### [Review] Physiology of Berry Set in Grapevines (1)

# Effect of Shoot and Cluster Nutrition on Grape Berry Set

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#### 1. Past and fundamental studies of grape berry set

Berry set in grapevines is one of the most important events in the annual regular production of quality grape clusters. It is significantly influenced not only by climatic conditions during blooming period but also by cultivars, vineyard managements, and vine and cluster nutrition. As specifying the cause of poor berry set is essential to maintaining annual production of the grapes, grape growers and horticulturists have been working hard to conduct a wide range of tests in vineyards world wide.

Oinoue (1940), a famous grape scientist who bred the excellent tetraploid cultivar cv. Kyoho, tested the effect of shoot pinching time on percentage berry set as well as on shoot nutrition in Muscat of Alexandria grapes. His work indicated that shoot pinching, treated five days before blooming time, gave the highest percentage berry set and high percentage pollen germination. Maximum carbohydrate content in shoots was also detected five days after shoot pinching. Injection tests of glucose and glutamic acid solutions independently via dormant canes showed that supplying glucose (a source of carbohydrate) increased ovule fertilization rate by 12%, compared with control, while supplying glutamic acid (a source of nitrogen) did not do so (Oinoue, 1951). From these results, a high C-N ratio of grape vines is expected to be the preferred nutritional condition for good berry set. This idea was supported by Tsuneya (1971) who was engaged in the successful production of Kyoho grapes. However, the C-N ratio is considered to be only one of the physiological indicators of the reproductive activity of grapevines, and is not an actual standard of good berry set (Okamoto, 1973).

Winkler (1974) demonstrated a significant effect of pruning severity on the berry set of Muscat of Alexandria grapes. Severe pruning, like short spur-pruning, caused severe flower shatter, while light pruning as cane pruning and non-pruning resulted in successful berry set in Muscat of Alexandria grape. He noted that the spur-pruning, cutting off large proportions of canes containing abundant food reserves, eliminates available carbohydrate (starch and sugar) during blooming time. He also commented the significance of "vine capacity" which means the capacity of total vine growth and fruit productivity. Severe pruning of vines results in poor berry set and fruit production as well as total shoot growth in the canopy, although the "vigor" of the individual shoot increases apparently. His findings are considered to be a general base to understand the relationship between winter pruning system and vine productivity. On the other hand, Japanese grape growers have improved berry set and fruit quality of tetraploid grape cultivars by developing new cultivation systems as canopy enlarging cultivation (Tuchiya, 1980) and root-zone restriction planting (Imai, 1991).

The author began to study grape berry set physiology in 1965 under instruction of Dr. Akira Kobayashi, a professor of the Pomology laboratory in Kyoto University. My early work was focused onto the effect of shoot pinch and cluster trimming on nutritional condition in blooming florets and the berry set in Muscat of Alexandria grape. The second stage of my works was turned to the causes of poor berry set observed in most tetraploid grape cultivars, such as Kyoho and Pione, of which cultivation developed rapidly in Japan around 1980. Anatomical analyses of ovule development and pollen tube penetration into pistils were intensively performed. The third stage of my work proceeded into the analyses of pollen tube growth regulators existed in diploid and tetraploid grape pistils. Anatomical and physiological studies of seedless berry setting caused by exogenous gibberellin applications were also conducted.

In this review, the main results of author's research and note unsolved but highly important ideas are discussed for future investigation.

## 2. Effect of pre-bloom shoot pinching and cluster trimming on berry set and cluster nutrition in Muscat of Alexandria grapes

# 1) Improved berry set by pre-bloom shoot pinching and cluster trimming

Muscat of Alexandria vines are usually trained to a multi-cordon system with annual spur-pruning, leaving only one or two basal buds. New shoots grow vigorously throughout the blooming period, causing a severe competition for photosynthates between shoot tips and clusters. Sometimes, most florets in a cluster abscise one to two weeks after anthesis, resulting in poor berry set ("excessive flower shatter" or "flower coulure" in English and "Hana-Burui" in Japanese). In order to minimize nutrient competition between clusters and shoot tips, removing the apical parts of a shoot (shoot pinching) has been known to be effective when treated before the blooming time. Okamoto (1973) examined the effects of shoot and/or lateral shoot pinching, treated at various times before and during bloom, using mature Muscat of Alexandria grapevines. As shown in Table 1, the highest percentage berry set was obtained when shoots were pinched one to three weeks before anthesis and all lateral shoots were also pinched successively. Percentage berry set was slightly decreased when the lateral shoots were not pinched. The current recommendation for Muscat of Alexandria growth is to pinch shoot tips when the 6th or 7th node from the second cluster has presented; this is 7 to 10 days before anthesis. Lateral shoots should be pinched, leaving one or two nodes.

Cluster trimming increases percentage berry

set because the number of florets is decreased, eliminating nutrient competition among florets in a cluster. Increased percentage berry set, accompanied by reduced cluster size, results in the production of compact clusters. Moderately compact clusters are recommended by most Japanese markets because dried rachis (cluster axis) and pedicels do not become visible even at several days after harvest. Table 2 shows the effects of severity and time of cluster trimming and the time of trimming on percentage berry set in Muscat of Alexandria grapes (Okamoto, 1973). Cluster trimming,

Table 1 Effect of time of shoot-tip pinching on percentage berry set (%) in Muscat of Alexandria grapes.

Shoot type and time of	Pinched node	Lateral shoot y		
shoot-tip pinching <sup>z</sup>	position from the 2 <sup>nd</sup> cluster	Pinched	Unpinched	
Vigorous shoot				
20 days before bloom	5	26.6*x	17.5	
13	8	20.8*	17.0*	
7	12	21.5*	19.4*	
3	14	14.8	16.5	
At bloom	15	11.3	11.6	
Full bloom	18	13.8	12.3	
Unpinched	-	12.3	11.4	
Medium shoot				
Unpinched	-	17.0	15.9	

<sup>z</sup> Vigorous shoot, longer than 100 cm at full bloom if not pinched; medium shoot, 60-80 cm at full bloom. Ten clusters were tested for each category.

<sup>y</sup> Each lateral shoot was pinched, leaving only one node.

x \* indicates that values are significantly higher than that of vigorous unpinched shoots ( $p \le 0.05$ ).

Table 2 Effect of time and severity of cluster trimming on percent berry set in Muscat of Alexandria grapes.

Time of cluster trimming <sup>z</sup>	No. of florets per cluster	No. of set berries per cluster	Percentage berry set (%)
15 days before bloom	350-400	128.8	35.0
10	350-400	120.4	32.1
5	450-500	116.3	24.5
	350-400	127.6	34.0
	250-300	119.5	43.6
	120-130	72.8	58.2
At bloom	350-400	94.6	25.2
Full bloom	350-400	91.2	24.3
Not trimmed	600-700	126.6	19.5

<sup>z</sup> Trimming was practiced by removing the apical half of basal blanches and the apical part of main cluster. Ten clusters were tested for each category.

which decreased the number of florets per cluster to approximately 350 to 400, was more effective when performed 5 to 15 days before bloom than at blooming time. The number of set berries per cluster was not affected by the severity of trimming if the floret number was more than 250, although it decreased when the floret number was decreased to 120-130. In the commercial production of Muscat of Alexandria grapes, 80 to 100 berries per cluster are usually needed at the berry set stage, because careful berry thinning is performed several times to choose the final 40 to 50 berries having a regular size and the desired density. In the commercial cultivation of Muscat of Alexandria grapes in Okayama, it is recommended that clusters are trimmed by cutting the apical part of basal branches one to two weeks before bloom and the cluster tip be removed at anthesis.

# 2) Effect of pre-bloom shoot pinching and cluster trimming on shoot and cluster nutrition

The improvement of berry set by pre-bloom shoot pinching and cluster trimming, as shown above, must be a result of modification of nutritional conditions in both shoots and clusters during blooming time. Oinoue (1940) stressed that the high C/N ratio in shoot, which was increased by pre-bloom shoot pinching, was responsible for the high percentage berry set. However, our analyses of sugar and nitrogenous compounds in florets from pre-bloom to post-



Fig. 1. Effect of pre-bloom shoot pinching on sugar and nitrogen (N) concentrations in Muscat of Alexandria grape florets during blooming period.

bloom stages revealed that sugar concentration in pinched shoot was higher than that in unpinched ones at the beginning of blooming time. However, sugar concentration in florets of pinched shoots was decreased more rapidly than that in unpinched shoots during blooming period (Fig. 1). Nitrogen concentration, on the other hand, was increased in pinched shoots, in contrast to unpinched shoots where both protein- and amino-N concentrations were decreased. From these, it is noted that to realize successful berry set as observed in pinched shoots, sugars in florets must be metabolized rapidly to produce protein for ovule fertilization and rapid ovary wall cell division.

Nutritional analyses of florets in trimmed and untrimmed clusters also indicated that cluster trimming decreases sugar concentration and increases N concentration during blooming period.

As regard minerals, P and B were found to increase a few days after shoot pinching and cluster trimming. These elements are important for sugar transport and metabolism in the plant body (Zittle, 1951; Gauch and Dugger, 1953; Dugger et al, 1957). Improved grape berry set after use of boric acid solution foliar sprays has been reported (Oinoue, 1938; Scott, 1944; Kobayasi and Okamoto, 1966). The accumulation of P and B in pinched shoots and trimmed clusters might be related to the pre-bloom increase and post-bloom decrease of sugars in those florets.

## 3) Effect of pre-bloom shoot pinching and cluster trimming on photosynthate translocation into clusters and its fate in florets

The fact that sugar concentration in florets was increased by pre-bloom shoot pinching might be an indication of the modification of photosynthate partitioning in shoot. We conducted two <sup>14</sup>C-tracer experiments; one involved feeding <sup>14</sup>CO<sub>2</sub> to Muscat of Alexandria vines in autumn to trace distribution among new shoots in the following spring (Okamoto, 1979); and the other involved feeding <sup>14</sup>CO<sub>2</sub> to pre-bloom shoots to detect distribution among full-bloom shoots (Okamoto, 1973).

# a) Translocation of reserved photosynthate into spring shoots

<sup>14</sup>C that was assimilated by autumn leaves and reserved in the vine during winter was distributed mainly into the stem and leaves of the basal part of a shoot. The effect of pre-bloom shoot pinching on the distribution was faint (Fig. 2). However, constitutional percentages of <sup>14</sup>C in blooming florets indicated that pre-bloom shoot pinching increased the percentage of amino- and protein-<sup>14</sup>C and decreased that of sugar-<sup>14</sup>C (Table 3), which corresponded to the analytical data of florets as discussed earlier. These results indicate that shoot pinching does not affect the distribution of the food reserves, assimilated in the previous autumn and stored in



Fig. 2. Radio-autographs showing distribution of previously assimilated <sup>14</sup>C in unpinched (left) and pinched (right) Muscat of Alexandria grape shoots at full bloom. Foliar feeding with <sup>14</sup>CO<sub>2</sub> was conducted on November 15, 1970, and shoot sampling was performed on June 1, 1971.

Table 3 Effect of shoot pinching and cluster trimming on distribution (%) of<br/>previously assimilated <sup>14</sup>C-activity among various fractions extracted<br/>from Muscat of Alexandria grape clusters before and at full bloom.<sup>z</sup>

Cluster stage and treatment <sup>y</sup>	Amino acid	Organic acid	Sugar	Protein	Poly- saccharide	Others
6 days before bloom	4.2	5.2	10.8	30.8	28.7	20.3
Full bloom Shoot pinched	2.6	5.2	4.9	32.6	38.7	16.0
Shoot pinch + cluster trimming	2.8	4.1	5.9	34.6	16.4	36.2
Untreated	1.4	4.2	9.5	31.2	34.3	19.4

<sup>z</sup> Mature leaves were fed  ${}^{14}$ C-CO<sub>2</sub> in previous autumn, October 15, 1970.

<sup>y</sup> Treated 6 days before bloom.

# b) Distribution of newly assimilated photosynthates among shoots

In the second test that involved feeding  ${}^{14}CO_2$  to variously positioned leaves in pre-bloom shoots, <sup>14</sup>C distribution in the shoots at full bloom was found to be significantly affected by shoot pinching and cluster trimming, although the effect differed depending on the position of leaf fed <sup>14</sup>CO<sub>2</sub> (Fig. 3). The translocation of photosynthates assimilated by basal first and second leaves into a cluster was increased markedly by pre-bloom shoot pinching. Interestingly, the translocation from the third leaf that developed from the same node of the cluster was also stimulated by cluster trimming. Analyses of <sup>14</sup>C in blooming florets suggested that cluster trimming as well as shoot pinching markedly increased amino-<sup>14</sup>C but not sugar-<sup>14</sup>C (Table 4). These findings indicate high metabolic activity for the conversion of sugar into amino acids and a sufficient supply of sugars to florets from leaves.

# 3. Anatomical events of berry set during blooming period in Muscat of Alexandria grapes

#### 1) Ovule development

To achieve successful berry set of a grape floret, normal

development of the ovary and the ovule is essential except for the case of seedless berry set, i.e., parthenocarpy. As noted in a review published by Platt (1971), a grape pistil contains four or five ovules in its. Each ovule usually contains an embryo sac with one fused polar nucleus, one egg cell, and two synergid cells after passing through the eight-nucleate stage. Some ovules, however, are malformed or lack an embryo sac or have an undeveloped embryo sac due to interruption of cell division at the two- or



Fig. 3. Effect of pre-bloom shoot pinching and cluster trimming on the translocation of <sup>14</sup>C-photosynthate into a cluster from basal 1<sup>st</sup> and 2<sup>nd</sup> leaves (●), 3<sup>rd</sup> (O), 4<sup>th</sup> (△), and 5<sup>th</sup> and 6<sup>th</sup> (▲) leaves. Values indicate percentages of <sup>14</sup>C remaining in fed leaves and translocated into cluster on each day after feeding. Foliar feeding with <sup>14</sup>CO<sub>2</sub> was conducted 8 days before bloom.

Treatment <sup>y</sup>	Amino acid	Organic acid	Sugar	Protein	Poly- saccharide	Others	
Shoot pinched	13.2	20.5	20.2	12.5	5.1	21.3	
Shoot pinch + cluster trimming	27.0	17.1	20.0	11.2	6.3	15.2	
Untreated	8.5	15.4	19.1	9.9	6.7	34.5	

Table 4 Effect of shoot pinching and cluster trimming on distribution (%) ofcurrently assimilated <sup>14</sup>C-activity among various fractions extracted fromMuscat of Alexandria grape clusters at full bloom<sup>z</sup>.

<sup>z</sup> Mature leaves were fed <sup>14</sup>C-CO<sub>2</sub> in previous autumn, October 15, 1970.

<sup>y</sup> Treated 6 days before bloom.

four-nucleated stage (Pratt and Einset, 1961; Pratt, 1973; Carraro et al, 1979). After ovule fertilization by pollen tube penetration into a micropyle, the endosperm nucleus (fertilized polar nucleus) begins to divide to form endosperm, while the fertilized egg cell is left to stand for several weeks (Pratt, 1971). Okamoto and Imai (1976) investigated the anatomical processes of berry set in Muscat of Alexandria grapes by comparing clusters in shoots treated with pinching and boric acid spray with those in untreated shoots. The division of endosperm nucleus, which is an indication of ovule fertilization, was found two days after pollination. At day 4 post-blooming, higher than 80% of the ovules were fertilized in both treated and untreated clusters, indication that three ovules of four ovules in an ovary are fertilized in Muscat of Alexandria grapes. The number of endosperm nuclei increased rapidly in both pinched and unpinched shoots, although the increase was more rapid in ovules that developed in pinched shoots than in those that

 Table 5 Effect of shoot pinching accompanied by cluster trimming and boric acid spray on endosperm nucleus division and ovule development in ovaries of Muscat of Alexandria grapes after bloom<sup>z</sup>.

Treatment <sup>y</sup>	No.	of endo	% of ovules with		
	1	2-4	5-7	8-10	shrunk nucellus
Shoot pinch + cluster trimming	9.8	14.5	34.4	35.0	6.3
Boric acid spray	10.8	27.4	33.0	19.3	9.2
Untreated	12.0	38.6	23.9	17.6	7.9
LSD (p<0.05)	NS	6.2	7.8	10.5	NS

<sup>z</sup> Ovules were examined anatomically 4 days after pollination.

<sup>y</sup> Shoot pinching, cluster trimming, and boric acid spraying (0.2 % H<sub>3</sub>BO<sub>3</sub>) were conducted 7, 3, and 7 days before anthesis, respectively.



Fig. 4. Normally developing (right upper and lower) and degenerating ovules with shrinking nucelli (left upper and lower) in a Muscat of Alexandria grape ovary observed one week after pollination.

developed in un-pinched ones (Table 5). Ovary drop was observed from days 5 to 13 after anthesis. Examination of the number of endosperm nuclei in dropped ovaries indicated that they had stopped nuclear division two or three days before abscission. Investigation of the developmental condition of ovules in both retained and dropped ovaries revealed that most retained ovaries contained more than two normally developing ovules, while in most dropped ovaries more than two ovules were found to be shrunk (Fig. 4,

#### Table 6).

From these results, it is concluded that poor berry set in unpinched Muscat of Alexandria shoots is caused not by failure of ovule fertilization but by interruption of ovule development after fertilization. Such interruption of fertilized ovule development may be caused by an insufficient supply of nutrients resulting from the severe competition between cluster and shoot tips. It is generally accepted that developing young seeds produce plant growth hormones such as auxin, cytokinin, and gibberellin, which stimulate ovary growth leading to berry set (Nitsch, 1960; Coombe, 1960; Iwahori, 1968; Matsui, 1976, 1991).

# 2) In vitro and in vivo pollen tube growth affected by

Table 6 Effect of shoot pinching accompanied by cluster trimming and boric acid spraying on distribution (%) of set and abscised ovaries with different numbers of developing ovaries of Muscat of Alexandria grapes after bloom<sup>z</sup>.

Treatment <sup>y</sup>	Set or	No. of developing ovules per ovary					No. of normal ovules	Final
abscised	abscised	4	3	2	1	0	per ovary	set (%)
Shoot pinch + cluster trim.	Set Abscised	39 0	35 6	19 19	5 66	0 9	3.0 1.2	28.6
Boric acid spray	Set Abscised	35 1	54 7	9 24	2 57	0 11	3.2 1.3	15.8
Untreated	Set Abscised	45 0	42 8	11 43	2 37	0 12	3.3 1.5	9.5

<sup>z</sup> Represent distribution of 100 ovaries for each treatment, collected 7-11 days after pollination for abscised samples and 15 days after pollination for set samples.

<sup>y</sup> Refer to Table 5.

## temperature conditions In the desire to realize

successful grape berry set, pollen tube growth rate has attracted growers' and horticulturists' attention. example. For low temperature conditions during blooming period is considered to cause poor berry set because pollen tubes cannot reach ovule micropyles, resulting in failure of ovule fertilization and berry set (Owada,

1956). Tube growth rate is usually measured in artificial culture media such as solidified 1% agar containing 15-20% sucrose at various temperatures. In this method, maximum

grape pollen tube elongation rate has been recorded at 25-30°C and no tube growth is observed at temperatures below 10°C. In actual grape vineyards in Japan, however,

 Table 7 Effect of vine growth temperature on pollen tube growth into various parts of a pistil and ovary growth in several table grapes<sup>z</sup>.

Cultivar	Tempera-	Sempera- No. of pollen tubes per pistil						
	(°C)	Middle style	Upper ovary	Middle ovary	Lower ovary	Micro- pyle	diameter	
Kyoho	15	70	29	12	11	1.8	1.76	
	20	75	40	12	8	2.0	2.12	
	25	63	21	14	8	2.0	2.08	
	30	75	31	18	10	1.2	1.98	
Muscat of	15	60	45	25	12	3.8	1.51	
Alexandria	20	58	28	17	14	4.0	1.72	
	25	78	31	19	17	3.9	2.02	
	30	75	40	21	18	4.0	2.10	
Campbell	15	107	78	41	12	3.8	1.28	
Early	20	115	68	45	15	4.0	1.84	
	25	80	59	42	19	4.0	1.91	
	30	25	20	9	6	3.1	1.48	
Delaware	15	21	10	4	2	2.0	1.18	
	20	51	18	9	5	2.1	1.28	
	25	50	19	13	7	1.9	1.60	
	30	11	5	5	2	1.8	1.20	

<sup>z</sup> Measured 3 days after pollination. Twenty pistils were examined.

 Table 8 Effect of temperature on *in vitro* pollen germination and tube length in several table grapes<sup>z</sup>.

Cultivar	15	20	25	30	35
Kvoho					
Germination (%)	10.6	34.5	71.2	65.0	70.8
Tube length (mm)	1.65	1.79	2.87	2.79	2.02
Muscat of Alexandria					
Germination (%)	0.0	37.2	71.2	65.0	70.8
Tube length (mm)	-	1.02	2.87	2.79	2.02
Campbell Early					
Germination (%)	11.3	50.1	52.2	45.6	-
Tube length (mm)	0.32	2.04	2.43	1.62	-
Delaware					
Germination (%)	4.3	11.6	10.4	12.0	-
Tube length (mm)	0.60	0.95	1.02	1.00	-
Hiro Humberg					
Germination (%)	35.7	70.2	80.0	91.0	-
Tube length (mm)	0.28	1.60	1.55	1.62	-

<sup>z</sup> Sucrose 20% + agar 1% medium. Counted after incubation for 20 hr at each temperature.

grape clusters reach blooming stage during late May or early June when the average day temperature is around 20°C on clear days, but below 15°C on cloudy and rainy days. That the optimum temperature for pollen tube growth in vitro is an indication of desirable vineyard temperature remains to be confirmed. We examined the pollen tube growth in grape pistils using a fluorescence microscope. Container-grown vines of several grape cultivars were placed in air-conditioned greenhouses whose temperatures ranged from 15°C to  $35^{\circ}$ C from anthesis to berry set. In vitro tests of pollen culture using agar-sucrose medium were also conducted at various temperatures to compare the results with those

obtained by *in vivo* tests. As shown in Table 7, temperature had little effect on the number of pollen tubes penetrating various parts of a pistil in most cultivars, although ovary growth was inhibited at 15°C. Meanwhile, *in vitro* pollen germination and tube elongation were markedly retarded at 15°C in each cultivar, and significantly retarded at 20°C in Kyoho and Muscat of Alexandria grapes (Table 8).

From these results, it is concluded that *in vitro* pollen tube growth rates at various temperatures is not a good indicator of actual pollen tube behavior in grapevines. Grape pollen tubes can grow into ovary tissues and reach ovules even at temperatures as low as 15 °C , where ovary growth is retarded significantly. Low temperature during

blooming period may not be a direct cause of poor beery set although it may affect negatively both nutrient translocation into florets and metabolic activities, resulting in poor berry set.

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### [総 説] ブドウの結実生理(1)

## 新梢、花穂の栄養条件と結実性

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ブドウ栽培において、良好な結実を確保すること は高品質果実を毎年生産する上で非常に重要である。 結実の良否は気象条件によって影響されるが、開花 期の樹体や花穂の栄養条件によっても大きく異なる。 結実不良の原因を明らかにする様々な試みや試験が なされてきた中で、文献的には Oinoue(1940)のマ スカット・オブ・アレキサンドリア(以下、マスカ ット)に対する摘心の効果を栄養生理学的に追及し た研究が最も古い。同氏は、開花5日前に新梢の摘 心を行うと結実率が高くなるが、それは新梢中の炭 水化物含量が最も高まることによると考えた。さら に、大井上静一(1951)が、休眠期の母枝にグルコ ース液を注入すると結実率が高まったが、グルタミ ン酸液の注入は効果がなかったことから、ブドウの 結実にはC/N比が高いことが重要であるとした。こ の考えは、国内の巨峰栽培家たちによって信奉され、 ブドウ栽培での樹勢調節や施肥などに対する認識が 進んだ。

一方、Winkler (1974) は、剪定の程度によってマ スカットの結実性と果実生産性が大きく異なること を示し、強剪定によって新梢の勢力(Vigor)は強く なるが、結実は非常に不良になり、果実生産が著し く劣ることを例証した。そして、剪定は、栄養の蓄 積機関である旧枝(母枝など)を切り捨てるもので あることから、樹全体の容量(Capacity)を低下さ せるものであると定義した。この考えは、その後、4 倍体ブドウの結実改善策として山梨の土屋氏によっ て開発された弱剪定によるX字型自然形整枝の理論 的基盤となった。

著者は、1960年代から始めた結実生理の研究において、まず、マスカットの結実機構を栄養生理学的に追及した。本稿では、摘心や整房などの新梢・花穂管理が結実を改善する機構について得られた知見を紹介する。

#### 概要

## 1)開花期前の摘心と整房がマスカット花穂の栄養生 理に及ぼす影響

新梢の摘心を行うと、開花期直前には小花中の糖 含量は高まるが、開花期中は無摘心区よりも糖含量 が低下する。一方、アミノ態やタンパク態の窒素(N) 含量は開花期中、無摘心区よりも高い。整房を行っ た場合もほぼ同様の影響が認められた。これは、摘 心や整房によって新梢や他の小花との競合が緩和さ れるとともに、糖の代謝が活性化され、アミノ酸や タンパク合成を活発に行っていると解釈される。こ の推察は<sup>14</sup>Cを用いたトレーサー実験によっても支 持された。さらに、摘心・整房によって新梢や小花 内にリンやホウ素などの無機成分が蓄積することも、 糖代謝の活性化に関連すると考えられた。

### 2) 開花から結実に至るマスカット胚珠の発育過程

開花(受粉)した雌ずいがどのような経過を経て 1~2週間後に離脱または着粒するかについて、組織 形態学的に調査した。併せて、結実を改善する摘心・ 整房、ホウ素散布の効果を検討した。その結果、受 粉1日後には、いずれの区でも全胚珠の約80%の珠 孔内に花粉管が進入しており、4 日後には受精した ことを示す胚乳核の分裂が確認された。しかし、そ の後の胚乳核の分裂は摘心・整房区の方が無摘心区 より活発で、無摘心区では胚珠内の珠心が収縮する ものが増加した。雌ずいの離脱は5日後から始まっ たが、雌ずい中にある4胚珠の内の3または4個が 正常に発達すると、その雌ずいは着粒し、1 個また は0個の場合はその雌ずいは離脱した。以上の結果 から、マスカットでは、受精後の胚珠が正常な発達 を続けられるか否かが最も重要な結実の条件であり、 小花への栄養の供給とその代謝が活発であるかが、 鍵となっていると考えられる。

### 3) 温度条件と in vitro および in vivo の花粉管生長

開花期が低温であると結実不良になりやすい。その原因が花粉の発芽や花粉管生長が遅れるためとされていた。しかし、開花期のマスカットなど数品種の個体を15~35℃の恒温室に搬入し、受粉後の雌ずい内への花粉管生長を調査した結果、15℃のような低温条件下でも20~30℃と同程度に花粉管が生長し、胚珠に到達することが確認された。一方、寒天

培地上の花粉発芽、花粉管生長は、15℃では非常に 不活発で、マスカットでは全く発芽しなかった。し たがって、人工培地で見られる温度と花粉管生長の 関係は、実際の雌ずい内での実態を示すものではな く、低温による結実不良の直接の原因は花粉管生長 の問題にあるのではなく、主として栄養の転流や代 謝活性の不活発に起因すると考えられる。