Theor Appl Genet (1994) 88:349–354

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Introgression of wild species into the cultivated strawberry using synthetic octoploids

Received: 5 June 1993 / Accepted: 27 September 1993

Abstract Synthetic octoploids reresent one method of integrating wild species germplasm into the cultivated octoploid strawberry. Several strawberry genotypes derived from Guelph synthetic octopoloids and 3–4 generations of outcrossing were evaluted for horticultural performance. Pollen stainability of the genotypes was improved by outcrossing and selection and was not considered a limiting factor to yield. Yield and berry weight of the genotypes improved to a level where several genotypes had yields as good as, or greater than, the mean of the check cultivars. There was no significant difference in the yield of genotypes that were either three or four outcrosses removed from the synthetic octoploids. Some genotypes displayed an everbearing habit accompanied by poor runnering characteristics which may have contributed to their reduced yield in the second season. Synthetic octoploids are composed of a diversity of germplasms distinct from the cultivated octoploid. However, by carefully selecting parents for the outcrossing program and rigorous selection for important horticultural traits, it was possible to restore performance close to the elite level in as few as three generations.

Key words *Fragaria* × *ananassa* Duch · Germplasm enhancement · Outcrossing · Selection · Yield

Introduction

The genetic base of the cultivated North American strawberry *Fragaria* × *ananassa* (Duch.) is narrow due to the limited number of founding clones present in the background (Sjulin and Dale 1987). There is also no evidence to suggest that octoploids other than *F. chiloensis* and *F. virginia*, or species with lower ploidy, contributed to modern strawberry cultivars (Bringhurst and Voth 1984). It is not surprising that broadening the genetic base of the cultivated strawberry, as well as creating useful germplasm with high economic potential, are major objectives in many strawberry breeding programs.

Interspecific hybridization among wild *Fragaria* species and octoploid *Fragaria* × *ananassa* (Duch.) via sexual crosses has recieved much attention by strawberry breeder's attempting to broaden the genetic base of strawberries. However, sexual incompatibility of species of different ploidy levels, resulting in either lack of seed set or sterile progeny, has limited the success of interspecific hybridization (Scott and Lawrence 1975). Niemirowicz-Szczytt (1978) and Wenzel (1978) reported unsuccessful attempts to induce octoploids of *Fragaria vesca* ($2n = 2x = 14$). Spiegler et al. (1986) obtained some crosses between *Fragaria* × *ananassa* ($2n = 8x = 56$) and *Fragaria vesca* ($2n = 2x = 14$) which produced decaploids after chromosome doubling (*Fragaria* × *vescana* $2n = 10x = 70$), but their further use in breeding work was not reported. When *F.* × *ananassa* ($2n = 8x = 56$) and *F. moschata* ($2n = 6x = 42$) were crossed, a new species called *Fragaria* × *anaschata* ($2n = 7x = 49$) resulted, which had a muscat fruit aroma as its main feature. However, its use in breeding was not successful because of low fertility when backcrossed to *Fragaria* × *ananassa* (Kantor 1983; Evans 1986). Other interspecific hybridizations have been accomplished but high levels of sterility have prevented their further exploitation in breeding programs (Turdykulou 1974; Zubov 1978; Kantor 1982).

The ploidy barrier was successfully overcome when Guelph synthetic octoploid 1 (SO1) and synthetic octoploid 2 (SO2) breeding clones were created (Evans 1982 a,b). Guelph SO1 is a hybrid of *Fragaria moschata* ($2n = 6x = 42$) and *Fragaria nubicola* ($2n = 2x = 14$) obtained after chromosome doubling of the interspecific hybrid. Guelph SO2 is the successful result of crossing *Fragaria vesca* ($2n = 2x = 14$) and *Fragaria viridis*

Communicated by A. L. Kahler

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($2n = 2x = 14$) which after chromosome doubling was crossed with *Fragaria moupinensis* ($2n = 4x = 28$). The interspecific hybrid was treated with colchicine to produce an octoploid plant ($2n = 8x = 56$) (Evans 1974, 1982a, b). Both clones have characteristics which are important in strawberry production, such as late flowering, upright flower stalks, a high number of flower stalks per plant, high plant vigor, and fruit with a distinctive aroma (Evans 1982a, b).

After obtaining both synthetic octoploid clones, introgression of this germplasm into cultivated strawberry became a primary objective of the strawberry breeding program at the University of Guelph. A simple form of recurrent selection known as outcrossing (Scott and Lawrence 1975) was employed. In each generation, selected progeny were crossed to a cultivar or advanced breeding line to strengthen perceived weaknesses.

This study was undertaken to measure the potential of S01 and S02 breeding clones to contribute useful horticultural traits for strawberry improvement and to measure the performance of genotypes derived from S01 and S02 relative to adapted cultivars.

Materials and methods

In this study, 19 breeding lines (see Table 1) were evaluated. All genotypes were derived from S01 (Evans, 1982a), S02 (Evans, 1982b), or both synthetic octoploid breeding lines. S01 and S02 are each composed of two or more wild *Fragaria* species and were developed via interspecific hybridization (Evans 1982a, b). Introgression of this germplasm was initiated in the mid-1970s using a classic outcrossing program (Scott and Lawrence 1975) in which crosses were made to several parents rather than a single recurrent parent. This approach was taken to avoid inbreeding depression (Evans 1982c). Progeny were tested and selected at the Cambridge Research Station, Cambridge, Ontario, in each generation. Crosses were made to selected progeny to increase strong characters and improve any perceived weaknesses. Emphasis during selection was placed on increased fertility, vigour, disease resistance, yield (as a visual assessment), and fruit quality. The advanced genotypes evaluated were three to five outcrosses from the original S0 parent (see Table 1). Bounty, Redcoat, Veestar, and Vibrant were chosen as checks because they are the best-performing and the most-widely-grown cultivars in Ontario (Evans et al. 1986).

The trial was planted in May 1986 on a Typic Hapludalf (Fox sandy loam soil) at the Cambridge Research Station. Plants were set 30 cm apart within the row, with 1.2 m between rows, and trained to a matted row. Each plot consisted of a matted row 3 m in length and 0.6 cm wide. A 2-m section of row was chosen for harvest. The field experimental design was a 5 × 5 lattice square with three replications. All 19 lines and five cultivars were present in each lattice square. Plants were grown according to standard commercial practices in Ontario (Evans et al. 1986). Fertilizers applied were 16-8-8 (N-P-K) at a rate of 300 kg ha^{-1} during early June each year and 34-0-0 (N-P-K) 112 kg ha^{-1} at mid-June 1986. Supplementary water was provided from May to September, according to plant needs, through a trickle irrigation system. A straw mulch was applied during November for cold protection.

Several measurements on vegetative and reproductive growth were made. Plant vigor was rated as a visual estimate of total leaf area, comparing only plants of similar age. An arbitrary rating scale was used, where low vigor = 1 and high vigor = 5. Vigor was rated three times at regular intervals during the entire season.

Runner number was measured as the average number of runners on ten primary plants (or mother plants) per plot at berry harvest. The height of upright peduncles and the number of trusses were obtained from a mean of ten randomly-selected plants of similar age in each plot prior to berry harvest.

Pedicel strength was measured as the force required to break the berry pedicel at harvest. A 1–5 subjective rating scale was used, where 1 = easy to break, and 5 = difficult to break.

Individual berries were picked when fully ripened on all plots every second day until harvest was completed. Harvest began on 11 June and continued for 25 days in 1987 and on 24 June and continued for 26 days in 1988. Data were collected on average berry weight during the 1987 season only.

The genetic contribution (GC) of S01 and S02 to each breeding genotype was obtained using the method presented by Sjulin and Dale (1987), employing the following formula:

$$GC = \Sigma(1/2)^{n}_{1\ldots x};$$

where n = number of generations in a pedigree pathway between the synthetic octoploid and the genotype, and x = total number of pathways between the synthetic octoploid and the genotype. Pedigree pathways ended when the synthetic octoploid parent was reached.

Pollen viability was assessed on all entries in the trial. Flowers were sampled, whenever possible, from original mother plants. Three primary, secondary and tertiary flowers per genotype were collected on three dates during 1987 and 1988. For each date, pollen from flowers of similar rank within a genotype was bulked and used for the pollen count. Flowers were collected when white petals began to show and refrigerated at 1.5 ± 0.5 °C until pollen counts could be made.

Pollen grains were stained with a solution of aniline blue (0.1 g aniline blue and 0.17 g K_3PO_4 in 100 ml H_2O), acetic acid (45%) and 80% ethanol in a 1:1:1 ratio (v:v:v). Only well-stained, plum pollen grains were considered viable. At least 500 pollen grains were counted in each sample. The analysis of variance was performed on the percentage viable pollen for each flower rank.

The data were analyzed as a mixed model, where years and blocks were considered random effects, and lines as fixed affects. Error terms and degrees of freedom were calculated according to Snedecor and Cochran (1982). Measurements over time for a given trait were considered as repeated measurements over time for purposes of analysis. Duncan's multiple range test was used for mean separation. Contrasts were used to compare specific groups of lines. Data were analysed as a lattice design using the GLM procedure of SAS.

Results

In the absence of significant interaction terms data for pollen stainability was pooled over flower types and years. Mean pollen stainability ranged from 67.7 to 83.2% with a mean of 75.3 and 75.2% for genotypes and cultivars, respectively (Table 1). There were no statistically-significant differences among ranks of flowers, between S01- and S02-derived genotypes or to the number of outcrosses separating the advanced genotype and S0 parent. No significant correlations were found between mean pollen stainability and yield or fruit characters. For instance, St. Clair and 4P33, which had high and low yields respectively, had similar pollen viability counts.

Only two genotypes, 81F52 and 4P33, produced anomalous flowers with relatively-short stamens and anthers which had difficulty shedding pollen, especially under greenhouse conditions. This, however, did not appear to affect yield potential.

The mean yield of S01- and S02-derived lines was 13.2 and 12.4 t/ha, respectively, compared to the mean of the cultivars which was 15.4 t/ha (Table 2). Although no

Table 1 Mean pollen stainability of strawberry genotypes derived from S01, S02 and cultivars

Genotype/ cultivar	Mean pollen stainability (%)
46G44	75
4P33	68
51F18	76
80F47	78
15G24	76
52P14	69
71F51	78
34P13	73
81F52	71
55F18	76
2P42	77
17Q39	82
16G16	83
67F40	75
2P41	80
24G19	79
3P33	71
77F9	75
67F47	75
62E55	71
Bounty	76
Vibrant	73
Veestar	74
Redcoat	77
SE	3

Table 2 Yield, berry weight, days to 50% yield and genetic contribution of synthetic octoploids for genotypes derived from S01 and S02

Genotype/ cultivar	Yield (t/ha)	Berry wt (g)	Days to 50% yield	Generations from		Genetic contribution	
				S01	S02	S01	S02
46G44	17.3	8.5	9	4	–	0.063	0
4P33	16.6	7.5	12	–	3	0.125	0
51F18	15.9	8.3	8	4	–	0.063	0
80F47	15.9	6.7	8	5	4	0.031	0.063
15G24	15.7	7.3	8	4	–	0.063	0
52P14	15.7	7.5	12	3	–	0.125	0
71F51	15.5	8.7	12	–	3	0	0.125
34P13	14.5	8.7	11	3	–	0.125	0
81F52	14.4	8.5	12	5	4	0.031	0.063
55F18	14.3	9.4	12	4	–	0.063	0
2P42	12.1	8.3	6	–	3	0	0.125
17Q39	11.1	7.5	8	–	3	0	0.125
16G16	10.8	7.7	6	4	–	0.063	0
67F40	9.7	6.4	8	4	–	0.063	0
2P41	9.5	5.8	4	–	3	0	0.125
24G19	9.2	8.1	6	4	–	0.031	0
3P33	8.5	6.6	6	–	3	0	0.125
77F9	7.9	9.5	8	–	3	0.031	0.125
67F47	4.9	7.9	6	4	–	0.063	0
St. Clair	18.8	8.5	8	–	–	–	–
Bounty	16.9	8.5	9	–	–	–	–
Vibrant	14.7	6.3	8	–	–	–	–
Veestar	13.8	7.9	8	–	–	–	–
Redcoat	12.6	7.9	8	–	–	–	–
SE	1.6	0.7	2.5				

Table 3 Several vegetative characters of strawberry genotypes derived from S01 and S02

Genotype/ cultivar	Vigor[a]	Truss no.	Runner no.	Peduncle length (cm)	Pedicel[b] strength	Ever-bearing habit
46G44	2.7	2.7	6.3	17.0	2.5	N
4P33	3.0	15.0	3.7	16.0	1.8	Y
51F18	2.9	6.3	6.0	25.0	2.1	N
80F47	3.3	29.3	3.8	19.0	2.3	Y
15G24	1.8	3.7	8.3	12.0	1.5	N
52P14	2.8	2.7	9.7	20.0	3.1	N
71F51	4.1	3.0	8.3	24.0	2.8	N
34P13	2.8	3.7	7.7	25.0	2.8	N
81F52	2.6	2.0	7.3	22.0	1.8	N
55F18	3.6	2.7	8.0	18.0	2.0	N
2P42	3.1	7.0	2.2	21.0	2.8	Y
17Q39	3.3	7.7	8.3	22.0	1.9	N
16G16	1.5	2.0	7.6	14.0	1.9	N
67F40	2.8	1.3	8.0	22.0	1.7	N
2P41	2.9	10.7	1.2	21.0	1.9	Y
24G19	2.8	1.7	8.3	15.0	3.0	N
3P33	2.9	13.5	0.0	18.0	1.8	Y
77F9	2.6	4.0	4.3	17.0	2.9	N
67F47	3.1	2.0	7.0	18.0	2.4	N
St. Clair	3.3	3.5	9.7	23.0	2.5	N
Bounty	3.0	3.3	8.7	20.0	2.8	N
Vibrant	2.8	4.7	9.3	15.0	1.9	N
Veestar	2.7	2.0	8.3	17.0	1.8	N
Redcoat	3.0	3.7	9.3	18.0	2.1	N
SE	0.1	1.3	0.8	0.7	0.2	

[a] Rated on a relative scale: 1 = low vigour to 5 = high vigour
[b] Rated on a relative scale: 1 = easy to break to 5 = difficult to break

significant genotype-by-year interaction was detected, the yield of some genotypes varied considerably between years. Five genotypes, 80F47, 67F40, 52P14, 2P42 and 3P33, showed yield declines of 50% on average from 1987 to 1988. This did not appear to be related to the synthetic octoploid parent because two genotypes were derived from each of S01 and S02, and the 80F47 pedigree contained both synthetic octoploid germplasms. One genotype 46G44 increased in yield 227% in the second harvest year. An increase in the vigor rating of 46G44 was also observed. Eight out of nineteen genotypes had 2-year average yields greater, although not significantly, then the mean of the cultivars. Eleven out of nineteen genotypes (i.e., 58%) were higher yielding than Veestar, a commonly grown cultivar in eastern Canada (the rank correlation for yield over the two years was $r^2 = 0.48$, $P = 0.0317$.) All genotypes displaying the everbearing habit (Table 3) declined in yield in the second year and produced the lowest number of runners per plant (Table 3). The genotypes evaluated were either three or four generations removed from the original synthetic octoploid parent. There was no significant difference in the yield of the genotypes that were three versus four outcrosses (12.3 vs 12.8 t/ha) from the synthetic octoploids.

The genotypes varied in maturity (i.e., days to 50% yield) from 4 days earlier to 4 days later than the mean of the cultivars. Selection favored both early and late maturity. S01-derived genotypes were, on average, 1.6 days later to 50% yield than the mean of S02-derived genotypes. Yield and days to 50% yield were significantly and positively correlated ($r^2 = 0.60$, $P = 0.0048$).

Average berry weight was only measured in 1987 and was significantly and negatively correlated ($r^2 = -0.44$, $P = 0.05$) with the number of trusses but not with yield. Three genotypes 80F47, 3P33 and 2P41, had the greatest number of trusses compared to the other genotypes or cultivars.

The number of runners produced by the original mother plants was measured only in 1987, the year after planting. Most genotypes produced runner numbers (Table 3) similar to the mean of the cultivars (i.e., 9.1 runners/plant). Genotypes exhibiting the everbearing habit (Table 3) produced a maximum of only 3.8 runners per plant while 3P33 produced no runners in the year of planting. S01-derived genotypes produced significantly more runners per plant (i.e., 7.3) than genotypes derived from S02 (i.e., 4.0). There was a significant and negative correlation ($r^2 = -0.70$, $P = 0.0001$) between the genetic contribution of S02 and runner number. In contrast, there was a significant and positive correlation between the genetic contribution of S02 and truss number ($r^2 = 0.47$, $P = 0.0172$).

Pedicel strength, an important characteristic for ease of harvest, was lowest in 67F40 (1.7) and 15G24 (1.5). In contrast, other genotypes, such as 52P14 and 24G19, required a force approximately 100% greater than 15G24 to break the pedicel. Values for cultivars ranged from 1.8 for Veestar to 2.8 for Bounty. Pedicel strength and berry weight were significantly and positively correlated ($r^2 = 0.45$, $P = 0.05$).

Peduncle height varied between 12 and 25 cm. Three genotypes, 51F18, 34P13 and 71F51, had peduncle lengths of 25, 25 and 24 cm, respectively. The longest peduncle among the cultivars was 20 cm for Bounty.

Those genotypes exhibiting the everbearing habit and reduced runnering also had truss numbers higher than the runnering genotypes. Average truss number per plant among the genotypes was 3.2 and 15.2 (Table 3) for non-everbearing and everbearing, respectively.

Discussion

Synthetic octoploids represent one of three breeding methods available to transfer strawberry germplasm from lower ploidy levels to cultivated octoploid species (Bringhurst and Voth 1984). Evans (1982a, b) has been the only strawberry breeder to successfully create and report synthetic octoploids of *Fragaria sp.* S01 was composed of 75% *F. moschata* and 25% *F. nubicola*, while S02 contained three species, *F. vesca* (25%), *F. viridis* (25%) and *F. moupinensis* (50%). The genetic contribution (Sjulin and Dale 1987) of S01 and S02 to the genotypes evaluated in the present study ranged between 3.12% and 12.5% depending on the number of outcrosses between the synthetic octoploid and genotype tested.

The five species originally used to create S01 and S02 are known to breeders and geneticists working with *Fragaria* (Reed 1966) but little is known about their actual breeding potential. For instance, Hancock and Bringhurst (1978) studied *F. vesca* L. (a diploid species) but this species was not described as part of a crossing program. Likewise, the characteristics of other species have been described but little is known about exactly what they might actually contribute to the cultivated octoploid strawberry.

Only 25% of the progeny from the first cross between the cultivar and the synthetic octoploid produced seed and set fruit (Evans 1986). Pollen stainability ranged from 4 to 90% among the F_1 progeny (Evans 1982a). Low pollen viability has been associated with lower yields in strawberry (Braak 1968). In the present study, pollen stainability averaged 75.5% and 76.0% for S01- and S02-derived genotypes respectively, and does not appear to be a limiting factor for yield or to contribute to yield differences. Flowers of all genotypes tested had functional anthers and ovaries compared to 75% of the progeny from initial cultivar × synthetic octoploid crosses which were staminate. Further outcrossing, and selection for yield and fruit size per se, favoured increased fertility and fully functional flowers. Although no empirical data were presented, Evans (1986) noted that the progeny of the third outcross had larger fruit and higher yields than the locally-adapted cultivars he used for comparison. These observations generally agree with the yield trial results produced in this study. Many of the genotypes evaluated had a yield that was as good as, or better than, the check cultivars. In 1987, 80F47 yielded 58% (i.e., 8.1 t/ha) more than the mean of Redcoat and Veestar, two cultivars adapted and widely grown in this geographic area. Yield components such as runner number had an impact on yield in the second year.

In some crosses between *F.* × *ananassa* nad *F. moschata*, Kantor (1982, 1983) attributed the yield increase to the *F. moschata* germplasm. Three lines, 51F18, 80F47, and 46G44, performed better than the average of the cultivars for two seasons. Although the genetic contributions of *F. moshata* to these genotypes via S01 was low (i.e., 4.15, 2.8 and 2.8%, respectively), increased heterozygosity after three or four outcrosses coupled with an increase in the frequency of superior alleles during selection could account for the improvement.

The yield results of the present study indicate that relatively high levels of performance can be restored to F_1 hybrids with as few as two outcrosses and intensive selection for horticultural performance. Wild species have many negative horticultural characters and may have few genes that could contribute to the high yields necessary in a cultivar. However, the process of restoring genotypes infused with wild species germplasm to an elite level of performance may require only three (Bringhurst and Voth 1984) or fewer generations. Evans (1982c) identified many genotypes during the early generations of the breeding program that lacked cultivar potential but were used extensively as parents in the crossing program.

Lacey (1973) found a positive correlation between vigor and yield; but, in the present experiment no correlation was found between these characteristics during either season. Vigor is normally associated with optimum plant growth rates, mainly due to increased efficiency at all physiological levels within the plant and positive interactions with the environment. Vigor is considered synonymous with yield in some breeding programs (Scott and Lawrence 1975), but partitioning of photoassimilates between vegetative and fruit tissues must also be taken into account. Good apparent external vigor could be due to poor partitioning or differences in the amount of interplant competition (Strik and Proctor 1988). An example of false vigor or luxuriance (Salisbury and Ross 1985) is given in the increased vigor of staminate plants, such as S01 and S02, or overfertilized plants. In this case, the lack of correlation seems to be related to the way yield was measured. Yield was measured on a plot basis, and vigor was measured on single plant basis. It is possible that yield could be the product of several runner plants originating from a relatively unvigorous mother plant (Olsen et al. 1985; Strik and Proctor 1988).

The number of trusses per plant has been positively correlated with yield (Strik and Proctor 1988). Four genotypes, 2P41, 3P33, 4P33 and 80F47, has truss numbers at least two-times higher than the mean of the cultivars. The synthetic octoploids were considered to have an abundance of trussses (Evans 1982a, b). S01-derived genotypes had, on average, 2.9 trusses and 7.6 runners per mother plant compared to 9.5 and 3.9 per plant, respectively, for S02. The high correlation between truss number and the genetic contribution of S02 suggests that S02 would be a source of increased yield potential through increased flower number. Truss number is only one yield component that must be balanced to maintain high marketable fruit number and weight. Those genotypes identified with high truss numbers also demonstrated compensation and had below average numbers of runners and lower berry weight.

The number of runners was significantly and negatively correlated with both the number of trusses and the everbearing habit. Truss number and the everbearing habit were strongly related. These findings agree with previous reports (Bedard et al. 1971; Scott and Lawrence 1975). The everbearing trait and the low number of runners seem to be inherited as a block. Contradictory results were shown in previous works on these two traits (Simpson and Sharp 1988). In *Fragaria vesca*, these traits are recessive and each is governed by a single gene segregating independently (Scott and Lawrence 1975). In polyploid *Fragaria* species, inheritance has not been clearly described (Scott and Lawrence 1975; Simpson and Sharp 1988) but the two traits are closely related. This is a good example of partitioning of growth factors as a whole-plant process. Although growth is controlled mainly by hormones, the principal determinant of hormone levels is genetic (Salisbury and Ross 1985). The everbearing trait is an example of the plant's genetic control over the timing and distribution of fruit development and the partitioning of growth substances. Axillary buds on the plant crown may develop into runners, branch crowns, or trusses, under different environmental conditions of temparature and daylength. The everbearing trait causes the preferential development of branch crowns and trusses at the expense of runner development (Simpson and Sharp 1988). In the field, the axillary buds which may develop into runners on a June-bearing genotype are induced to develop into trusses under long days (Dana 1981) and produce a second crop of flowers in everbearing genotypes. Many of the genotypes with the everbearing habit produced few if any runners but produced more crowns per plant. Crown number per plant is an important yield component and has an optimum value above which berry yield and size decline (Strik and Proctor 1988).

Pedicel strength and peduncle height are two traits that may be significant to facilitate machine harvesting of strawberries. Berry pedicel strength increased significantly as berry weight increased. A greater pedicel diameter which does not restrict translocation could facilitate greater berry weights (Gardner et al. 1985). However, for mechanical picking a pedicel that breaks easily may contribute to less berry damage. A long or tall peduncle that could keep fruit off the ground would increase the efficiency of some mechanical harvesters by increasing harvestable yields and reducing berry damage.

In summary, the genotypes evaluated in this study represent germplasm selected for three to four generations after the original cultivar synthetic octoploid cross. In their present state, these genotypes are performing at the elite germplasm or pre-cultivar level. Breeding progress has been rapid due, in part, to intense selection pressure for good horticultural performance. Evans (1986) suggested that S01 and S02 had high levels of homozygosity due to chromosome doubling and, in theory, would be excellent testors in a breeding program (Hallauer and Miranda 1981). The potential of the synthetic octoploids as testors, may have contributed to high genetic variance in these initial generations and to the rapid progress realized. The use of synthetic octoploids represents an efficient method for broadening the genetic base of the cultivated strawberry. One advantage is the ability to bring together germplasm from two or more species into a genotype at the octoploid level that is crossable to modern octoploid cultivars. This approach warrants continued and further use.

Acknowledgements The authors thank Mr. Simon van Schyndel for technical assistance and acknowledge the Ontario Ministry of Agriculture and Food and Ontario Berry Growers' Association for financial assistance.

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