Relationship between Flower–bud Differentiation and Carbohydrate Contents in Spring Shoots of Very–early, Early and Late Maturing Cultivars of Satsuma Mandarin

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Summary

Seasonal changes in the types of bud, vegetative, mixed or generative (reproductive), and carbohydrate contents in three satsuma mandarin (*Citrus unshiu* Marc.) cultivars, ‘Yamakawa Wase’, ‘Okitsu Wase’ and ‘Aoshima Unshiu’, were investigated. Shoots from these very–early, early and late maturing cultivars, respectively, were excised and examined for bud types from the pre–harvest period of the previous year to just before bud break in the spring (2001–2002). Tree growth of each cultivar in 2001 showed aspects of nearly the heaviest on–year of alternate bearing for the previous 10 years, so that a poor return bloom was expected in 2002. Shoots that sprouted in the spring of 2001 were sampled at monthly intervals from early–November to mid–March, 2002, defoliated, placed in a vase and sprayed with 100 ppm benzyladenine (BA) to force them into growth in a chamber kept at 28°C. After 8–14 days of incubation, developing buds were tallied whether they were vegetative, mixed or generative. In every cultivar, nearly all buds of shoots excised in early–November were vegetative; those with an inflorescence constantly increased up to mid–March. Shoots of ‘Yamakawa Wase’, whose trees were harvested in late–October, progressed from the vegetative to the generative phase most rapidly, followed by those of ‘Okitsu Wase’ and ‘Aoshima Unshiu’, whose trees were harvested in mid–November and mid–December, respectively. There was no significant difference in the bud types between ‘Okitsu Wase’ and ‘Aoshima Unshiu’ throughout the experimental period. From December to February, the starch concentrations in the spring shoots of ‘Yamakawa Wase’ were significantly higher than those of the other two cultivars. Spring shoots of ‘Okitsu Wase’ had the highest total sugar contents from December to January, but the least number of inflorescences. Higher total sugar accumulation in spring shoots after harvest seemed to have no promotive effect on flower–bud formation. Our data indicate that earlier harvest of satsuma mandarin induces rapid starch accumulation in spring shoots, resulting in a progressive differentiation of flower buds on inflorescences.

Key Words: carbohydrate, flower–bud differentiation, harvest time, satsuma mandarin.

Introduction

Satsuma mandarin (*Citrus unshiu* Marc.) exhibits marked alternate bearing habit, such that a heavy crop suppresses flower bud formation for the following year. Early thinning of fruit increases flowering in the following year (Garcia–Luis et al., 1986; Okuda et al., 1996). Many studies were conducted on the inhibitory effect of fruit load on flowering in satsuma mandarin trees as related to carbohydrate levels (Okuda et al., 2002; Shimizu et al., 1978) and plant growth regulators (Ogata et al., 1996; Okuda, 2000). However, information on the influence of fruit load and harvesting timing on the progress of flower–bud differentiation is limited (Iwasaki, 1959). We suggested in our previous works that the experimental method using excised shoots was useful to investigate the progress of flower–bud differentiation in satsuma mandarin trees (Yahata et al., 1995;

Yahata, 1997).

In this study, we examined the seasonal changes in the number of sprouted shoots with inflorescence on the excised shoots of three satsuma mandarin cultivars which matured at different times. In addition, starch and sugar contents in the shoots were quantified to seek the effect of the previous crop on the suppression of the flower–bud differentiation in the following season.

Materials and Methods

Plant materials

Three trees each of 19–year–old ‘Yamakawa Wase’ (very early maturing), 22–year–old ‘Okitsu Wase’ (early maturing) and ‘Aoshima Unshiu’ (late maturing) grafted on trifoliate orange rootstocks in an orchard at Fukuoka Agricultural Research Center were used. The trees with a good balance of vegetative and generative growth were selected for the investigation in 2001; trees were grown under customary field management in Japan. Fruit thinning to adjust the leaf–to–fruit ratio to

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nearly 30 was done in late-August for all cultivars. All fruits of each cultivar were picked at the customary time for the area: 'Yamakawa Wase', October 24; 'Okitsu Wase', November 15; and 'Aoshima Unshiu', December 11. Tree height and width were measured in November; canopy volume was calculated by the following formula: canopy volume = tree height $\times$ tree long-width $\times$ tree short-width $\times$ 0.7 (Kawase et al., 1987).

Flower-bud development in excised spring shoots

From early-November in 2001 to mid-March in 2002, 20 spring shoots (10–20 cm long) were sampled at monthly intervals from each tree. The shoots were defoliated and separated into two lots. One lot of 10 shoots was stored at -80°C for carbohydrate analysis; the other 10 shoots were placed in a vase, sprayed with 100 ppm benzyladenine (BA), and incubated in a growth chamber to induce bud break under continuous light from a 60 W incandescent lamp at 28°C (Kawano, 1987; Yahata, 1997). After 8–14 days incubation, new shoots emerged were counted and classified as follows: vegetative, bearing leaves and no flowers; generative, with no leaves and a single flower; or mixed, with leaves and a flower at the terminal position (Okuda, 2000). The results were expressed as number of shoots per 100 nodes.

During the following flowering season in 2002, 20 spring shoots which were 10–20 cm long and 1–1.5 m above the soil surface were selected at random from each tree in the orchard. The bud types of the newly sprouting shoots were counted on April 24.

Carbohydrate analysis

Soluble sugars were extracted by homogenizing the frozen shoot samples in 80% ethanol and heating the homogenate for 30 min at 80°C . After centrifugation, the supernatant was decanted and the precipitate washed with 80% ethanol; the process was repeated 2 more times. The combined supernatant was evaporated to the aqueous phase and diluted with distilled water to a given volume. An aliquot of the diluted solution was injected into an HPLC (LC-10A, Shimadzu Co.) equipped with a refractive index detector. Sugars were separated by using an Asahipak NH2P-50 4E column (Shodex), that was maintained at 30°C and eluted with 75% acetonitrile at a flow rate of $0.6\text{ ml}\cdot\text{min}^{-1}$. Sucrose, glucose, fructose and sorbitol were identified and quantified.

The residue after sugar extraction was resuspended in distilled water and boiled for 30 min. Starch in the suspension was hydrolyzed by a combination of glucoamylase and maltase at 40°C for 2.5 hr (Hase and Yasui, 1980). The mixture was centrifuged; the supernatant was decanted, and the precipitate washed with distilled water. The process was repeated and the supernatants combined. The water-soluble proteins in the supernatant were precipitated with 2.8% ZnSO_4 and 0.15N $\text{Ba}(\text{OH})_2$, and removed by filtration. Glucose content in the filtrate was determined by a Somogyi-Nelson method. The starch content was calculated by multiplying the glucose content by 0.9.

Results

Yield (kg) per tree of 'Yamakawa Wase' was significantly less than those of 'Okitsu Wase' and 'Aoshima Unshiu', whereas the yield ($\text{kg}\cdot\text{m}^{-3}$) per canopy volume of 'Yamakawa Wase' was more than twice those of the other two cultivars (Table 1). This is because trees of 'Yamakawa Wase' were shortest and the canopy volume the smallest. No significant difference in yield per tree and per canopy volume was found between 'Okitsu Wase' and 'Aoshima Unshiu'. In the same orchard, the coefficients of variation (C.V.) in yield per tree of 'Okitsu Wase' and 'Aoshima Unshiu' were larger between 1991 and 2000 than that of 'Yamakawa Wase' (Table 2). In 2001, the yields of 'Yamakawa Wase' and 'Okitsu Wase' were almost the same as the highest values for 10 years, while the yield of 'Aoshima Unshiu' was slightly less than that in its maximum year.

Buds on almost all nodes in the excised spring shoots broke normally, regardless of the sampling timing for all cultivars (Table 3). In all the cultivars, nearly all shoots that emerged in early-November were vegetative; the number of shoots bearing flowers increased after early-December. In 'Yamakawa Wase', the bud types shifted from vegetative to generative gradually from early-December to mid-March, and especially generative shoots increased in mid-March. Contrarily, in 'Okitsu Wase' and 'Aoshima Unshiu', flower initiation progressed slowly, as the frequency of shoots with mixed buds slowly increased after early-December. The number of flowering shoots was significantly fewer than that of 'Yamakawa Wase' after January. There was no significant difference in the total number of flowers between 'Okitsu Wase' and 'Aoshima Unshiu' through-

Table 1. Varietal differences in harvest date, yield, tree height and canopy volume of satsuma mandarin trees in 2001.

Cultivar	Harvest date	Yield per tree (kg / tree)	Yield per canopy volume ($\text{kg}\cdot\text{m}^{-3}$)	Tree height ^z (cm)	Canopy volume ^z (m^3)
Yamakawa Wase	Oct. 24	47.0b ^y	8.25a	167b	5.7c
Okitsu Wase	Nov. 15	88.3a	4.01b	243a	22.0b
Aoshima Unshiu	Dec. 11	108.7a	3.55b	263a	30.6a

^z Tree height and canopy volume were measured at November in 2001.

^y Mean separation within columns by Tukey's multiple range test at $P=0.05$ ($n=3$).

Table 2. Fluctuation in yield of three satsuma mandarin cultivars from 1991 to 2000.

Cultivar	Standard harvest date	Yield (kg / tree) ^z			Coefficient of variation (%)
		Maximum year	Minimum year	Average 10 years	
Yamakawa Wase	Oct. 20	50.7	28.3	39.0	19.8
Okitsu Wase	Nov. 20	89.6	35.1	65.3	28.3
Aoshima Unshiu	Dec. 20	122.8	45.7	75.6	29.1

^z The mean value of 10–15 adult trees of each cultivar.**Table 3.** Varietal differences in flower–bud development in excised spring shoots of satsuma mandarin trees. Excised shoots were defoliated, treated with 100 ppm BA, then kept at 28°C for 8–14 days with their bases in water.

Sampling date (2001–2002)	Cultivar	Percentage of bud break nodes (%)	Number of shoots formed per 100 nodes			Number of flowers per 100 nodes
			Vegetative	Mixed–type	Generative	
Nov. 6	Yamakawa Wase	99.0	129.8a ^z	3.0a	0	3.0a
	Okitsu Wase	98.9	128.8a	0 a	0	0 a
	Aoshima Unshiu	95.1	125.0a	5.5a	0	5.5a
Dec. 3	Yamakawa Wase	100	106.7a	61.1a	6.7a	67.8a
	Okitsu Wase	100	111.9a	21.9a	6.6a	28.5a
	Aoshima Unshiu	100	81.5a	45.9a	3.1a	49.0a
Jan. 7	Yamakawa Wase	100	57.4b	92.7a	23.9a	116.6a
	Okitsu Wase	97.8	128.5a	33.0b	1.1b	34.1b
	Aoshima Unshiu	100	75.9b	64.5ab	4.2b	68.7b
Feb. 4	Yamakawa Wase	100	40.0b	124.4a	60.0a	184.4a
	Okitsu Wase	100	109.9a	64.6b	1.1b	65.7b
	Aoshima Unshiu	100	70.5b	84.4ab	3.3b	87.7b
Mar. 11	Yamakawa Wase	100	12.0c	110.9a	188.5a	299.4a
	Okitsu Wase	100	114.4a	88.9a	6.7b	95.6b
	Aoshima Unshiu	100	76.7b	86.7a	26.7b	113.4b

^z Mean separation within columns by Tukey's multiple range test at $P = 0.05$ ($n=3$). **Fig. 1.** Varietal differences in starch contents in spring shoots of satsuma mandarin trees. Vertical bars represent SE ($n=3$).

out the investigation period.

In 'Yamakawa Wase', starch accumulation in the shoots was markedly accelerated from early–December, whereas it remained low until early–January in 'Okitsu Wase' and 'Aoshima Unshiu' (Fig. 1). Between December and February, the starch contents in shoots of 'Yamakawa Wase' exceeded those of the other two cultivars. However, total sugar contents of 'Okitsu Wase' were markedly higher than those of the other cultivars from December to January (Fig. 2). By mid–March, starch was accumulated to its maximum, while total sugar contents decreased rapidly in all cultivars.

During the second flowering period of this experiment, the percentages of bud break nodes in the spring shoots were 86.0% in 'Yamakawa Wase', 63.9% in 'Okitsu Wase' and 69.1% in 'Aoshima Unshiu' (Table 4). Few vegetative shoots were observed in 'Yamakawa Wase', whereas the frequency of generative shoots in

Fig. 2. Varietal differences in sucrose (left) and total sugar contents (right) in spring shoots of satsuma mandarin trees. Total sugar content was expressed as the sum of sucrose, glucose, fructose and sorbitol contents. Vertical bars represent SE ($n=3$).

Table 4. Varietal differences in number of shoots and flowers in spring shoots of satsuma mandarin trees in spring, 2002.

Cultivar	Percentage of bud break nodes (%)	Number of shoots formed per 100 nodes				Total flowers per 100 nodes
		Vegetative	Mixed-type	Generative	Total	
Yamakawa Wase	86.0a ²	1.0b	12.8c	183.5a	197.3a	196.3a
Okitsu Wase	63.9b	26.2a	29.9b	17.4b	73.5b	47.3b
Aoshima Unshiu	69.1b	10.8b	43.7a	26.7b	81.2b	70.4b

² Mean separation within columns by Tukey's multiple range test at $P = 0.05$ ($n=3$).

'Okitsu Wase' and 'Aoshima Unshiu' was less than that in 'Yamakawa Wase'. The number of flowers in 'Yamakawa Wase' was about 3–4 times more than those in the other two cultivars. No significant difference in the number of flowers was observed between 'Okitsu Wase' and 'Aoshima Unshiu'.

Discussion

Morphologically flower-bud differentiation of satsuma mandarin becomes visible from late-December to late-March, so that the physiological/biochemical induction occurs during October to November prior to this stage (Inoue, 1989; Inoue, 1990; Iwasaki, 1959; Osaki and Sasou, 1940). Some researchers correlated the presence of endogenous gibberellin to the inhibition of flower-bud initiation, whereas others showed the inhibitory effect of flowering by exogenous application of GA₃; that in citrus plants extends from early-November until bud sprouting (Goldschmidt et al., 1985; Guardiola et al., 1982; Hirose, 1968; Monselise and Halevy, 1964). In this study, we examined the changes in the type of sprouted shoots on the excised spring shoots of three satsuma mandarin cultivars which differ in harvest time from early-November to mid-March. In all cultivars, no or very few shoots with inflorescence emerged on the excised spring shoots in early-November, then the number of flowers increased after early-December. Therefore, it was estimated that the morpho-

logical differentiation of flower bud in bearing satsuma mandarin trees became possible after around early-November.

Okuda et al. (2000, 2002) reported the effect of the fruit load on subsequent flowering cycle in the several cultivars with different degrees of alternate bearing. However, the varietal differences in the progress of flower-bud differentiation in various satsuma mandarin cultivars from harvest to the next sprouting time have not been sufficiently explored, especially with very early maturing cultivars, e.g., 'Yamakawa Wase'. Thus, our data show significant differences on the flower-bud differentiation among 'Yamakawa Wase', 'Okitsu Wase' and 'Aoshima Unshiu'. It seems that the flower buds which attained the physiological differentiation stage and shifted to the morphological differentiation stage increased in 'Yamakawa Wase' from January to March in comparison with the other cultivars.

The total number of excised spring shoots bearing inflorescences of each cultivar in mid-March was more than that on comparable shoots on the mother trees at the following season because of the high percentages of the nodes induced to sprout by the BA treatment. But the proportions of bud types in the tested cultivars were similar between the flowering in the orchard and that on the excised spring shoots. Because the generative shoots are most sensitive to the presence of the fruit, defruiting in late-September results in an increase in the number

of this type of shoots for the next flowering period in comparison to thinning in early–November (Garcia–Luis et al., 1986). We found a marked increase in flower buds on excised shoots of ‘Yamakawa Wase’ in mid–March, followed by a large number of generative shoots, in contrast with ‘Okitsu Wase’ and ‘Aoshima Unshiu’ which we attribute to the early harvesting of ‘Yamakawa Wase’.

Our orchard data reveal that annual fluctuations in yield per tree of ‘Okitsu Wase’ and ‘Aoshima Unshiu’ were larger than that of ‘Yamakawa Wase’ during the past 10 years. The investigation was carried out in on–year of alternative crop variation. Furthermore, yields of the three tested cultivars in 2001 were nearly the highest values for the past decade, especially the fruit load of ‘Yamakawa Wase’ was the heaviest among the three cultivars because of the highest yield per canopy volume. In satsuma mandarin trees, an early removal of fruits enhances the next flowering (Garcia–Luis et al., 1986; Okuda et al., 1996), such that an early harvest in October increases the number of flowers in the following season compared to the late harvest in December (Ogata et al., 1996). From December to February, the starch contents of ‘Yamakawa Wase’ were significantly higher than those of the other two cultivars. Carbohydrate content of the bearing satsuma mandarin trees increases rapidly after harvest (Shimizu et al., 1978). The removal of fruits increases starch content and flowering in citrus trees (Goldschmidt and Golomb, 1982; Goldschmidt et al., 1985; Jones et al., 1974). These results indicate that earlier harvesting in satsuma mandarin induces rapid accumulation of starch in spring shoots, resulting in a progressive differentiation of inflorescence even if the crop load was high.

Shoots of ‘Okitsu Wase’ accumulated from December to January much sugar compared with the other two cultivars, but its starch content remained low by January. Iwasaki (1959) observed that the morphological flower–bud differentiation of early and late maturing cultivars advanced simultaneously, or that of an early maturing cultivar rather retarded. We obtained similar results in that there was no significant difference in the number of shoots bearing inflorescences between ‘Okitsu Wase’ and ‘Aoshima Unshiu’ throughout the investigation period. Therefore, higher total sugar accumulation in spring shoots after harvest seemed to have no promotive effect on flower–bud formation.

The most important period for the physiological flower–bud differentiation of satsuma mandarin appears to be about mid–November. Hence, flower induction is markedly decreased by defoliation, and increased by ringing or defruiting before mid–November (Iwasaki, 1959). In this study, the flower–bud differentiation seemed to be suppressed by the fruit load in cultivars harvested after mid–November. It seems that we need to investigate the effects of fruit load before or after mid–November on the changes in carbohydrates in early and

late maturing satsuma mandarin cultivars to clarify the control mechanism of the flower–bud differentiation.

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収穫期の異なるウンシュウミカン3品種の花芽分化と春枝中の炭水化物含量との関係

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摘 要

ウンシュウミカンの収穫期の異なる3品種, '山川早生', '興津早生', '青島温州'の切り枝から発生する無着花枝, 有葉花, および直花数と炭水化物含量の時期的変化を2001年11月上旬から2002年3月中旬まで調査した。調査には2001年が隔年結果の表年にあたる樹を用いたが, 各品種の2001年の収量は過去10年間の最高に近い値であった。1か月間隔で, 各品種の結果樹から切り取った春枝を摘葉し, 100 ppmのBA水溶液で処理後, 水挿して28°Cの定温器内に置き, 8~14日後に萌出した芽のタイプを調査した。各品種とも, 11月上旬の切り枝では無着花枝の発生が多く, 花らいの発生がみられないか, あるいはごくわずかな数の花が着生した程度であった。その後は, 3月中旬にかけて花らいの発生が増加したが, 花芽数の増加程度は品種によって著しく異なった。10月下旬に収穫した極早生品種の'山川早

生'の切り枝では, 11月中旬に収穫した早生品種の'興津早生'や12月中旬に収穫した晩生品種の'青島温州'に比べて, 1月から3月まで無着花枝の発生が減少して花らい数が急激に増加した。'興津早生'と'青島温州'の間では調査期間中, 花らいの発生数に有意な差が認められなかった。春枝のデンプン含量は, 12~2月に'山川早生'が他の品種より著しく多くなった。一方, '興津早生'の春枝では12月から1月にかけて全糖含量が他の2品種よりも顕著に多かったが, 同品種では1月以降の無着花枝の発生が3品種中で最も多かったことから, 収穫後の春枝への糖集積は花芽分化を促進しないものと思われた。ウンシュウミカンでは, 早期収穫による春枝へのデンプン集積が花芽分化の進行に対して促進的な作用を及ぼしていることが推察された。