Changes in Sugar and Starch Concentrations of Forced June-bearing Strawberry Plants as Influenced by Fruiting

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ABSTRACT. June-bearing strawberry plants (*Fragaria × ananassa* Duch. 'Morioka 16') were forced in a greenhouse and either allowed to fruit or deflowered continuously. Plants were harvested at the start of the experiment (day 0), at full bloom (day 35), during rapid growth of green fruit (day 53), at first fruit coloring (day 63), at full coloring of the primary and some secondary fruit in the primary and secondary inflorescences (day 68), and at overripe of many primary and secondary fruit in the primary and secondary inflorescences (day 81). Dry matter accumulation in the vegetative organs in fruiting plants was less than that in deflowered plants as the fruit matured, but the total plant dry mass did not differ significantly between treatments throughout the forcing period. Reducing sugar and sucrose concentrations in roots, crown, and old leaves decreased continuously until day 68, particularly in roots. The concentrations did not differ between treatments. Starch concentrations in roots declined rapidly in both treatments between day 0 and day 35, and then the decline slowed. Starch level was significantly lower in the roots of fruiting plants from day 35 through fruit harvest. These results suggest that carbohydrate reserves in roots of forced June-bearing strawberry plants are used primarily to support the growth of inflorescences and developing leaves. They are less available for fruit growth and maturation since the levels are already relatively low by this stage.

Dry mass and carbohydrate concentrations of June-bearing strawberry plants increase rapidly during autumn, particularly in roots (Anderson, 1982; Gagnon et al., 1990). In the following spring, these levels greatly decrease at fruit coloring of the primary inflorescence (Nishizawa, 1994). However, to our knowledge, there has been no study of the changes in carbohydrate reserves between fruiting and deflowered strawberry plants at different times in fruit development.

In rabbiteye blueberry plants, the initial growth of flowers in spring depends on carbohydrate reserves in the vegetative organs and photoassimilates produced by the newly matured leaves (Darnell and Birkhold, 1996; Hansen and Grauslund, 1971; Vemmos, 1995). However, it is not yet clear whether the carbohydrate reserves in June-bearing strawberry plants are important for fruit development. Our objective was to elucidate the role of carbohydrate reserves in forced June-bearing strawberry plants.

Materials and Methods

PLANT MATERIALS AND GROWTH CONDITIONS. On 1 Oct. 1993, 60 runners of June-bearing strawberries ('Morioka 16') were planted in 2.5-L pots containing a 4 sandy soil : 1 peat (v/v) mixture and were grown under outdoor conditions. On 1 Mar. 1994, plants were transplanted into 3.5-L pots without removing and disturbing the soil around the roots. On 4 Mar., they were brought into a greenhouse and maintained at 24 ± 3 °C day / 18 ± 3 °C night under 14-h photoperiod (forcing). Light was that of natural daylength supplemented with 60-W incandescent lamps ($15 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux at the surface of leaves). A slow-release fertilizer (20N-8.7P-16.6K) (MMB-20, Zennoh Co-op.,

Tokyo) was added (3 g/pot) on 1 Oct. and 1 Mar. Runners were removed as soon as they emerged.

A completely randomized block design was used with five single-plant replicates per treatment. Half of the plants were allowed to fruit; flowers on the primary and secondary inflorescences were pollinated using a small paintbrush (fruiting). Tertiary inflorescence with only a few flowers formed in some plants was removed before blooming. All inflorescences of the remaining half of plants were removed as soon as they emerged (deflowered). Plants from each treatment were harvested on day 0 (4 Mar.), day 35 [8 Apr.; 70% to 80% anthesis of inflorescences of the plants (full bloom)], day 53 (26 Apr.; growing stage of green fruit), day 63 (6 May; coloring stage of the primary fruit in the primary inflorescence), day 68 (11 May; fully colored stage of the primary and some secondary fruit in the primary and secondary inflorescences), and day 81 (24 May; overripe stage of many primary and secondary fruit in the primary and secondary inflorescences) after forcing. Each inflorescence bore eight to 10 fruit. Plants then were divided into roots, crowns (including the plant apices), leaves that unfolded before forcing (old leaves), leaves emerged during forcing (new leaves), and inflorescences including fruit.

CARBOHYDRATE MEASUREMENTS. Roots, crowns, and leaflets of old and new leaves were lyophilized at -50 °C and were ground. A total of 150 to 200 mg of ground sample was extracted 3 times in 80% boiling ethanol. The homogenates were centrifuged at $2400g_n$ after each extraction. The pellets were saved for starch determination. The ethanol extracts were evaporated to dryness, then solubilized in 25 mL of water. An 1.0 mL aliquot of the supernatant and AG11-A8 resin (0.5 mL; Bio-Rad Lab., Hercules, Calif.) were mixed and shaken for 1 min, and then 100- μL aliquot of the supernatant was analyzed by a spectrophotometer (model UV-1200; Shimadzu Co., Kyoto, Japan) for glucose and sucrose using the sucrose/d-Glucose test kit (Boehringer Mannheim Biochem., Mannheim, Germany). Fructose was determined by adding

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Fig. 1. Comparison of dry matter accumulation in plant parts and total of fruiting and deflowered June-bearing 'Morioka 16' strawberry plants. *Significant treatment differences at $P=0.05$ and 0.01 , respectively, in dry mass using a paired t test.

30 μ L (50 units/mL) of phosphoglucose isomerase (enzyme code 5.3.1.9) (Boehringer Mannheim Biochem., Mannheim, Germany) and measured using the above kit.

The pellet was boiled in 2.0 mL of water for 10 min. The mixture was suspended in 4.0 mL 0.2 N KOH and exposed to ultrasonic waves for 10 min. After boiling the mixture for 30 min, the contents were cooled, the pH was adjusted to 4.5 with 1 M acetic acid, and 8 mL amyloglucosidase (EC 3.2.1.3, 2.0 unit/mL; Wako Pure Chemical Co. Ltd., Osaka, Japan) were added. After incubating for 2 h at 55 °C, the mixture was centrifuged at 2400 g_n , and the volume of the supernatant brought to 20 mL with water. A 200- μ L aliquot of the supernatant was analyzed by the previously mentioned spectrophotometer using the glucose b-test kit (Wako Pure Chemical Co.). Inflorescences were dried in an oven at 85 °C for 48 h and were weighed.

DATA ANALYSIS. Differences between treatments in plant dry mass, leaf area, and carbohydrate concentrations were analyzed using a paired t test.

Results

DRY MATTER. Dry matter partitioning was strongly influenced by fruiting. The dry mass of roots in fruiting and deflowered plants decreased similarly during the first 53 d of forcing (Fig. 1A). Root dry mass of fruiting plants maintained a constant level thereafter until day 68 and then decreased again. However, root dry mass of the deflowered plants increased rapidly after day 53. A significant difference between treatments was apparent after day 63.

The dry mass of crowns in fruiting plants did not change, while

the dry mass of deflowered plants increased slightly after day 63 (Fig. 1B). The dry mass of old leaves was almost constant throughout the forcing period, irrespective of treatments (Fig. 1C). The dry mass of new leaves in deflowered plants increased continuously throughout the forcing period, but that increase in fruiting plants ceased after day 53 (Fig. 1D). Dry matter accumulation of the inflorescences increased rapidly after day 35 (Fig. 1E), reaching 48% (19.6 g) of the total plant dry mass (40.8 g) on day 81 (Fig. 1F). There was no significant difference, however, in the total plant dry mass between treatments throughout the forcing period.

LEAF AREA. The total area of the new leaves in fruiting plants increased gradually throughout the forcing period, while that in deflowered plants increased similarly until day 53, and more rapidly thereafter, reaching 158% (19 dm²) of fruiting plants (12 dm²) on day 81 (Fig. 2).

CARBOHYDRATES. Reducing sugar (glucose + fructose) and sucrose concentrations in roots, crown, and old leaves tended to decrease continuously to day 68, irrespective of treatments (Fig. 3A–C and E–G). Reducing sugar and sucrose concentrations in new leaves increased during the first 35 d of forcing and then decreased thereafter (Fig. 3D and H). With a few exceptions, there was no difference in soluble sugar concentrations between treatments throughout the forcing period, irrespective of plant parts. Contrary to soluble sugars, starch concentrations of all plant parts of deflowered plants were significantly higher than those of the fruiting plants after day 35 (Fig. 3I–L). In both treatments, root starch concentrations decreased more than 65% during the first 35 d of forcing and remained low after day 53.

Discussion

The lack of difference in total plant dry mass between fruiting and deflowered strawberry plants throughout the entire experimental period (Fig. 1F) was reported previously (Forney and Breen, 1985; Nishizawa, 1994; Schaffer et al., 1986), and this lack

Fig. 2. Comparison of leaf area of newly emerged leaves after forcing in fruiting and deflowered June-bearing 'Morioka 16' strawberry plants. *Significant treatment difference at $P=0.05$ in leaf area using a paired t test.

Fig. 3. Comparison of carbohydrate concentrations on a dry mass basis in fruiting and deflowered June-bearing 'Morioka 16' strawberry plants. * Significant treatment differences at $P = 0.05$ and 0.01 , respectively, in carbohydrate concentration using a paired t test.

of difference might be due to the enhanced photosynthetic rate of each leaf in fruiting plants (Choma et al., 1982; Sruamsiri and Lenz, 1985; Wolkowa et al., 1974).

The declining levels of sugars in roots, crowns, and old leaves during the first 63 d suggest that soluble sugars stored in vegetative organs of forced June-bearing strawberry plants are probably important, not only for flower development but for the early phases of vegetative growth.

Root starch concentration decreased >65% between day 0 and 35 (full bloom) (Fig. 3I), suggesting the conversion of starch to sugars and their movement to the growing organs. Similarly, Darnell and Birkhold (1996) reported that starch contents in the roots of dormant rabbiteye blueberry plants 'Bonita' decreased by 80% between dormancy and anthesis, and the subsequent decrease was low. Therefore, starch reserves in the roots were important to forced June-bearing strawberry plants during spring growth, even if the plants were deflowered.

Forney and Breen (1985) found that the root starch concentration at fruit maturation was higher in fruiting than in deflowered day-neutral strawberry plants. In our study, however, the significant difference of root starch concentrations between fruiting and deflowered plants were observed at and after full bloom (day 35). Strawberry leaves are major sinks for photoassimilates during the early stage of development (Nishizawa and Hori, 1988; Schaffer et al., 1985). In our study, a rapid decrease in root starch concentrations between day 0 and day 35 correlated with an increasing soluble sugar concentrations in the new leaves (Fig. 3D, H, and I), suggesting that the developing leaves may be a major sink organ for reserve carbohydrates in the roots. Therefore, a greater decrease in starch concentrations in fruiting than that in deflowered plants is probably due to the stronger sink demand of the inflorescences. In contrast to the roots, starch and sugar concentrations in

the crowns decreased more gradually, irrespective of treatments (Fig. 4B, F, and J), suggesting that the reserve carbohydrates in the crowns may be less important than the roots.

Fruit bearing inflorescences made up 48% of total plant dry mass on day 81 (Fig. 1E and F). Strawberry fruit are the predominant sink organ for photoassimilates, and >50% of the total exported carbon from the most recently expanded leaf accumulates in inflorescences during the maturation stage (Nishizawa and Hori, 1988). Nishizawa (1994) reported that 'Yachiyo' fruit-bearing strawberry plants had less white roots and more black roots than nonbearing plants. Thus, the shortage in the photoassimilate supply from leaves to roots during fruit maturation may induce the death of old roots, and this result may explain the decrease in root dry mass after day 68 in fruiting plants (Fig. 4A).

In our previous report (Nishizawa, 1994), we hypothesized that the carbohydrate reserves of forced June-bearing strawberry plants might be used for fruit growth during maturation since carbohydrate concentrations in roots and crown at coloring of the fruit were significantly lower than those at the onset of forcing. However, study of the changes in carbohydrate reserves at various stages of fruit development indicate that a large amount of carbohydrate reserves was depleted before coloring of the primary fruit in the primary inflorescence (Fig. 3). Therefore, we conclude that carbohydrate reserves, especially in the roots, in forced June-bearing strawberry plants are used primarily to support the early phases of spring growth, even if the plants were deflowered. They are less important for fruit growth and maturation.

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