Heritability of Sugar Contents in Strawberry Fruit in the F₁ Populations Using a Common Pollen Parent

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Summary

The heritability values of sugar contents in strawberry fruit were estimated from the parent-offspring regression of seven F₁ populations, obtained from a common pollen parent 'Toyonoka'. The estimated heritability values for total sugar, hexose (fructose plus glucose) and sucrose contents were 0.568, 1.153 and 0.004, respectively; high additive genetic effects were found in total sugar and hexose contents. Therefore, an optimum method for breeding strawberry cultivars that contain large amounts of sugar and hexose may be to use parental lines with high total sugar and hexose contents, and to select F₁ individuals with high sugar contents. The low heritability of sucrose content in this experiment may be attributable to the cultural practices and environmental factors because harvesting strawberry fruits took a long time.

Key Words: heritability, parent-offspring regression, strawberry, sugar content.

Introduction

The qualities of strawberries are determined by their taste and flavor, i.e., aroma, sweetness, acidity, texture; appearance, e.g., size, shape, gloss and skin color; storage and transportability; all involve physical properties and chemical compositions (Mochizuki, 1991). In Japan, most strawberries are consumed fresh (Morishita, 1994); sugar content is the key factor that determines their palatability. New strawberry cultivars have been bred in Japan by propagating a large number of seedling progenies, measuring, and selecting individuals based on high soluble solids content. Several new strawberry cultivars with high soluble solids content, such as 'Akihime' (Hagiwara, 1995), 'Tochiotome' (Ishihara et al., 1997) and 'Sachinoka' (Morishita et al., 1997) have been established.

Estimated heritability of the soluble solids content in strawberry fruit have been reported (Spangelo et al., 1971; Shaw et al., 1987; Sato and Yamakawa, 1989; Shaw, 1990; Monma and Takada, 1991; Morishita, 1994). However, the heritability of soluble solids content varied from 0.14 (Spangelo et al., 1971) to 0.69

(Morishita, 1994); the correlation coefficient between soluble solids content and total sugar content was low ($r = 0.579$) (Ogiwara et al., 1998b). Moreover, Shaw (1988) indicated that selecting individuals with high sugar content from soluble solids content only was difficult. Therefore, the modes of inheriting sugar content of fruit should be understood to efficiently breed strawberry cultivars with high sugar content.

Sugars that accumulate in mature strawberry fruit consist mostly of fructose, glucose and sucrose but the accumulation is influenced by cultivar, cultural practices and environmental conditions (Inaba et al., 1977; Reyes et al., 1982; Forney and Breen, 1985; Yoshida et al., 1992; Hamano and Imada, 1994; John and Yamaki, 1994; Ogiwara et al., 1998a, b, c, 1999a). However, the inheritance of the contents and composition of sugars in strawberry fruit has been studied little, except those by Shaw (1988) and Sone et al. (2002). Since fructose, glucose and sucrose differ in the degree of sweetness, the proportion of each sugar in fruit critically affects palatability. Thus, cultivars should be bred not only for total sugar content but also the content of each sugar.

In this study, the heritability of each sugar content was investigated, using the parent-offspring regression of F₁ populations, which were obtained from a common pollen parent.

Materials and Methods

Seven strains (No.1–7), sampled at random from 'Toyonoka' × 'Reiko' or 'Reiko' × 'Toyonoka', were chosen as seed parents, and 'Toyonoka' was used as the pollen parent. 'Toyonoka', which was bred in 1973, is a major cultivar grown in Japan and has been widely used for breeding. F₁ populations were obtained by crossing

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Table 1. Parent values, mid-parent values and mean values of F_1 populations of sugar contents in strawberry fruit.^z

Parent ^y	Number of parent plant	Number of F ₁ plant	Total Sugar ^x						Hexose ^w						Sucrose					
			P ^v		MP ^w	F ₁ ^v		P		MP	F ₁		P		MP	F ₁				
			Mean ^u			C.V. ^l	Mean	C.V.	Mean		C.V.	Mean	C.V.	Mean		C.V.				
			Mean ^u	C.V. ^l													Mean	C.V.	Mean	C.V.
Toyonoka	15		60.0	8.6				38.2	7.5				21.8	15.3						
No.1	11	19	55.5	23.0	57.8	49.4	20.0	35.0	26.6	36.6	34.2	24.3	20.5	25.1	21.1	15.2	34.3			
No.2	10	24	53.0	21.4	56.5	51.6	20.5	37.5	22.5	37.9	34.8	22.4	15.5	22.8	18.6	16.9	27.0			
No.3	9	20	36.2	16.7	48.1	42.4	19.3	23.8	13.6	31.0	25.4	14.9	12.5	23.6	17.1	16.9	36.8			
No.4	10	26	24.6	32.6	42.3	46.8	14.8	21.1	28.1	29.7	30.8	16.0	3.5	82.5	12.6	16.0	36.4			
No.5	4	23	54.3	8.5	57.1	49.0	16.2	30.5	6.1	34.3	32.7	18.2	23.8	13.3	22.8	16.3	33.2			
No.6	7	18	51.2	21.2	55.6	53.4	17.3	35.0	19.6	36.6	37.2	19.4	16.2	26.1	19.0	16.2	29.9			
No.7	10	19	53.9	17.2	57.0	60.8	9.3	37.5	13.2	37.9	40.0	10.4	16.4	28.7	19.1	20.8	27.4			
Mean			48.6	—	53.5	50.5	—	32.3	—	34.9	33.6	—	16.3	—	18.6	16.9	—			

^z F_1 s were made by crossing between 'Toyonoka' as pollen parent and No.1 to No.7 as seed parent.^y No. 1–7 were parents which sampled at random from between 'Toyonoka' × 'Reiko' or 'Reiko' × 'Toyonoka'.^x Total sugar content is indicated as the sum of fructose, glucose and sucrose.^w Hexose is indicated as the sum of fructose and glucose.^v P, parent value; MP, mid-parent value; F_1 , mean value of F_1 population.^u The sugars are expressed as mg · g⁻¹FW.^l Coefficient of variation (%).

the seven strains with 'Toyonoka' (Table 1). The crosses were made in April 1995 and the mature seeds were sown in July after treating them with concentrated sulfuric acid to raise the germination rate (Yamakawa et al., 1987). F_1 progenies were transplanted to a greenhouse in August to generate runners. Three to five runner plants per progeny were harvested in July 1996 and cultured in nursery boxes (length 60 cm, width 45 cm, depth 10 cm) until they were transplanted to the greenhouse.

One-runner plants with 4 to 5 leaves were selected from each progenies and planted in the greenhouse in two rows (40 cm between rows, 20 cm between plants) in early October 1996. Plants were covered with vinyl film on October 30, and the temperature in the greenhouse was maintained between 5 and 28 °C (night / day) using a heater and a ventilator from November. Fertilizers of 1.7 N, 2.0 P₂O₅, and 1.7 K₂O (kg/a) were applied two weeks before planting.

For sugar analysis, three to five primary, secondary and tertiary fruits on the first inflorescence were harvested between early January to early April 1997. These fruits were harvested when the entire surface of the fruits had just turned red; they were immediately frozen at -80 °C for 2 days, and stored at -30 °C until analyzed. Sugars were extracted and analyzed as described by Ogiwara et al. (1999b). For each plant, 3 to 5 frozen fruits were diced to a size of about 100 mm³ and mixed; a 20 g sample was collected at random. Sugars in the sample were extracted with water, heated in a microwave oven, and analyzed, using HPLC (Pump: Shimadzu LC-9A, Column: Shim-pack SCR-101N, Detector: Shimadzu RID-6A (refractive index detec-

tor), Mobile phase: water).

Sugar contents are expressed in milligrams of sugar per gram of fresh weight. Total sugar content is the sum of fructose, glucose and sucrose, and fructose plus glucose indicates as hexose. Parent-offspring correlation coefficient (r_{MPF_1}) and parent-offspring regression coefficient (b_{MPF_1}) were estimated from:

$$r_{MPF_1} = \frac{W_{MP \cdot F_1}}{\sqrt{V_{MP} \cdot V_{F_1}}}$$

$$b_{MPF_1} = \frac{W_{MP \cdot F_1}}{V_{MP}}$$

where, $W_{MP \cdot F_1}$, V_{MP} and V_{F_1} indicate the covariance of mid-parent value and mean value of F_1 population, the variance of mid-parent value, and the variance of mean value of F_1 population, respectively.

Results and Discussions

The relationships between the parent and mid-parent sugar content values of the seven strains and 'Toyonoka' and the mean sugar content values of the F_1 populations (Table 1) are shown in Fig. 1 for each cross combination.

The mean total sugar content in the F_1 populations was lower than their mid-parents in five combinations (No. 1, 2, 3, 5 and 6). The mean value in the F_1 populations was especially low in No. 1, 5 and 3. The mid-parent total sugar content and the mean total sugar content in the F_1 populations have a parent-offspring correlation of $r=0.584$ and a moderate heritability value of $b=0.568$ (Fig. 1). A negative apparent-dominant genetic effect was possibly involved in this charac-

Fig. 1. Parent-offspring regression and correlation for sugar contents in strawberry fruit related to mid-parent values and mean values of F_1 populations. b : parent-offspring regression coefficient. r : parent-offspring correlation coefficient. NS, *: Non-significant or significant at $P < 0.05$.

teristic expression because most combinations have a lower total sugar content in the F_1 populations than their mid-parents (Fig. 1). Just for reference, we note that the dominant genetic effect in this case was likely to be an apparent-dominant genetic effect because it differed from the dominant genetic effect by hybridization between pure line parents (Morishita, 1994).

In all combinations except No. 3, the mean hexose content in the F_1 populations was similar to their mid-parents. In No. 3, the mean value in the F_1 population was lower than the mid-parent. From the relationship between the mid-parent hexose content and the mean hexose content in the F_1 populations, the parent-offspring correlation is $r = 0.820$; the heritability is $b = 1.153$, showing an additive genetic effect (Fig. 1). An estimated heritability of over 1.0 probably indicates not only an additive genetic effect but also a non-additive effect (dominance and epistasis effect) by genetic interaction (Morishita, 1994). 'Toyonoka', a cultivar with high hexose content, was selected in 1973 from F_1 populations of 12 combinations, obtained by crossing 'Himiko' and 'Harunoka'. Both cultivars have high hexose content (Honda et al., 1985; Ogiwara et al., 1998b). That was reflected in the progenies. Therefore, to breed strawberry cultivars with high total sugar and hexose contents, parental lines with these characteristics should be used. Individuals with high sugar contents should be then selected from F_1 progenies. However, we must further investigate the inheritance of sugar contents since the heterosis was observed in the sugar content of a specific combination (Ogiwara, 1997).

The mean sucrose content in the F_1 populations of No. 2, 3, 6 and 7 was similar to their mid-parents, but the mean value in the F_1 populations of No. 1 and 5 was lower than their mid-parents. In No. 4, the mean value in the F_1 populations was higher than the mid-parent. The coefficient of variation of sucrose content in each F_1 population was larger than those of total sugar and

hexose contents (Table 1). The mid-parent sucrose content and the mean sucrose content in the F_1 populations yielded a low parent-offspring correlation of $r = 0.007$ and a low heritability of $b = 0.004$; no additive genetic effect was observed (Fig. 1). However, our previous study showed heritability values of 0.42 and 0.39 for the F_1 populations between 'Toyonoka' and 'Reiko' and between 'Toyonoka' and 'Nyoho', respectively (Ogiwara, 1997). Sone et al. (2002) estimated a heritability value of 0.592 for sucrose content using Japanese and foreign cultivars and strains. The heritability of sucrose content in this current experiment is lower than the results of Ogiwara (1997) and Sone et al. (2002). In this experiment, we estimated the heritability values of sugar contents by using the primary, secondary and tertiary fruits on the first inflorescence to eliminate the factor of plant vigor by the fruit loading. Sumida (1997) suggested that the soluble solids content in strawberry fruit was influenced more by 1) the distribution of photosynthate and 2) the difference on the fruit load than by the temperature during harvesting. However, the fruits of the F_1 populations were harvested from early January to early April during which sucrose level is influenced by the environment more so than hexose content (Inaba et al., 1977; Ogiwara et al., 1998a, 1999). Ogiwara et al. (1999a) also reported that strawberry fruit, cultivated at high temperatures and under high solar radiation during late March and April, did not accumulate sucrose to its maximum potential even when the surface of the fruit turned uniformly red. Thus, the low heritability of sucrose content in this experiment may be attributable to the influence of extended harvest period during which the plants were exposed to varying environmental factors, such as high temperatures and solar radiation. Hence, the coefficient of variation of sucrose content in each population was larger than those of total sugar and hexose contents (Table 1).

Lastly, the differences in estimated the heritability values of sugar contents in previous studies, in which soluble solids content was used as an index, ranged from 0.14 (Spangelo et al., 1971) to 0.69 (Morishita, 1994). In these studies, various materials and methods were used to estimate the heritability, such as cultivars used for parents and methods of cultural practices and for calculating heritability. While, in which sugar content was used as an index, Sone et al. (2002) estimated heritability values for the total sugar, fructose, glucose and sucrose contents to be 0.312, 0.326, 0.360 and 0.592, respectively, whereas this report produced results that are different because of differences in cultivars/strains and environment (sampling time). In the future, we need to pay special attention to the sampling method for estimating the heritability of sugar content in strawberry fruit under forcing cultivation because the harvest period lasts as long as 4 to 6 months. It will be necessary to determine the heritability of sugars by considering the above-mentioned problems.

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共通花粉親を使用した F_1 からみたイチゴ果実中の糖の遺伝力

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摘 要

イチゴ果実中の糖含量の遺伝的特性を明らかにするため、共通花粉親として‘とよのか’を用い、得られた F_1 集団から親子回帰により糖含量の遺伝力を推定した。その結果、全糖含量、ヘキソース(フルクトース+グルコース)含量およびスクロース含量の遺伝力は、それぞれ 0.568, 1.153 および 0.004 となった。全糖含量およびヘキソース含量で相加的遺伝子効果が認められたことから、ヘキソース含量が高く、全

糖含量も高い品種を育成するには、ヘキソース含量が高く、全糖含量も高い特性を有する個体を交雑親に用い、その後代からそれら糖含量の高い個体を選抜する方法が効果的であると考えられた。一方、スクロース含量の遺伝力が低かったのは、収穫期間が長期にわたった結果、栽培環境の影響を受けたためと思われた。