副梢葉が‘巨峰'ブドウの生長と品質に及ぼす影響

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Contribution of Lateral and Primary Leaves to the Development and Quality of 'Kyoho' Grape Berry

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Summary

The contribution of lateral and primary leaves to the growth and quality of 'Kyoho' (*Vitis vinifera* × *V. labrusca*) berries was investigated. The total leaf area on each bearing shoot was adjusted to ca. 1500 cm^2 by removing primary or lateral leaves at veraison so that the percentage of lateral leaf area (LL) beyond or distal to the cluster was : ca. 100 (100-LL), 70 (70-LL), 30 (30-LL), and 0 (0-LL) of the ca. 1000 cm^2.

The net photosynthetic rate (Pn) of the primary and lateral leaves on treated and intact shoots were determined.

1. The berries on 100- and 70-LL shoots ripened faster than they did on 30- and 0-LL shoots. Berries on 100- and 70-LL shoots accumulated total soluble solids (TSS) and anthocyanin faster than they did on 30- and 0-LL shoots. Contrarily, titratable acidity of the berries on 100- and 70-LL shoots decreased more rapidly than they did on 30- and 0-LL shoots.

2. During the ripening stage of the berry, the Pn of lateral leaves was faster than that of primary leaves. The Pn of basal primary leaves was significantly slower which may be responsible for the retarded ripening of berries on 0-LL shoot.

3. No significant difference was found in the leaf structure or the mineral nutrient content between primary and lateral leaves when measured before the veraison.

Introduction

In spur pruning system of grapevine, primary shoots are generally pinched on or about anthesis, thus forcing lateral shoots which also pinched. The new growth after the first pinching is ordinarily suppressed by successive pinchings throughout the season. Therefore, most of leaf area is provided by leaves which unfolded on primary shoots before anthesis. Kriedemann et al. (1970) reported that the photosynthetic activity of grapevine leaves reached a peak when they were fully expanded, approximately 40 days after they began to unfold. Subsequently, Pn declined gradually. Therefore, Pn of leaves on bearing shoots is less than maximum at the ripening stage of berries. Recently, restricting the rooting volume of some trees was tried to improve the fruit quality. In grapevines, the restriction of rooting volume increased the numbers of seeded berries and improved berry quality (Okamoto and Imai, 1989), but the primary leaves began to senesce during ripening; this phenomenon was attributed to water stress during the summer season (personal communication).

In this study, we examined the role of lateral leaves, which developed after primary leaves, in accelerating the berry ripening process and improving the berry quality. The trial also included restricting the rooting volume.

Materials and Methods

Four-year-old, own-rooted 'Kyoho' grapevines (*Vitis vinifera* × *V. labrusca*) were planted in isolated soil beds set in a plastic house at the Fruit Tree Research Institute, Hiroshima Agricultural Research Center. The rooting volume was restricted to 60 liter per vine using plastic sheets. Six shoots per vine and one cluster per shoot were

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allowed to develop. After the berries set, shoot length was shortened to 12 nodes; each cluster was thinned to about 35 berries. Lateral shoots were cut back to the first node every two weeks. Vines were watered automatically using a irrigation equipment, Takemura DM-103 (Takemura Electric Works, Ltd., Tokyo, Japan) synchronized with a soil tensiometer. Watering was started at pF2.2 from budbreak to berry set, at pF1.5 from berry set to veraison, and at pF2.2 after veraison. At veraison (21 July, 1992), cluster was rethinned to 15 berries each. The leaf area per shoot was limited to ca. 1500 cm^2 and the percentage of lateral leaf area beyond the cluster was adjusted to ca. 100, 70, 30, and 0 by removing excess apical leaves as shown in Figure 1. One lateral and two primary leaves were retained on the basal part of shoots below the cluster leaving a leaf area of approximately 500 cm^2 in all treatments. The leaf area was estimated from the length of leaf blade using following regression equations :

Primary leaf ; $A=0.612+1.015X^2$

Lateral leaf ; $A=2.254+1.004X^2$

The above equations were obtained from the length of a leaf blade (X) for 30～50 leaves sampled from another vine and its actual leaf area (A) measured with a leaf area meter. Hayashi Denkoh AAM-8 (Hayashi Denkoh Co., Tokyo, Japan). For each treatment, the average diameter of ten berries was measured once or twice a week until harvest. Six berries were sampled biweekly from each treatment and anthocyanin contents in skin, total soluble solids (TSS) and titratable acidity in the juice were determined. The anthocyanin was extracted with 1% hydrochloric acid in methanol and the spectrometric absorbance of the extract measured at 535 nm.

The Pn was measured for primary and lateral leaves at each node on treated and intact shoots during ripening, using a portable photosynthesis and transpiration analyzer, Shimadzu SPB-H3 (Shimadzu Co., Kyoto, Japan).

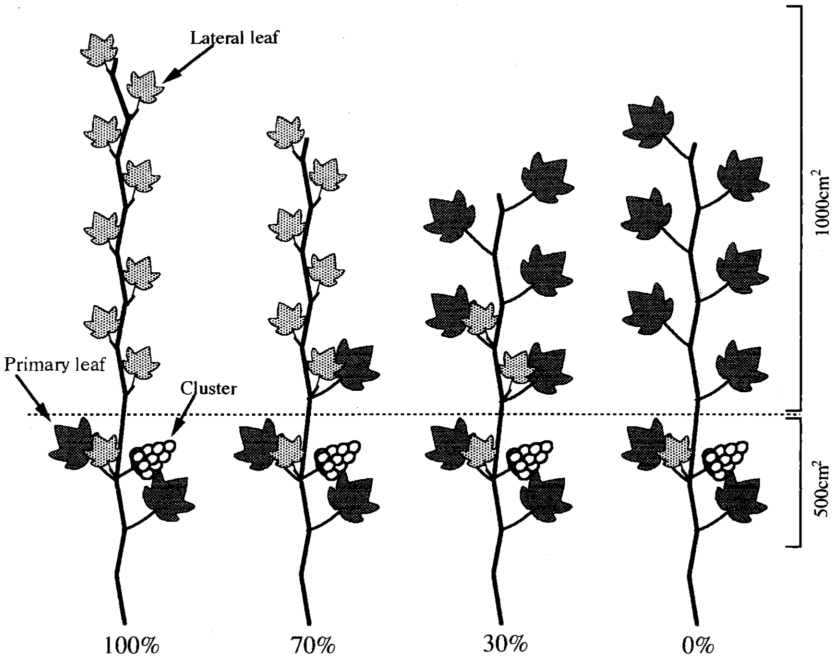

Fig. 1. Illustration showing the position of the cluster and primary and lateral leaves on the treated shoots. Each shoots had a leaf area of ca. 500 cm^2 proximal to the cluster and ca. 1000 cm^2 distal to the cluster. The percentage of lateral leaf area beyond the cluster was adjusted to ca. 100, 70, 30, and 0 (left to right) of the total leaf area at veraison. The primary and lateral leaves on first node are removed.

Both lateral and primary leaves on intact shoots were sampled before veraison for leaf tissue thickness measurements and mineral content analysis. For anatomical study, leaf samples were fixed with FAA, dehydrated with EtOH-BtOH series, and embedded into paraffin blocks. Samples were sliced into transverse sections of 10 μm thick and stained with alcian blue and basic fuchsin. The thickness of each tissue was measured under a microscope. Leaves were dried at 60 °C for mineral nutrient assay. The nitrogen content was measured by a CN corder. Yanako MT-600 (Yanagimoto Kogyo Co., Tokyo, Japan). After ashing at 550 °C, the phosphorous content was measured by a vanadomolybdate method. The potassium, calcium, and magnesium contents were determined with an atomic absorption spectrophotometer. Hitachi 170-40 (Hitachi, Ltd. Tokyo, Japan).

Results

There were no significant differences among treatments in the rate of berry growth; however, berry development on the shoot, adjusted to 100% of lateral leaf area (100-LL shoot), tended to be retarded (Fig. 2). Titratable acidity of berries on 100- and 70-LL shoots decreased faster than it did on 0- and 30-LL shoots, but there were no statistical differences among treatments (Fig. 3). TSS of berries on 100- and 70-LL shoots was higher than it was on berries on 0- and 30-LL shoots (Fig. 4). The rate of anthocyanin formation was faster in the clusters on 100- and 70-LL shoots than it was in those on 0- and 30-LL shoots (Fig. 5). Berries on 30- and 0-LL shoots did not fully color.

On a sunny day, 1, Sept., the Pn increased rapidly after 6 : 00, reached a plateau between 8 : 00 to 10 : 00, and then declined (Fig. 6). Photosynthetic photon flux (PPF) density increased from 6 : 00 until 11 : 00 and then declined. Pn of lateral leaves on the 11th and 7th nodes were faster than it was on leaves at other nodes. Pn of the primary leaf on the 3rd node was extremely low. On a rainy day, 19, Aug., Pn was low compared to that on a sunny day. No significant differences among leaf positions were observed when PPF was under 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 7). However, Pn of lateral leaves rose markedly at 11 : 00 when

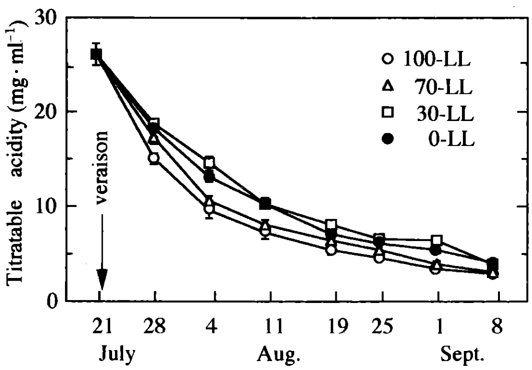

Fig. 3. Seasonal changes in titratable acidity of 'Kyoho' grape juice as affected by the percentage of lateral leaf area. Vertical bars indicate standard errors (n =3). (See Fig. 1 for lateral leaf area)

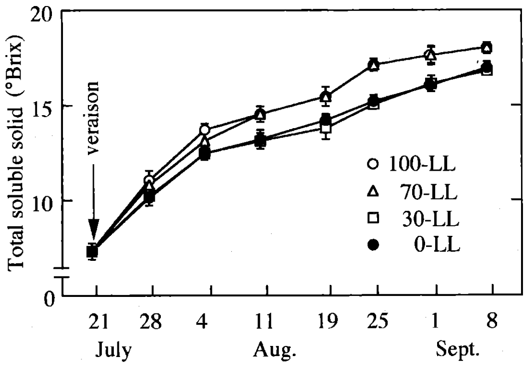

Fig. 4. Seasonal accumulation of TSS in the juice of 'Kyoho' grape as affected by the percentage of lateral leaf area. Vertical bars indicate standard errors (n=3). (See Fig. 1 for lateral leaf area)

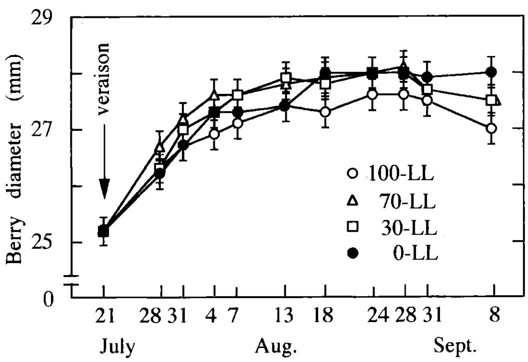

Fig. 2. Growth curve of 'Kyoho' grape berries as affected by the percentage of lateral leaf area. Vertical bars indicate standard errors (n = 10). (See Fig. 1 for lateral leaf area)

PPF exceeded 650 $\mu E \cdot m^{-2} \cdot s^{-1}$; such an increase did not occur in primary leaves.

The Pn of leaves on an untreated shoot was measured repeatedly during berry ripening (Fig. 8). Relative photosynthetic rate (node 11 = 100%) was about 75～80% in the basal lateral and apical primary leaves. In the basal primary leaves, relative Pn was as low as 50%.

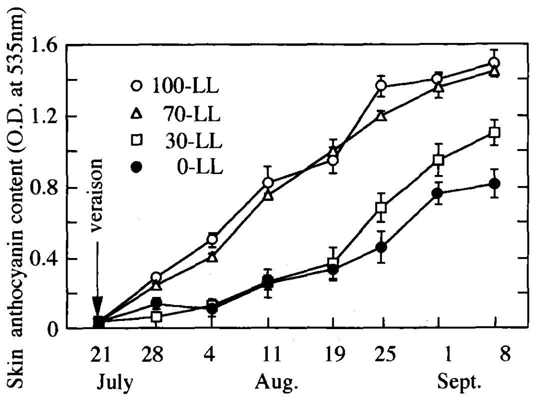

Fig. 5. Seasonal increase in the anthocyanin content in the skin of 'Kyoho' grape as affected by the percentage of lateral leaf area. Vertical bars indicate standard errors (n = 3). (See Fig. 1 for lateral leaf area)

There were no significant differences between primary and lateral leaves with respect to P, K, Ca and Mg contents before veraison. In the 1st～4th leaves on the primary shoot, N content was lower than it was in the 5th～12th leaves (Table 1). Mg content tended to be higher in lateral leaves than it was in primary leaves but no such differences were found in P, K and Ca contents. Anatomically, no differences were found between primary and lateral leaves with respect to the thickness of the various tissues (Table 2).

Discussion

By varying the percentage of lateral leaf area on bearing 'Kyoho' grape shoot, we found that increasing the lateral leaf area accelerated berry ripening, accumulated TSS more rapidly, reduced the titratable acidity, and enhanced berry color.

Pn measurements of lateral and primary leaves revealed that photoysnthesis was faster in the lateral leaf during berry ripening than it was in the primary leaves. Kriedemann et al. (1970), Kumashiro et al. (1990), and Takagi and Inoue (1982) reported that a peak of photosynthetic activity of grape leaves occurred when the leaves became fully expanded. In Japan, primary leaves of grapevine near the cluster unfold in the mid-April,

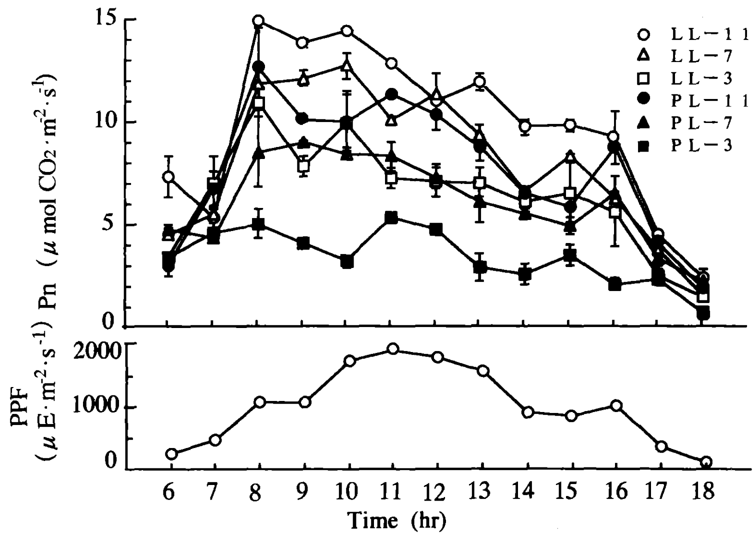

Fig. 6. Diurnal changes of photosynthetic photon flux (PPF) density (lower) and photosynthetic rate (Pn) (upper) in primary (PL) and lateral (LL) leaves on, 1, Sept. a sunny day. Numbers in legend are node number on shoot. Vertical bars indicate standard errors (n=3).

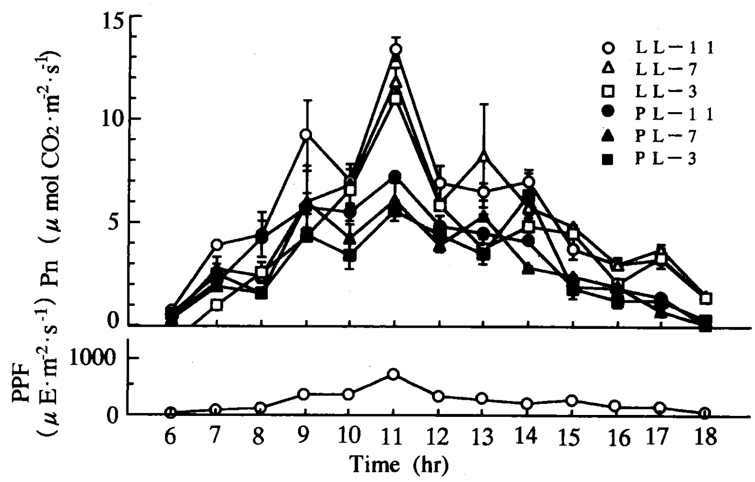

Fig. 7. Diurnal changes of photosynthetic photon flux (PPF) density (lower) and photosynthetic rate (Pn) (upper) in primary (PL) and lateral (LL) leaves on, 19, Aug. a rainy day. Numbers in legend are node number on shoot. Vertical bars indicate standard errors (n=3).

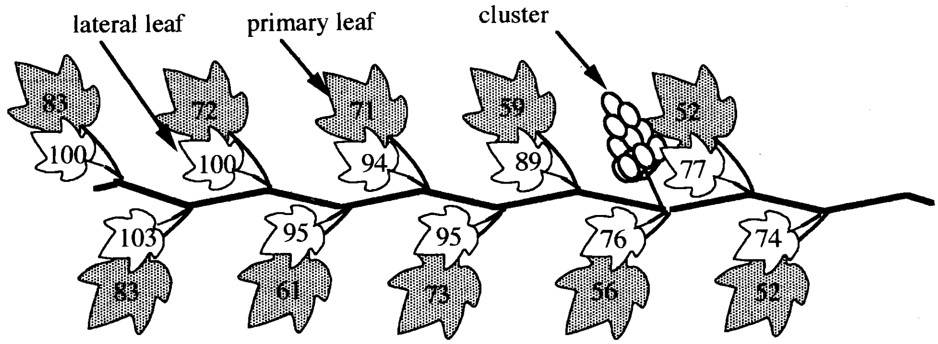

Fig. 8. Relative photosynthetic rates of the primary (shaded) and lateral (unshaded) leaves at different nodes of an intact shoot during berry ripening stage. The rate of lateral leaf on 11th node is taken arbitrarily as 100%. The primary and lateral leaves on first node are removed.

about ninety days before veraison. Therefore, the contribution of photosynthesis by primary leaves is declining during later growth and ripening stages of the berries. In this experiment, the Pn of the basal primary leaves was about half that of the apical lateral leaves. Hence, the stimulation of berry ripening on 100- and 70-LL shoots is attributed to the high Pn of lateral leaves.

TSS of berry increased faster on 100- or 70-LL shoots than it did on 30- or 0-LL shoots after treatment. When Matsui et al. (1985) tracted the distribution of ^{14}C-assimilate in potted 'Delaware' grapevines after exposure to $^{14}CO_2$, they found that the amount of ^{14}C-assimilate translocated into berrries became maximum at the early period of stage III; the rate of import was minimum at harvest. They also noted that ^{14}C-assimilate in berries was mainly in the sugar fraction. Their findings indicate that the rate of sugar accumulation at the early stage III depends on the amount of photosynthates available. This would account for the rapid increase of TSS in berries on 100- and 70-LL shoots. Kurooka et al. (1990) reported that CO_2 enrichment of the atmosphere accelerated Pn and stimulated berry ripening.

Anthocyanin in the skin was more concentrated

Table 1. Mineral nutrient contents (% DW) of primary and lateral leaves before the veraison.

Leaf	N	P	K	Ca	Mg
1st～4th leaves					
Primary	2.36	0.51	1.17	1.34	0.14
Lateral	2.61	0.48	1.21	1.20	0.19
F significance	NS[z]	NS	NS	NS	NS
5th～8th leaves					
Primary	2.67	0.44	1.22	1.21	0.15
Lateral	2.59	0.43	1.13	1.31	0.22
F significance	NS	NS	NS	NS	*
9th～12th leaves					
Primary	2.89	0.40	1.22	1.36	0.16
Lateral	2.55	0.40	1.21	1.25	0.17
F significance	NS	NS	NS	NS	NS

[z] NS and * are not significant and significant at $P = 0.05$, respectively.

Table 2. Thickness (μm) of various tissues of primary and lateral leaves before the veraison.

Leaf	Epidermis (upper)	Palisade parenchima	Spongy tissue	Epidermis (lower)	Total
1st～4th leaves					
Primary	15.1	54.3	58.5	9.9	137.8
Lateral	15.0	53.8	57.0	10.0	135.8
F significance	NS[z]	NS	NS	NS	NS
5th～8th leaves					
Primary	15.0	53.9	57.5	10.1	136.4
Lateral	14.9	53.6	58.2	10.1	136.8
F significance	NS	NS	NS	NS	NS
9th～12th leaves					
Primary	15.5	53.7	56.8	10.3	136.3
Lateral	14.8	52.5	55.9	9.9	133.1
F significance	NS	NS	NS	NS	NS

[z] Not significant.

in berries on 100- and 70-LL shoots. The close correlation between TSS and anthocyanin content in skin was found at the early stage III (Ono et al., 1993); a similar tendency was observed in this study. Smart et al. (1988) noted that the anthocyanin increased with more exposure of fruit to light. The 100-LL shoot, having small lateral leaves instead of large primary ones near the cluster may have exposed clusters to the sunlight. This would explain in part the good coloration of berries on 100-LL shoots.

On a sunny day, the Pn reached maximum in mid-morning, and gradually declined thereafter. There was little correlation between Pn and PPF. On the contrary, on a rainy day, the Pn depended on PPF. Kumashiro et al. (1990) reported that the light-saturation point of 'Kyoho' grape was about 900 $\mu E \cdot m^{-2} \cdot s^{-1}$. On a sunny day, PPF between 8 : 00 and 16 : 00 exceeded this level, whereas on a rainy day, PPF level was below this level throughout the day. Küppers et al. (1986) found a concurrent decline in Pn of *Eucalyptus* spp. on a sunny day, but not on a day with intermittent clouds. Chaves et al. (1987) reported similar results in grapevines. Thus our agreement here suggests that supra-optimum light intensity may have a negative effect on Pn.

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副梢葉が'巨峰'ブドウの生長と品質に及ぼす影響

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摘　要

果実の成熟促進を目的として，着色開始期から結果枝上の葉面積を約 1500 cm^2 に制限し，果房着生節より先端部（約 1000 cm^2）の本葉と副梢葉の葉面積の割合を変えて果実の成熟を調査し，本葉と副梢葉の特性を比較した．

1．副梢葉 0％区と 30％区に比べ，副梢葉 70％区と 100％区では成熟が早く進み，果汁の糖含量，果皮のアントシアニン含量の蓄積や滴定酸度の減少が早かった．

2．成熟期に，処理に用いた新梢と無処理の新梢の本葉と副梢葉の光合成速度を測定した．副梢葉は本葉よりも光合成速度が高く，新梢の基部付近の本葉の光合成速度は著しく低かった．この本葉と副梢葉の光合成活性の違いが成熟の早晩につながったと思われる．

3．硬核期における葉の内部形態，無機成分含量には本葉と副梢葉の間で差異は認められなかった．