectional areas of different tissues within the peduncle of cv. Roter Gutedel.

Messung der Querschnittsfläche einzelner Gewebe des Traubenstiels der Sorte Roter Gutedel.

The growth of the peduncles was observed and recorded and, at specified times, samples of rachis were removed for sectioning from between the 1st (tendril-like) and 2nd primary lateral branches of the peduncle (B in Fig. 3). Cross sections were made with a cryostat microtome and the areas of the tissues and of the parts shown in Fig. 1 were measured using a Wild M-20 microscope and a Leitz-ASM Image Analysis system [1]) from an image magnified 25-fold.

In one series the cambial region was also measured and in all sections the number of primary and secondary vascular bundles were counted. In general, cross sections of 5 peduncles were measured from each treatment.

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[1]) Kindly provided by Wild & Leitz AG, Zürich.

Results

Development of the rachis

Rachis length and the course of development in the total cross-sectional area of the peduncle and of its constituent tissues, from 1 month before flowering until berry ripeness, are shown in Fig. 2. After an initial rapid increase in length, the peduncle thickened, attaining 75 % of its final cross-sectional area by the middle of flowering. After flowering, there were further small increases in length and area. The pith and cortical parenchyma and collenchyma comprise the bulk of the area.

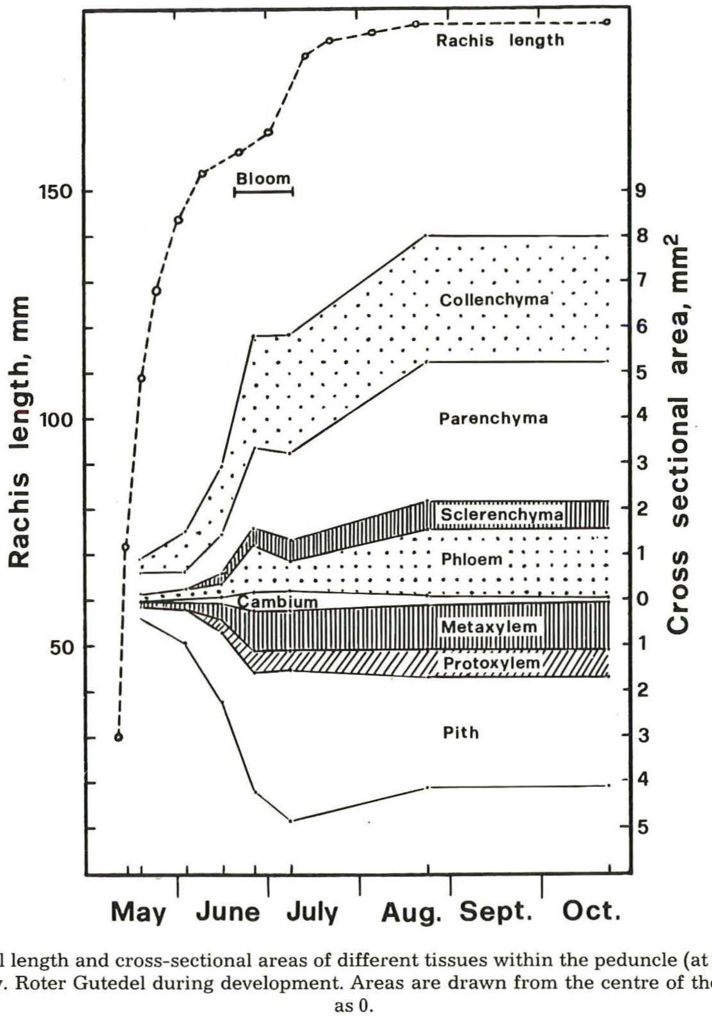

Fig. 2: Total length and cross-sectional areas of different tissues within the peduncle (at position B, Fig. 3) of cv. Roter Gutedel during development. Areas are drawn from the centre of the cambium as 0.

Gesämtlänge und Querschnittsfläche einzelner Gewebe des Traubenstiels (Schnittposition B, Abb. 3) der Sorte Roter Gutedel während der Entwicklungsperiode. Die Mitte des Kambiums wurde als Nullinie gesetzt, von der aus die übrigen Gewebeflächen dargestellt sind.

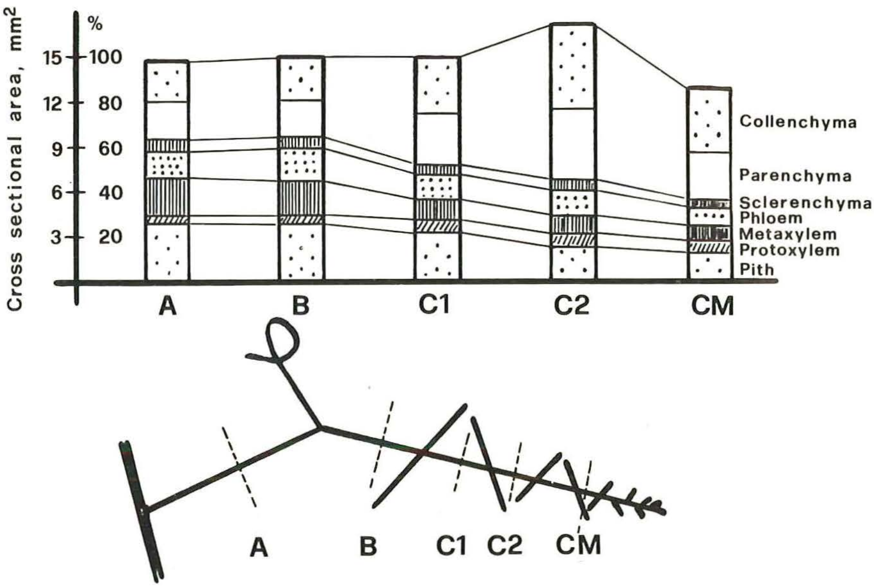

Fig. 3: Cross-sectional areas of tissues at five positions along the peduncle of cv. Roter Gutedel 20 d after flowering. Percentage scale relates to total area at position B.

Flächenanteil verschiedener Gewebe in Querschnitten an fünf verschiedenen Stellen eines vollentwickelten Traubenstiels. Die Prozentskala bezieht sich auf die Gesamtfläche des Querschnittes B.

Formation of secondary tissue (metaxylem and sclerenchyma) began well before flowering when the peduncle was 2/3 of its final length but only 1/5 of its final area. Cambial area was greatest during flowering, then gradually diminished until it was practically 0 when the berries entered the ripening phase of growth.

Measurements taken at different positions along the peduncle during August (Fig. 3) showed trends towards the tip for a declining proportion of pith and an increasing one of cortex.

Effect of berry removal

The effect of the presence and absence of berries on the area of peduncle and of its constituent tissues were measured by removing berries 10 d after flowering; the effects of flowers could not be assessed because of the resultant death and abscission of the peduncle. The results (Fig. 4) show that during the 15 weeks after treatment deberried peduncles only increased by 10 % in total cross sectional area (compared to 25 % in control). Except for the pith, which decreased in area, all tissues expanded: the smallest increase occurred in cortical collenchyma and sclerenchyma and the greatest in the phloem and protoxylem (neither increased as much as control, however). Removal of berries led to a decline in cambial area.

The effects of time of flower and berry removal on death and abscission of the rachis are shown in the next experiment where the treatments were combined with growth regulator treatments.

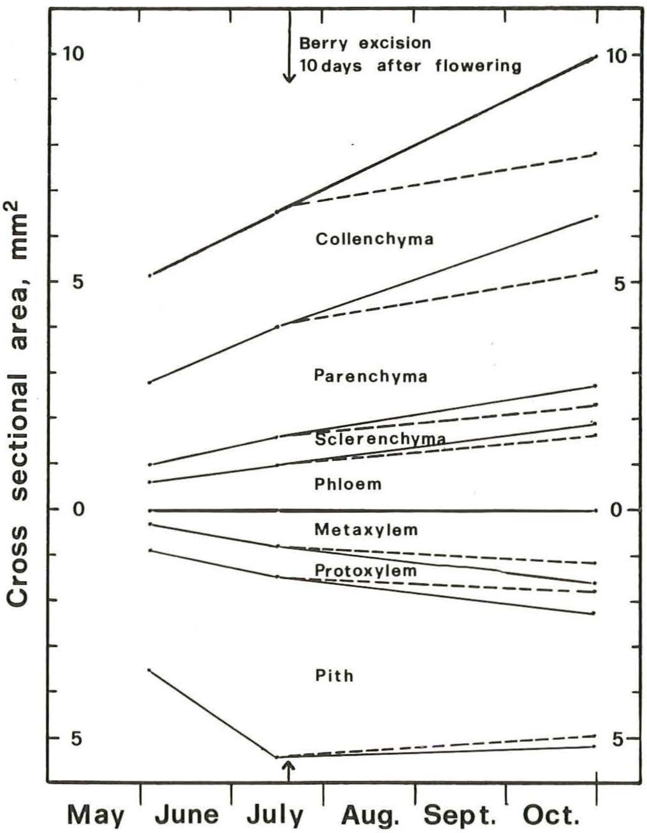

Fig. 4: Cross-sectional areas of different tissues of the peduncle (position B) at three times showing the effect of removal of berries 10 d after flowering as dashed lines.

Querschnittsfläche verschiedener Gewebe des Traubenstiels (Schnittposition B) zu drei Zeitpunkten; die gestrichelten Linien stellen den Einfluß der Beerenentnahme (10 d nach 70 % Vollblüte) auf die Gewebeentwicklung dar.

Combination of flower and berry removal with growth regulator treatments

Clusters of cv. Roter Gutedel were deflowered 10 and 3 d before 70 % capfall and 4 days after, or deberried 10 d after 70 % capfall. At the latter stage, berries were 3—4 mm in diameter. The treated peduncles were dipped in 100 ppm solutions of IAA, IBA, NAA, BA, CCC or GA; their subsequent fate is recorded in Fig. 5.

Deflowered peduncles treated with IAA, IBA, BA and CCC were not different from the untreated controls. In this group of treatments, removal of flowers (times 1 and 2) resulted in decline of the growth of the peduncle leading to death and abscission within 3—7 weeks. The removal of flowers/berries at +4 d (treatment 3) had similar effects but the reactions were slower, while removal of berries (treatment 4) did not lead to any decline.

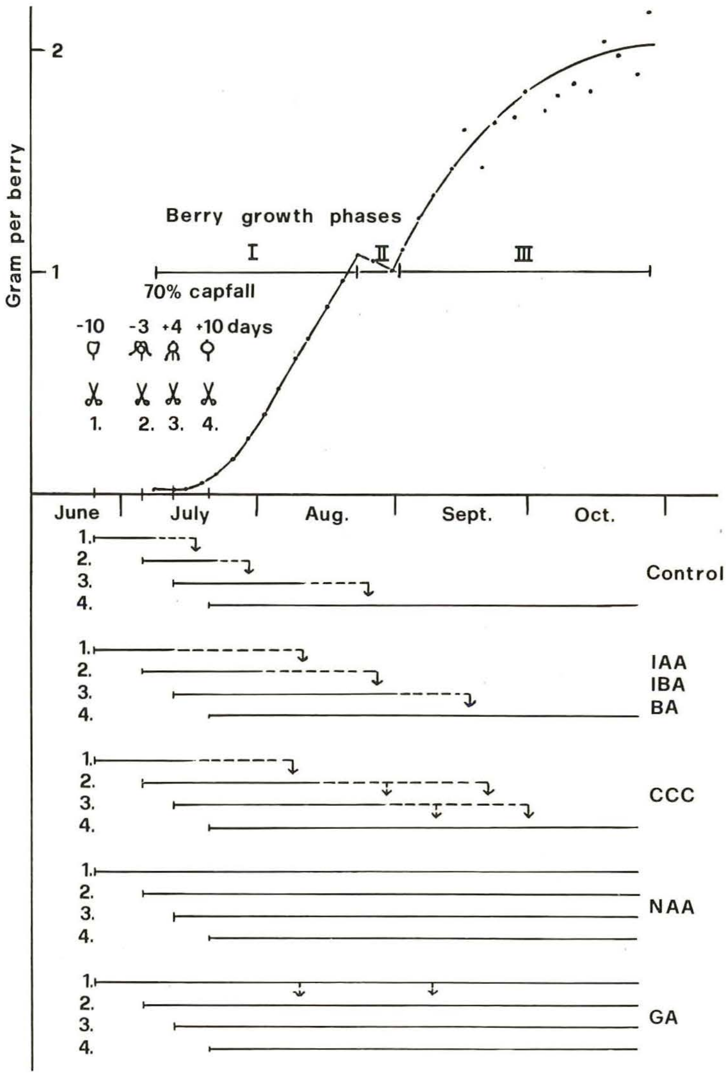

Fig. 5: Effect of flower and berry removal on the peduncle of cv. Roter Gutedel. Flowers were removed 10 or 3 d before flowering (70 % capfall) and berries 4 and 10 d after flowering during fruit set. Growth regulators (BA, IAA, IBA, NAA, CCC or GA) were superimposed by dipping of the bare peduncles. Horizontal solid lines denote living peduncles, dashed lines dying and abscising peduncles, and the arrows when the peduncles abscised. Dashed arrows indicate partial abscission of lateral branches of peduncles (GA, 1.).

Auswirkungen der Entfernung von Blüten und Beeren auf die Traubenstiele der Sorte Roter Gutedel. Die Blüten wurden 10 bzw. 3 d vor der Vollblüte (70 % offene Blüten) und die Beeren 4 bzw. 10 d nach der Vollblüte während des Fruchtansatzes entfernt. Die behandelten Traubenstiele wurden in die Lösungen der Wachstumsregulatoren (BA, IAA, IBA, NAA, CCC oder GA) getaucht. Die ausgezogenen horizontalen Linien repräsentieren lebende, die gestrichelten Linien absterbende und abfallende Traubenstiele. Die Pfeile markieren den Zeitpunkt der Abszission. Gestrichelte Pfeile geben an, daß nur einzelne Seitenverzweigungen der Rispe abfielen (GA, 1.).

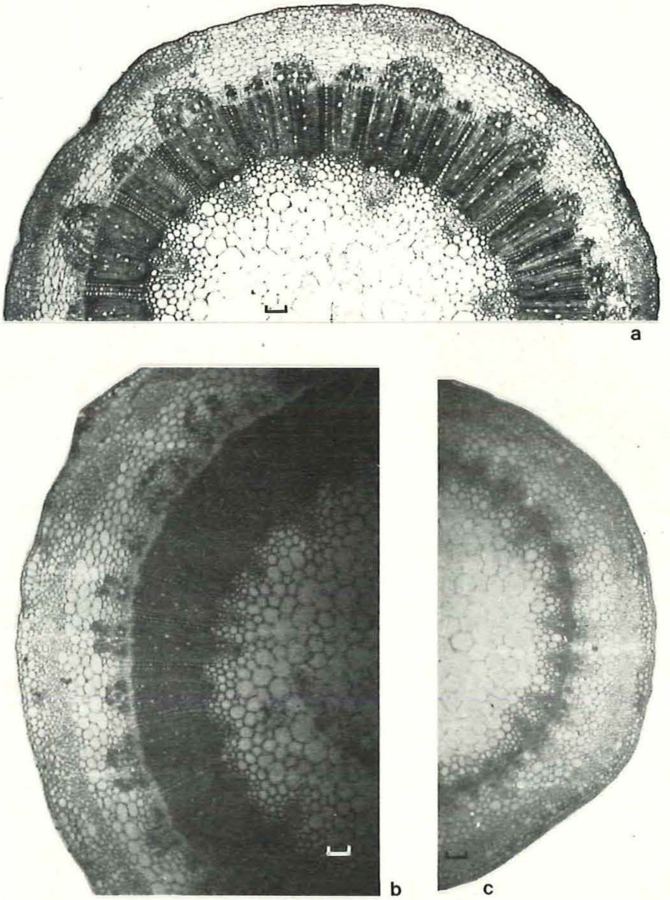

Fig. 7: Composite photographs of sections made at harvest. — a) Deflowered and GA-treated peduncle 10 d before flowering. b) Coiled, c) uncoiled type of tendrils. Bars indicate 150 µm.

Teilaufnahmen von Querschnitten, Ende Oktober geschnitten. — a) Traubenstiel, bei dem 3 d vor der Blüte die Blüten entfernt und anschließend GA appliziert wurde. b) Haftender, c) nichthaftender Rankentyp. Die Balken entsprechen 150 µm.

had a pronounced effect on the area of the metaxylem, as shown in the table and in Figs. 6 and 7 (composite photographs of sections). The increase generally represented a doubling in metaxylem area; treatment applied 10 d before flowering had an especially large effect. It was noted that GA-treated peduncles resembled tendrils, and this is supported by the appearance of coiled tendril cross sections (Fig. 7).

In another series of treatments, growth regulators were applied to intact inflorescences and clusters. Again, GA treatment had the greatest effect: area of metaxylem was increased, though less so than with berries removed (Table). GA treatment before or during flowering led to shot berries and reduced fruit set, while treatment during fruit set had only a slight effect on berry development but caused a significant decrease in stiellaehme. NAA also reduced fruit set markedly, but had no effect on the occurrence of stiellaehme.

Areas (%) of metaxylem in cross sections of the rachis at harvest, after treatments on various dates with growth regulators, with and without flower/berry removal (values are means out of 5 replicates ± S.E. of the mean)

Prozentualer Flächenanteil des Metaxylems in Querschnitten durch Traubenstiele zur Erntezeit nach Behandlung mit Wachstumsregulatoren zu verschiedenen Zeitpunkten, mit und ohne Entfernung von Blüten bzw. Beeren (Durchschnittswerte aus 5 Wiederholungen ± Standardabweichung)

Growth regulators [1])	Berries intact and treated	Berries removed and treated			
	10 d before flowering (−10)	10 d before flowering (−10)	3 d before flowering (−3)	4 d after flowering (+4)	10 d after flowering (+10)
Nil (control)	10.7 ± 1.1	6.1 ± 1.4	6.6 ± 1.1	6.6 ± 0.8	8.9 ± 1.3
CCC	9.2 ± 2.7	10.2 ± 2.1	9.1 ± 2.2	10.2 ± 2.1	9.9 ± 3.4
NAA	9.1 ± 1.6	9.8 ± 2.3	10.8 ± 2.4	11.2 ± 1.9	11.1 ± 2.2
GA	14.4 ± 4.3	32.2 ± 3.9	18.4 ± 1.8	18.3 ± 2.7	19.1 ± 1.4

[1]) Applied immediately after flower/berry removal.

Discussion

The hypothesis that the flowers are required for the continuous health of the peduncle and that the flower set effect can be substituted by treatment with a growth regulator is sustained. The substance which most closely matched the flower effect was NAA. Two other auxins IAA and IBA did not equal the effect of NAA; possibly they were too readily metabolized.

NAA-treated, deflowered peduncles grew like the peduncles on intact bunches with respect to length, thickness and expansion of the constituent tissues in cross section. There are reports of auxin activity in flowers of grape before anthesis (4) and in developing berries immediately after setting (9, 12); thus it is possible that the flower effect on the peduncle is due to its production of auxins.

GA was the other growth regulator to prevent abscission and death of deflowered peduncles. This treatment had the additional effect of causing cambial activity and enlargement of the metaxylem tissues (Table and Figs. 6 and 7; see also 8 under Literature). Gibberellin activity occurs in grape flowers and increases rapidly as fruits set (5, 6, 7, 13). Whether GA can be considered as another endogenous effector from the flowers is not clear. Such an inference would depend on whether low concentrations of GA prevented peduncle abscission and death without increasing metaxylem area; or that endogenous gibberellin activity was balanced by the antagonist; abscisic acid, which is also abundant in young grape seeds (3).

GA applications during the setting period, either to intact clusters or to whole vines in the field, have resulted in a significant decrease of stiellaehme whereas NAA and CCC have had no effect. Furthermore, it is known that berry weight within a cultivar is positively correlated with seed number per berry (10) and also that developing grape seeds are rich in gibberellins (see above). Thus it is suggested that disposition of peduncles to the development of stiellaehme is associated with a deficiency of gibberellins (15).

From the growth cycle of peduncles (Fig. 2) and the effects of flower and berry removal on peduncle development (Fig. 5) the most critical growth period which influences the occurrence of stiellaehme (visible during the fruit ripening period) is that of flowering and fruit set.

The anatomical resemblance shown in cross sections of tendrils and of GA-treated peduncles matches other observed similarities, including toughness and wiriness. Probably the most distinctive property of tendrils is thigmotropism and this is also displayed by berry-bearing peduncles after treatment with GA (1, 2). These facts suggest a hormonal role for GA in the growth and developmental behaviour of tendrils.

Summary

Removal of grape berries (cv. Roter Gutedel) after setting (10 d after anthesis) had just a slight effect on the subsequent health of the peduncle. But if younger berries of flowers were removed before this stage the peduncle formed abscission layers along its length, and/or it died. Treatment of deflowered peduncles with α-naphthalene acetic acid (NAA) prevented peduncle abscission and death; it is suggested that auxins produced by flowers have a hormonal role in maintaining normal development of the peduncle. Treatment with 2-chloroethyltrimethyl ammonium chloride (CCC), benzyladenine (BA), indole-3-acetic acid (IAA) or 3-indolebutyric acid (IBA) did not give these effects. The lack of effect of the latter two compounds (auxins) is possibly due to their catabolism.

Treatment with gibberellic acid (GA) resembled NAA in that it also maintained the health of deflowered peduncles, but GA had the additional effect of causing prolonged development of metaxylem. Gibberellin produced by developing berries may also have a hormonal role in peduncle development. The occurrence of grape peduncle necrosis (stiellaehme), which appears associated with a gibberellin deficiency during setting, supports this idea.

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