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ORIGINAL PAPER

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AGRONOMIC PERFORMANCE AND HETEROSIS OF STRAWBERRY INBRED HYBRIDS OBTAINED BY TOP-CROSS MATING SYSTEM

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ABSTRACT

The aim of this study was to develop an inbred lines from octoploid strawberry and to determine their breeding value by estimating the effects of general combining ability (GCA) and mid-parent heterosis. All inbred lines were obtained through selfing using five cultivars. The number of inflorescences, number of flowers per inflorescence, fruit yield, fruit number per plant, average fruit weight, number and weight of leaves as well as number of runners per plant were recorded from 2014 to 2015. The highest breeding value was estimated for maternal forms of 'Senga Sengana' 17 for six important traits. The lowest GCA effects were exhibited by inbred lines derived from clone 1387 18. Degree of heterosis for a given trait differed greatly among hybrids. The highest heterosis in terms of a number of inflorescences, fruit yield, number of fruits per plant and leaf weight occurred in the Kent 7-14 × 'Dukat' progeny. The results obtained could be used to evaluate the agronomic performance and to make more efficient choices of parents in current strawberry breeding programs.

Key words: *Fragaria* × *ananassa* Duch., GCA, heterosis, top-cross mating design

INTRODUCTION

Cultivated strawberry (*Fragaria* × *ananassa* Duch.) is an octoploid species of the family *Rosaceae* that has economic importance related to the fruit yield. The cultivated species is a hybrid between *F. virginiana* Duch. and *F. chiloensis* Duch. [Hancock et al. 1991], and it is produced in various regions and climates, including temperate, Mediterranean, and subtropical zones and taiga areas [Hancock and Luby 1993]. The world production of strawberry has recently reached nine million tons [FAO 2016], and Poland is the second country in strawberry production in Europe.

During the twentieth century, the efficiency of strawberry production and fruit quality have been greatly improved by development of superior production environments and breeding of cultivars specifically adapted to these superior environments. In this context, breeders must integrate their research into production physiology and cultural practices in order to optimize their selection strategies [Davis et al. 2007, Fernandez 2016, Van Delm et al. 2017].

At present, several hundred strawberry cultivars are commercially grown. Their share in total fruit production is strongly correlated with the acceptance of their phenotypical traits by producers and consumers on national levels [Korbin and Mezzetti 2010]. From a breeder's point of view, phenotypic characteristics is very useful for planning the introgression of novel traits.

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Large genetic variability among strawberry progenies is a major factor in the selection of desirable characteristics. Traditionally, the best cultivars are crossed and the best genotypes are selected from their progenies. The succession of crosses between the best genotypes and selection in the progeny is a recurrent breeding associated with a pedigree selection, in which the selection of parents and the best combination are critical.

Breeding values of important agricultural traits can be obtained, e.g. by applying suitable schemes of parental forms crossings. If the number of inbred lines is great, experiments with hybrids obtained from line × tester crosses are usually performed. In this procedure, a number of inbred lines tested may be higher than that using diallel crosses. The effects of general combining ability (GCA), clearly show the potential values of inbred lines in hybrid combinations and it depends on the additive genetic effects [Poehlman 1979].

The aim of our studies was to develop inbred lines from octoploid strawberry. All inbred lines were obtained through selfing using five cultivars. They were produced by selecting the best individuals for further inbreeding from each of previous generations. Then, obtained lines were crossed with a tester in top-cross mating system generating F_1 hybrids. Previously, we assessed general combining ability of 29 S_4 inbred lines on the basis of phytochemical properties. In particular, we estimated acidity, soluble solids and dry matter contents in fruits [Kaczmarska et al. 2016] as well as vitamin C, total anthocyanin and phenol contents in fruits and antioxidant activity [Kaczmarska et al. 2017] in parental genotypes and F_1 hybrids. Furthermore, we determined the usefulness of established lines for heterosis breeding based on the estimated level of heterosis.

In current study, we evaluated 29 S_4 inbred lines for their GCA in relation to the agronomical characteristics such as: number of inflorescences, number of flowers per inflorescence, fruit yield per plant, number of fruit per plant, weight of a single fruit, number of leaves and weight of leaves per plant, as well as number of runners per plant. Additionally, we determined: (1) mid parent heterosis regarding to S_4 inbred lines and (2) regarding to cultivated strawberry (S_0). The results obtained will enable the selection of the most valuable inbred lines in order to obtain new strawberry cultivars well adapted to Polish and European agro-ecosystems and climatic conditions.

MATERIAL AND METHODS

Plant material

The experiment was conducted in the Experimental Farm Felin of the University of Life Sciences in Lublin (Poland, 51°23'N, 22°56'E) in 2014 and 2015. Twenty nine selected S_4 inbred lines derived from four strawberry cultivars ‘Senga Sengana’, ‘Kent’, ‘Chandler’, ‘Teresa’ and one breeding clone – 1387 – were used in this study. The full pomological description of parental genotypes is given as follows: ‘Senga Sengana’ [Szczygieł and Pierzga 1999], ‘Kent’ [Żurawicz 2005], ‘Chandler’ [Pudelski and Lisiecka 1995], ‘Teresa’ [Żurawicz 2000]. The S_4 progeny marked with corresponding numbers was derived from the same S_3 parental plants on the basis of vigor, yielding performance and uniformity. The S_3 lines were selected as previously described by Kaczmarska [2012] during three generations of inbreeding.

Twenty-nine inbred lines S_4 were crossed following a top-cross mating design, producing 29 F_1 hybrids. The pollinizer (tester) was a Polish cultivar ‘Dukat’, selected on the basis of high values of most horticultural traits. The crosses were made in spring of 2011. Seedlings of all families were propagated in a greenhouse from February to May 2012. They were planted in the field in August and September 2012 in a completely randomized block design with 40 entries (29 hybrid families, 5 parental genotypes inbred lines S_4 and 6 cultivars S_0) in 4 replicates (blocks). Each plot consisted of 30 plants in a row spaced by 0.3 × 0.5 m. Plants were protected against pests and diseases, while weeds were controlled mechanically and using herbicides.

Observations. In the years 2014 and 2015, the following indices were recorded: number of inflorescences, number of flowers per inflorescence, fruit yield per plant, fruit number per plant, average fruit weight, number and weight of leaves as well as number of runners per plant. Data on growth and productivity traits were collected for individual plants (F_1 hybrids, non-inbred S_0 control and S_4 inbreeding populations) for two years following the plantation establishment and are shown as the average of two growing seasons. The number and weight of leaves per plant

Table 1. Means for cultivars, S_4 plants and 29 strawberry hybrids grown in the Experimental Farm Felin in 2014 and 2015

Genotype	Number of inflo-rescences	Number of flowers per inflo-rescence	Fruit yield per plant (g)	Number of fruit per plant	Weight of single fruit (g)	Number of leaves per plant	Weight of leaves per plant (g)	Number of runners per plant
Chandler S_0	8.33 bc*	7.12 a	112.27 bc	39.33 c	2.16 abc	17.67 a	36.00 a	7.00 a
Kent S_0	8.00 bc	5.81 b	154.48 ab	42.00 bc	2.23 abc	26.33 a	31.00 a	9.67 a
Senga S. S_0	9.00 ab	8.16 a	208.63 a	70.00 a	2.45 ab	26.00 a	37.33 a	5.00 a
Teresa S_0	8.00 bc	7.95 a	184.99 a	58.67 ab	2.09 bc	25.33 a	41.33 a	13.67 a
Clone 1387 S_0	6.33 c	7.11 a	66.07 c	37.67 c	1.93 c	17.00 a	24.00 a	7.33 a
Dukat S_0	11.00 a	7.83 a	161.91 ab	57.67 ab	2.60 a	28.00 a	46.33 a	9.00 a
Chandler S_4	7.00 b	6.35 ab	111.20 b	40.33 b	2.19 ab	15.67 a	28.33 a	6.00 a
Kent S_4	6.33 b	4.87 c	149.96 a	21.00 c	1.83 bc	22.00 a	26.67 a	7.00 a
Senga S. S_4	11.00 a	5.35 bc	106.12 b	55.00 a	2.31 a	23.67 a	30.33 a	8.67 a
Teresa S_4	5.66 b	6.64 a	120.73 ab	27.67 c	1.65 c	21.00 a	35.67 a	12.00 a
Clone 1387 S_4	6.00 b	5.06 c	51.29 c	28.00 c	1.78 bc	15.33 a	20.33 a	9.00 a
Chandler 123-2 × Dukat	6.20 d	6.27 ab	124.28 cd	37.71 bc	3.57 ab	23.86 abc	42.43 a	12.79 ab
Chandler 123-5 × Dukat	8.00 cd	7.09 ab	124.66 cd	46.00 bc	4.09 a	33.83 a	49.67 a	14.83 a
Chandler 123-7 × Dukat	9.4 cd	5.48 bc	115.99 cd	49.80 bc	2.18 cd	20.73 bc	32.67 a	7.27 cd
Chandler 123-8 × Dukat	7.8 d	6.51 ab	96.45 cd	47.14 bc	2.03 cd	20.86 bc	32.21 a	9.00 bcd
Chandler 123-11 × Dukat	13.0 bc	6.09 ab	198.08 bc	75.20 b	2.79 bc	23.20 bc	43.20 a	12.00 abc
Chandler 123-18 × Dukat	6.43 d	5.77 abc	53.12 d	29.36 c	2.27 cd	21.36 bc	41.71 a	5.64 d
Chandler 123-22 × Dukat	15.0 b	5.31 bc	241.19 ab	78.00 b	3.11 abc	24.00 abc	41.20 a	9.30 bcd
Chandler 123-23 × Dukat	8.7 cd	6.02 ab	102.43 cd	51.23 bc	1.91 cd	16.46 c	41.69 a	10.69 abc
Chandler 123-32 × Dukat	17.7 a	7.60 a	311. 24 a	134.20 a	2.34 cd	27.60 ab	44.47 a	10.93 abc
Chandler 123-35 × Dukat	9.50 cd	7.63 a	54.74 d	37.13 bc	1.50 d	20.63 bc	34.50 a	8.38 bcd
Mean for Chandler 123	9.62 BC	6.38 A	146.31 B	60.53 A	2.52 B	22.74 B	40.02 B	9.88 B
Kent 7-2 × Dukat	7.50 d	6.26 ab	79.04 cd	45.43 bc	1.74 b	10.93 c	18.07 b	5.14 c
Kent 7-5 × Dukat	5.50 d	5.16 ab	46.65 d	20.79 c	2.49 a	15.14 c	21.29 b	6.21 c
Kent 7-6 × Dukat	13.20 bc	5.41 ab	179.12 b	69.40 b	2.69 a	38.33 a	61.60 a	22.53 a
Kent 7-14 × Dukat	19.40 a	6.60 a	317.95 a	126.80 a	2.56 a	36.60 a	62.13 a	22.13 a
Kent 7-26 × Dukat	15.6 b	4.85 b	196.39 b	73.07 b	2.92 a	25.21 b	44.14 a	17.36 ab
Kent 7-35 × Dukat	9.10 cd	6.00 ab	180.33 b	53.20 bc	3.10 a	28.73 ab	54.07 a	14.93 b
Mean for Kent 7	11.72 AB	5.71 AB	168.62 B	65.41 A	2.59 B	26.13 B	44.09 AB	14.90 A
Senga S. 17-2 × Dukat	20.50 a	4.21 a	245.75 ab	85.93 a	2.67 bc	33.43 ab	48.36 a	7.21 ab
Senga S. 17-4 × Dukat	19.12 a	4.21 a	233.04 ab	78.00 a	3.86 abc	42.57 a	63.86 a	10.86 a
Senga S. 17-12 × Dukat	11.31 bc	5.09 a	133.74 b	56.31 a	2.49 c	28.23 ab	43.31 a	5.00 ab
Senga S. 17-19 × Dukat	11.50 bc	4.69 a	152.97 b	50.20 a	3.00 bc	20.07 b	38.80 a	1.80 b
Senga S. 17-20 × Dukat	14.20 b	5.57 a	341.23 a	78.20 a	4.31 ab	41.53 a	62.13 a	10.00 a
Senga S. 17-24 × Dukat	9.00 cd	5.84 a	150.48 b	46.50 a	3.32 bc	36.00 a	54.33 a	9.00 a
Senga S. 17-36 × Dukat	16.70 ab	4.67 a	330.61 a	73.88 a	5.23 a	41.13 a	61.50 a	10.88 a
Mean for Senga S. 17	14.62 A	4.88 B	227.84 A	67.65 A	3.44 A	33.36 A	51.53 A	7.18 B
Teresa 18-4 × Dukat	4.42 d	6.56 a	48.64 b	23.75 b	1.82 a	11.17 b	24.58 b	5.50 c
Teresa 18-15 × Dukat	12.00 bc	3.93 b	98.89 ab	45.40 ab	2.32 a	41.87 a	64.27 a	23.53 a
Teresa 18-27 × Dukat	14.80 b	3.32 b	110.20 a	48.00 a	2.33 a	18.29 b	21.00 b	9.86 bc
Mean for Teresa 18	10.41 B	4.74 B	83.48 C	38.29 B	2.15 B	26.18 B	41.35 AB	14.35 A
Clone 1387 18-4 × Dukat	6.14 d	5.18 ab	59.25 ab	26.14 a	2.16 ab	24.50 a	39.21 a	12.14 a
Clone 1387 18-15 × Dukat	7.27 d	4.68 b	32.17 b	17.18 a	1.82 b	14.46 b	21.27 b	6.73 b
Clone 1387 18-16 × Dukat	5.42 d	6.26 a	74.61 a	26.36 a	2.94 a	21.14 ab	26.50 ab	9.64 ab
Mean for clone 1387 18	6.21 C	5.43 AB	57.13 C	23.69 B	2.34 B	20.46 B	29.59 C	9.72 B

The means for cultivars (S_0), S_4 plants and top-cross progeny were tested separately
* The means followed by the same letters do not differ at $\alpha = 0.05$

Table 2. Estimates of GCA effects averaged for 2014 and 2015 for eight agronomic traits in a set of 29 strawberry inbred lines

Genotype	Number of inflore-scences	Number of flowers per inflorescence	Fruit yield per plant	Number of fruit per plant	Weight of single fruit	Number of leaves per plant	Weight of leaves per plant	Number of runners per plant
Chandler 123-2	-3.48 ij*	0.67 abc	-29.45 c-h	-19.47 d-g	0.89 b-e	-2.06 d-l	-0.05 a-f	1.88 cde
Chandler 123-5	-0.55 d-j	1.49 ab	-29.08 c-h	-11.18 c-g	1.41 bc	7.91 a-f	7.19 a-d	3.93 cd
Chandler 123-7	-2.55 g-j	-0.12 b-e	-37.74 d-h	-7.38 b-g	-0.50 f-i	-5.19 f-l	-9.81 c-g	-3.64 e-h
Chandler 123-8	-2.05 f-j	0.91 abc	-57.28 d-h	-10.04 c-g	-0.65 ghi	-5.06 f-l	-10.26 c-g	-1.91 d-g
Chandler 123-11	0.52 b-i	0.49 a-d	44.35 bcd	18.02 bcd	0.11 d-h	-2.72 e-l	0.72 a-f	1.09 c-f
Chandler 123-18	-2.12 f-j	0.17 b-e	-100.61 gh	-27.83 fg	-0.41 f-i	-4.56 f-l	-0.76 a-g	-5.26 gh
Chandler 123-22	1.25 b-g	-0.28 b-e	87.46 ab	20.82 bc	0.43 c-g	-1.92 d-l	-1.28 a-g	-1.61 d-g
Chandler 123-23	-0.70 d-j	0.42 a-d	-51.30 d-h	-5.95 b-g	-0.77 ghi	-9.46 h-l	-0.79 a-g	-0.21 d-g
Chandler 123-32	5.65 a	2.00 a	157.51 a	77.02 a	-0.34 e-i	1.68 c-j	1.99 a-f	0.03 d-g
Chandler 123-35	0.95 b-h	2.03 a	-98.99 gh	-20.06 efg	-1.18 i	-5.30 f-l	-7.98 c-g	-2.53 efg
GCA for Chandler 123	**-0.36 B**	**0.78 A**	**-7.42 B**	**3.35 A**	**-0.16 B**	**-3.18 B**	**-2.46 B**	**-1.03 B**
Kent 7-2	-3.19 h-j	0.66 a-e	-74.69 e-h	-11.75 c-g	-0.94 hi	-14.99 l	-24.41 g	-5.76 gh
Kent 7-5	-3.05 g-j	-0.43 cde	-107.08 gh	- 36.40 fg	-0.19 e-i	-10.78 i-l	-21.19 fg	-4.69 fgh
Kent 7-6	1.92 a-f	-0.18 b-e	25.39 b-f	12.22 b-e	0.02 d-i	12.41 abc	19.12 ab	11.63 ab
Kent 7-14	4.52 ab	1.00	164.22 a	69.62 a	-0.12 e-i	10.68 a-d	19.66 ab	11.23 ab
Kent 7-26	0.81 b-i	-0.75 c-f	42.66 b-e	15.89 b-e	0.24 c-h	-0.71 d-j	1.66 a-f	6.45 bc
Kent 7-35	-0.42 d-j	0.40 a-d	26.60 b-f	-3.98 b-g	0.42 c-g	2.81 b-h	11.59 abc	4.03 cd
GCA for Kent 7	**0.16 AB**	**0.12 B**	**14.89 B**	**8.23 A**	**-0.09 B**	**0.21 B**	**1.61 AB**	**3.99 A**
Senga S. 17-2	3.45 a-d	-1.38 def	92.02 ab	28.75 b	-0.01 d-i	7.51 a-f	5.88 a-e	-3.69 e-h
Senga S. 17-4	4.02 a-c	-1.39 def	79.31 abc	20.82 bc	1.18 bcd	16.65 a	21.38 a	-0.05 d-g
Senga S. 17-12	1.30 b-g	-0.51 c-f	-20.00 b-h	-0.87 b-f	-0.19	2.31 d-i	0.83 a-f	-5.91 gh
Senga S. 17-19	-1.75 f-j	-0.90 c-f	-0.76 b-g	-6.98 b-g	0.32 c-h	-5.85 g-l	-3.68 b-g	-9.11 h
Senga S. 17-20	4.45 ab	-0.03 b-e	187.50 a	21.02 bc	1.62 ab	15.61 a	19.66 ab	-0.91 d-g
Senga S. 17-24	-1.22 e-j	0.24 a-e	-3.25 b-h	-10.68 c-g	0.64 b-f	10.08 a-e	11.86 abc	-1.91 d-g
Senga S. 17-36	2.95 a-e	-0.93 c-f	176.88 a	16.69 b-e	2.55 a	15.21 ab	19.02 ab	-0.03 d-g
GCA for Senga S. 17	**1.92 A**	**-0.70 C**	**74.10 A**	**10.47 A**	**0.76 A**	**7.44 A**	**9.05 A**	**-3.73 B**
Teresa 18-4	-4.13 j	0.96 abc	-105.09 gh	-33.43 fg	-0.86 hi	-14.75 kl	-17.89 efg	-5.41 gh
Teresa 18-15	0.18 c-j	-1.66 ef	-54.85 d-h	-11.78 c-g	-0.36 e-h	15.95 a	21.79 a	12.63 a
Teresa 18-27	2.74 a-e	-2.27 f	-43.53 d-h	-9.18 c-g	-0.34 e-h	-7.63 h-l	-21.48 fg	-1.05 d-g
GCA for Teresa 18	**-0.81 BC**	**-0.99 C**	**-0.99-70.25 C**	**-18.89 B**	**-0.53 B**	**0.26 B**	**-1.13 AB**	**3.45 A**
Clone 1387 18-4	-2.41 f-j	-0.42 cde	-94.48 gh	-31.04 fg	-0.52 f-i	-1.42 d-k	-3.26 b-g	1.24 c-f
Clone1387 18-15	-1.28 e-j	-0.92 c-f	-121.57 h	-40.00 g	-0.86 hi	-11.47 jkl	-21.21 fg	-4.18 e-h
Clone 1387 18-16	-3.12 h-j	0.66 abc	-79.12 fgh	-30.83 fg	0.26 c-h	-4.78 f-l	-15.98 d-g	-1.26 d-g
GCA for clone 1387 18	**-2.34 C**	**-0.22 BC**	**-96.60 C**	**-33.49 B**	**-0.34 B**	**- 5.46 B**	**-12.89 C**	**-1.19 B**

* The means followed by the same letters do not differ at α = 0.05

was obtained on 20−26 July, after harvest. Yields and fruit counts were recorded for each plant for 4 consecutive weeks starting from the first week of June. Weight of a single fruit was calculated by dividing weekly yields by corresponding fruit numbers.

Heterosis assessment. Data obtained for F_1 offspring, original cultivars and inbred lines were used to calculate two types of heterosis: heterosis relative to the cultivars (Mid S_0 parent heterosis − MS_0PH) using the following equation:

$$MS_0PH = \frac{Xhybrid - xS_0}{xS_0} \cdot 100\ \%$$

and heterosis relative to the inbred lines (Mid S_4 parent heterosis − MS_4PH):

$$MS_4PH = \frac{Xhybrid - xS_4}{xS_4} \cdot 100\ \%$$

where:
Xhybrid – top-cross (F_1) hybrid mean,
xS_0 – mean of maternal cultivars (S_0) used to obtain inbred lines and the pollinizer (cv. 'Dukat'),
xS_4 – mean of the inbred line (S_4) used to create F_1 hybrids and the pollinizer (cv. 'Dukat').

Statistical analysis. Results from the field experiment were statistically processed applying analysis of variance. Duncan confidence half-intervals were calculated to analyze in detail the significance of differences between mean values at a significance level of $p = 0.05$. General combining ability effects were estimated using the formula provided by Ubysz-Borucka et al. [1985]. The cluster analysis was conducted using the average linkage method available in STATISTICA 13.1.

RESULTS

In a view of a large number of observations and measurements performed in 2014 and 2015, this report contains results of analyses carried out on the basis of average trait values obtained during two years of the study (Tabs. 1−2).

Phenotypic features

Table 1 shows that of the five strawberry cultivars tested, cv. 'Dukat' produced the highest number of inflorescences (11.0 on average), whereas among the hybrids, the highest value of this trait was noted in the seedlings of 'Senga Sengana' 17 × 'Dukat' (average 14.62). Number of flowers per inflorescence ranged from 3.32 in the progeny 'Teresa' 18-27 × 'Dukat' to 8.16 in the cultivar 'Senga Sengana' S_0. Hybrids of 'Senga Sengana' 17 × 'Dukat' had higher yields (from 133.74 g to 330.61g per plant) compared to the average yield obtained from plants of all evaluated hybrid families (136.68 g, data not shown). In this experiment, the highest number of fruits per plant was estimated for the progeny 'Senga Sengana' 17 × 'Dukat' (67.65), while the lowest was recorded for clone 1387 × 'Dukat' hybrids (an average of 23.69). The average weight of a single fruit was from 2.15g for 'Teresa' 18 × 'Dukat' hybrid (Tab. 1) to 3.44 g for seedlings of 'Senga Sengana' 17 × 'Dukat'. The highest plant vigor manifested as the number and weight of leaves per plant was measured for 'Senga Sengana' 17 × 'Dukat' progeny, while the lowest values of these features were estimated for the hybrid clone 1387 18 with cv. 'Dukat'. Among the analyzed offspring, the highest number of runners per plant was observed in 'Kent' 7 × 'Dukat' and 'Teresa' 18 × 'Dukat'.

GCA analysis of inbred lines

Estimates of GCA effects for eight agricultural traits of 29 strawberry inbred lines are presented in Table 2. The positive and the highest GCA value among parental forms was obtained for 'Senga Sengana' 17 for the following traits: number of inflorescences (mean 1.92), fruit yield per plant (mean 74.10), number of fruits per plant (mean 10.47), weight of single fruit (mean 0.76), number of leaves per plant (mean 7.44), as well as leaf weight per plant (mean 9.05). In terms of the number of flowers per inflorescence, a positive GCA value (mean 0.78) was estimated for the female forms of 'Chandler'123 and 'Kent' 7 (mean 0.12), and the average value of GCA for other parental forms was negative. The GCA values for the number of runners per plant indicated a positive effect in inbred lines 'Kent' 7 and 'Teresa' 18 (3.99 and 3.45, respectively).

Cluster analysis

Figure 1 presents the relationships between 40 genotypes (cultivars – S_0, inbred lines – S_4 and hybrids – F_1) revealed by the cluster analysis based on eight agricultural traits. Three main groups of clusters were distinguished. The smallest group was Cluster I containing four hybrids that showed high GCA effects in terms of the fruit yield (from 157.51 to 187.50) as well as the number of fruits per plant (from 16.69 to 77.02). Cluster II consisted of two cultivars: 'Senga Sengana S_0' and 'Teresa S_0' and seven F_1 offsprings. The third, largest group included other twenty-seven accessions, among which two sub-clusters could be distinguished.

Mid-parent heterosis

Heterosis relative to the S_4 and S_0 parents was estimated for each trait. As shown in Figure 2, positive and negative values were obtained. MS_0PH for the number of inflorescences, for example, ranged from −53.47% ('Teresa' 18-4 × 'Dukat') to 104.21% ('Kent' 7-14 × 'Dukat'). In the case of the number of flowers per inflorescence only the 'Chandler' 123-35 × 'Dukat' offspring was characterized by positive MS_0PH (7.62%) and MS_4PH (34.95%). The highest heterosis value for fruit yield was estimated for the 'Kent' 7-14 × 'Dukat' offspring (199.0%) in relation to S_0 and for 'Senga Sengana' 17-20 × 'Dukat' (154.61%) in relation to S_4. As regarding the number of fruits per plant, the highest MS_4PH (222.37%) was recorded for the 'Kent' 7-14 × 'Dukat' progeny. All progeny of clone 1387 18 crossed with cv. 'Dukat' revealed negative values of heterosis relative to the S_4 inbred lines in terms of all examined characteristics.

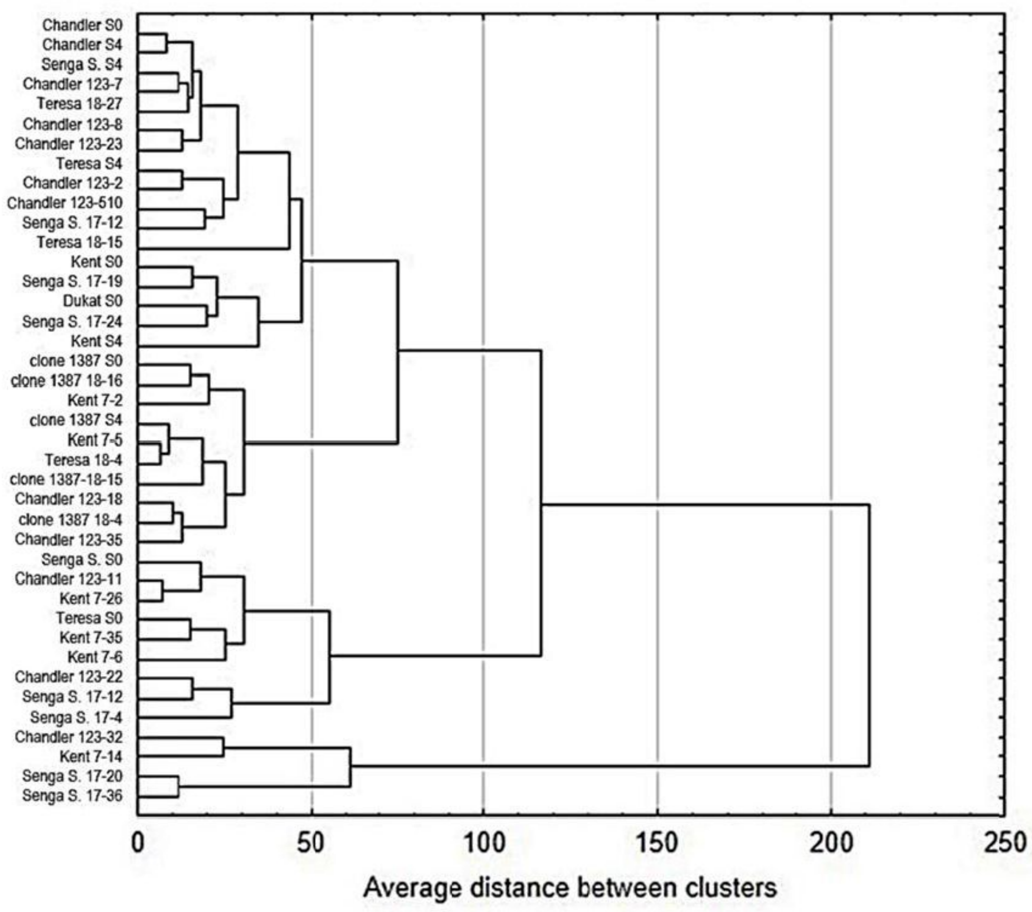


Fig. 1. Dendrogram estimating distance among strawberry cultivars (S_0), inbred progeny (S_4) and F_1 hybrids. Genotype with double numbering are hybrids with cv. 'Dukat'

DISCUSSION

Agricultural characteristics

Two-year observation showed statistically significant differences between tested genotypes for all studied traits. The average fruit yield per plant varied considerably from 32.17 g to 341.23 g. Similar results were obtained by Masny et al. [2016], who studied offspring obtained from a half-diallel mating design among 13 dessert strawberry parental genotypes. The average marketable yield (2012−2013) was from 51 g/plant to 392 g/plant. In the present study, an inbreeding depression (ID) was observed for all traits in the S_4 progeny in comparison to cultivars (S_0). In previous experiment, ID for fruit weight per plant decreased in successive inbreeding generations and amounted to 52.5 for S_1, 36.6 for S_2, and 22.0 for S_3 [Kaczmarska 2012]. Noticeable fruit size depression compared to the parental cultivar 'Alpha' was also observed by Shokaeva et al. [2014]. Bellusci et al. [2009] indicated that the magnitude of trait mean depression depended on the rate, at which homozygosity was accumulated and the strength of selection pressure counteracting this depression. Additionally, it is believed that the reciprocal recurrent selection would give more viable and homogeneous inbred lines and as stated by Dale et al. [2016], such lines are required to ensure genetic uniformity.

Clustering based on agronomic traits

Relationships among the 40 genotypes revealed by average linkage method based on agricultural characteristics are presented in Fig 1. Only in the case of clone 1387 18, single cluster included both: S_0, S_4 and hybrid plants, suggesting only a minor variation between the analyzed genotypes. On the contrary, grouping of 'Senga Sengana', 'Teresa' cultivars, their inbred lines and F_1 hybrids in separate clusters proves their high diversity and hence suitability in breeding works. The cultivars 'Dukat' and 'Kent' were grouped together, while the 'Senga Sengana' separately, similarly as in the work of Sieczko et al. [2015]. Also the high inter-cluster distance was observed between 'Senga Sengana' and 'Chandler' both in the present study and that by Singh et al. [2013]. In general, belonging genotypes to distant clusters means that there is a wide range of variability for most of characteristics tested, thus the selected genotypes can be used in future breeding programs, as also Kuras and Korbin [2010], Mishra et al. [2015] pointed out.

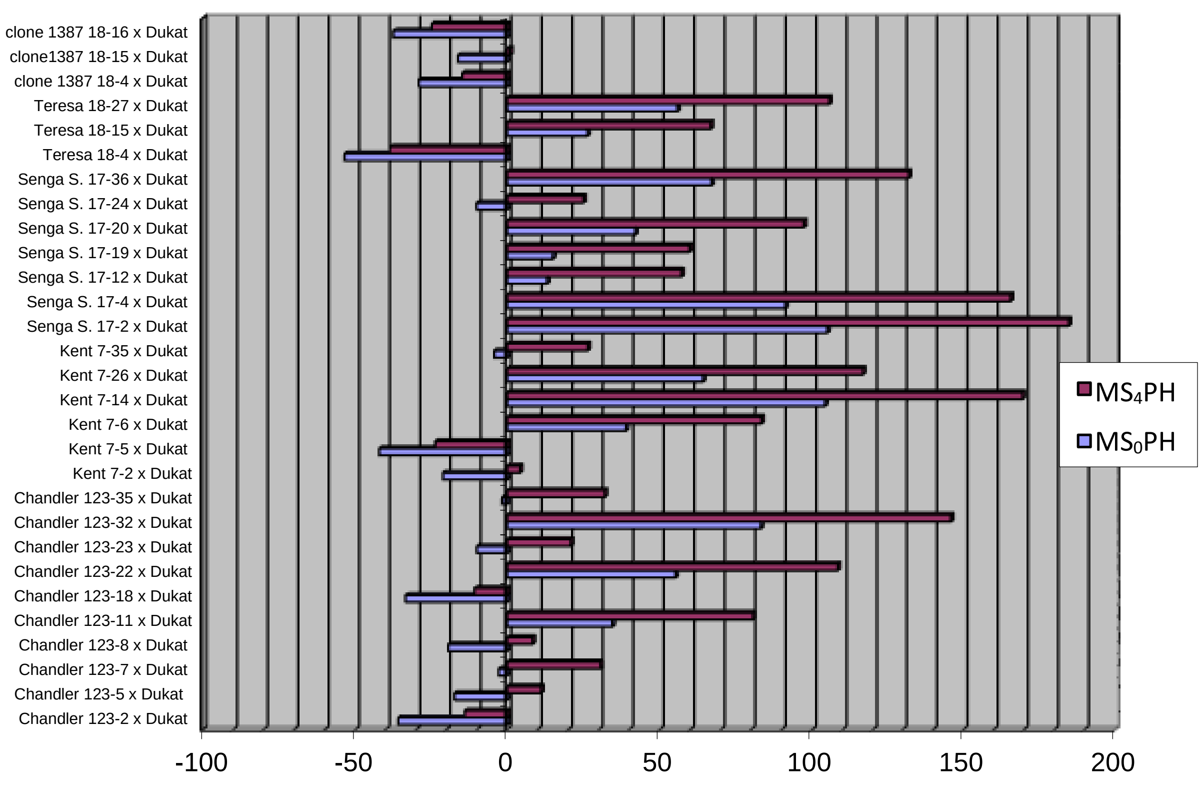
Breeding value of strawberry inbred lines

GCA effects of fruit yield per plant estimated in this study highly varied and ranged from minus 96.60 (in parental form clone 1387 18) to 74.10 (in 'Senga Sengana' 17). Differentiated GCA effects for fruit yield, mean weight of single fruit, number of inflorescences per plant and leaf weight per plant when crossed with two testers were also observed by Gawroński [2014]. Masny et al. [2016] obtained both negative and positive GCA values for marketable yield. The high positive effect on this trait was determined for cv. 'Camarosa', which was not consistent with previous results of these authors [Masny et al. 2008]. Hence the authors argued that these contradictory findings indicated that breeding value estimates for a given variety could be subjected to modification depending on a gene pool composition. Low, negative GCA values for all studied traits were found in maternal forms inbred lines obtained from clone 1387 18. Like in previous studies [Kaczmarska et al. 2016 and 2017], these inbred lines exhibited negative GCA values for soluble solids, total acidity, dry matter, vitamin C, FRAP, DPPH, phenolic contents, and total anthocyanin content in fruits. This means that these lines pass on a tendency towards low productivity, vigor as well as phytochemical fruit properties to their progeny. Mathey et al. [2014] point out that trait with a significant genotype × environment interaction will need to be selected at this location to make breeding progress.

Heterosis

This study was conducted to estimate the heterotic effect in strawberry to identify combinations expressing high hybrid vigor and productivity. Heterotic responses for composition traits varied greatly in this experiment. In previous studies by Kaczmarska et al. [2016], all inbred lines derived from clone 1387 had negative MS_0PH and MS_4PH in terms of soluble solids, total acidity and dry matter. At present, all these lines have shown positive MS_4PH in terms of eight agronomic features. This means that even though the strawberry is predisposed to inbreeding depression, some inbred lines may exhibit an above-average value of the characteristics, as illustrated by Kataoka and Noguchi [2016] on the example of plant vigor. Such extraordinary genotypes can be easily vegetatively propagated or inbred lines can be used for development of seed propagated F_1 hybrid cultivars, the number of which is currently limited [Mahoney and Davis 2016].

a)



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clone 1387 18-4 x Dukat
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Teresa 18-15 x Dukat
Teresa 18-4 x Dukat
Senga S. 17-36 x Dukat
Senga S. 17-24 x Dukat
Senga S. 17-20 x Dukat
Senga S. 17-19 x Dukat
Senga S. 17-12 x Dukat
Senga S. 17-4 x Dukat
Senga S. 17-2 x Dukat
Kent 7-35 x Dukat
Kent 7-26 x Dukat
Kent 7-14 x Dukat
Kent 7-6 x Dukat
Kent 7-5 x Dukat
Kent 7-2 x Dukat
Chandler 123-35 x Dukat
Chandler 123-32 x Dukat
Chandler 123-23 x Dukat
Chandler 123-22 x Dukat
Chandler 123-18 x Dukat
Chandler 123-11 x Dukat
Chandler 123-8 x Dukat
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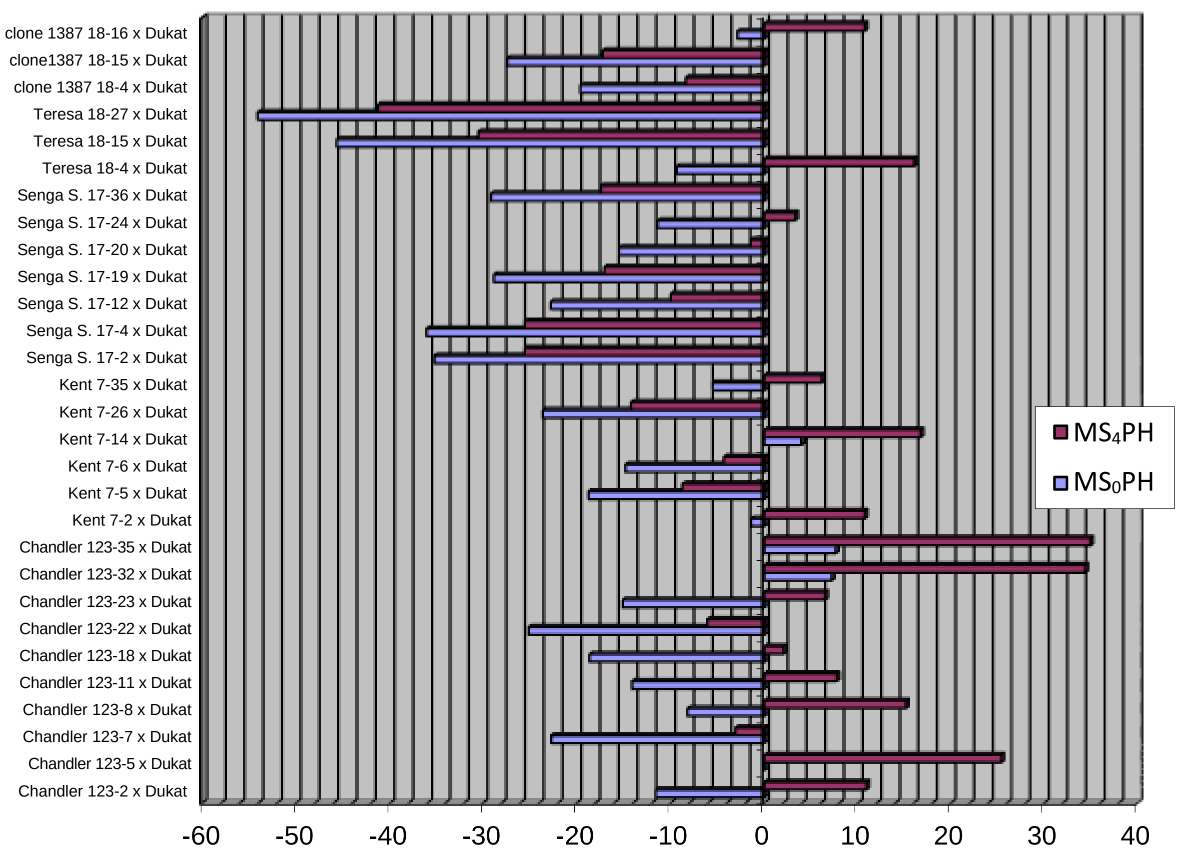
MS_4PH
MS_0PH

b)



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Teresa 18-4 x Dukat
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Senga S. 17-12 x Dukat
Senga S. 17-4 x Dukat
Senga S. 17-2 x Dukat
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Kent 7-26 x Dukat
Kent 7-14 x Dukat
Kent 7-6 x Dukat
Kent 7-5 x Dukat
Kent 7-2 x Dukat
Chandler 123-35 x Dukat
Chandler 123-32 x Dukat
Chandler 123-23 x Dukat
Chandler 123-22 x Dukat
Chandler 123-18 x Dukat
Chandler 123-11 x Dukat
Chandler 123-8 x Dukat
Chandler 123-7 x Dukat
Chandler 123-5 x Dukat
Chandler 123-2 x Dukat
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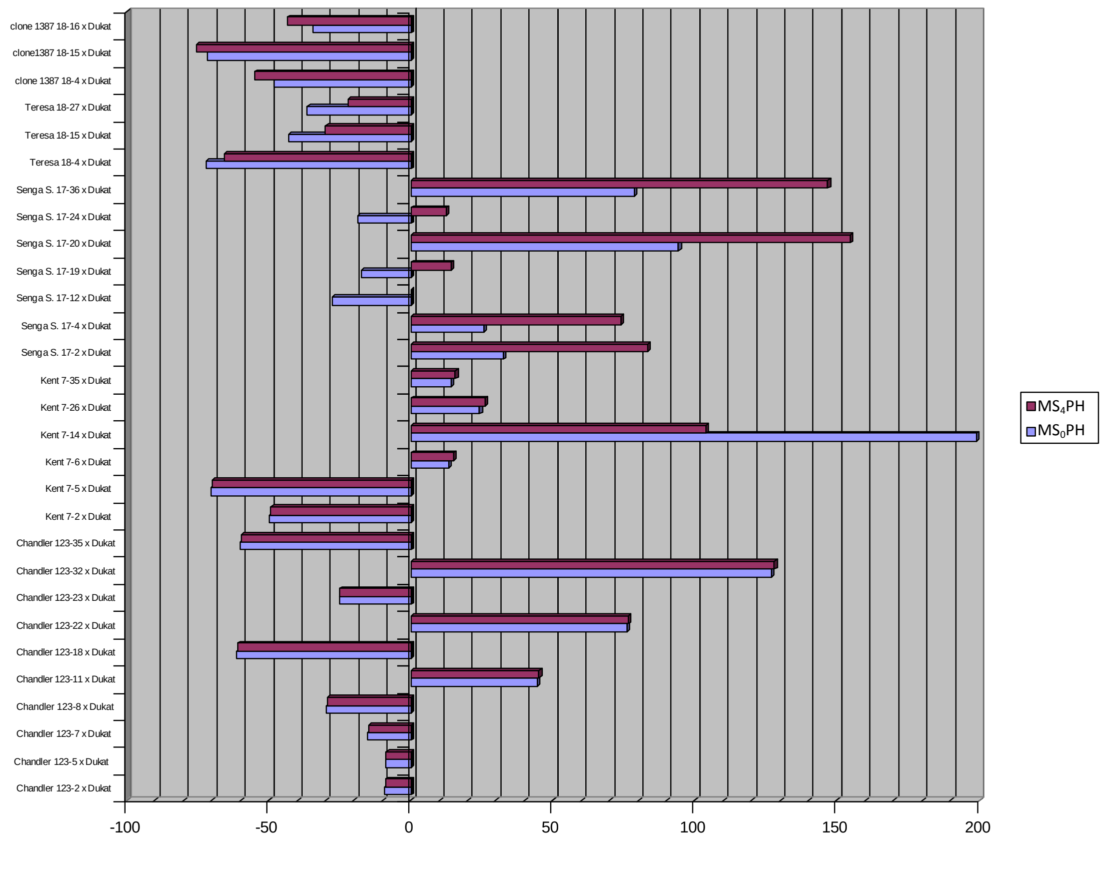
10
20
30
40
MS_4PH
MS_0PH

c)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Chandler 123-32 x Dukat
Chandler 123-23 x Dukat
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Chandler 123-18 x Dukat
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MS_4PH
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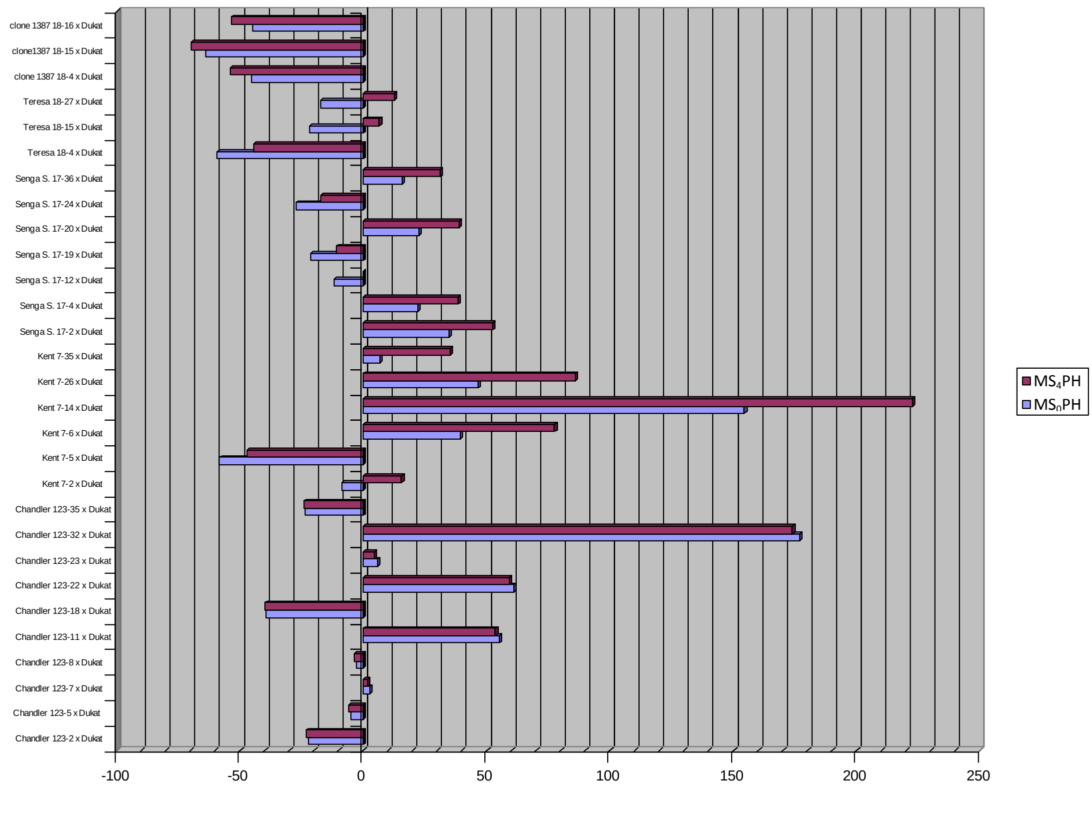
d)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Kent 7-2 x Dukat
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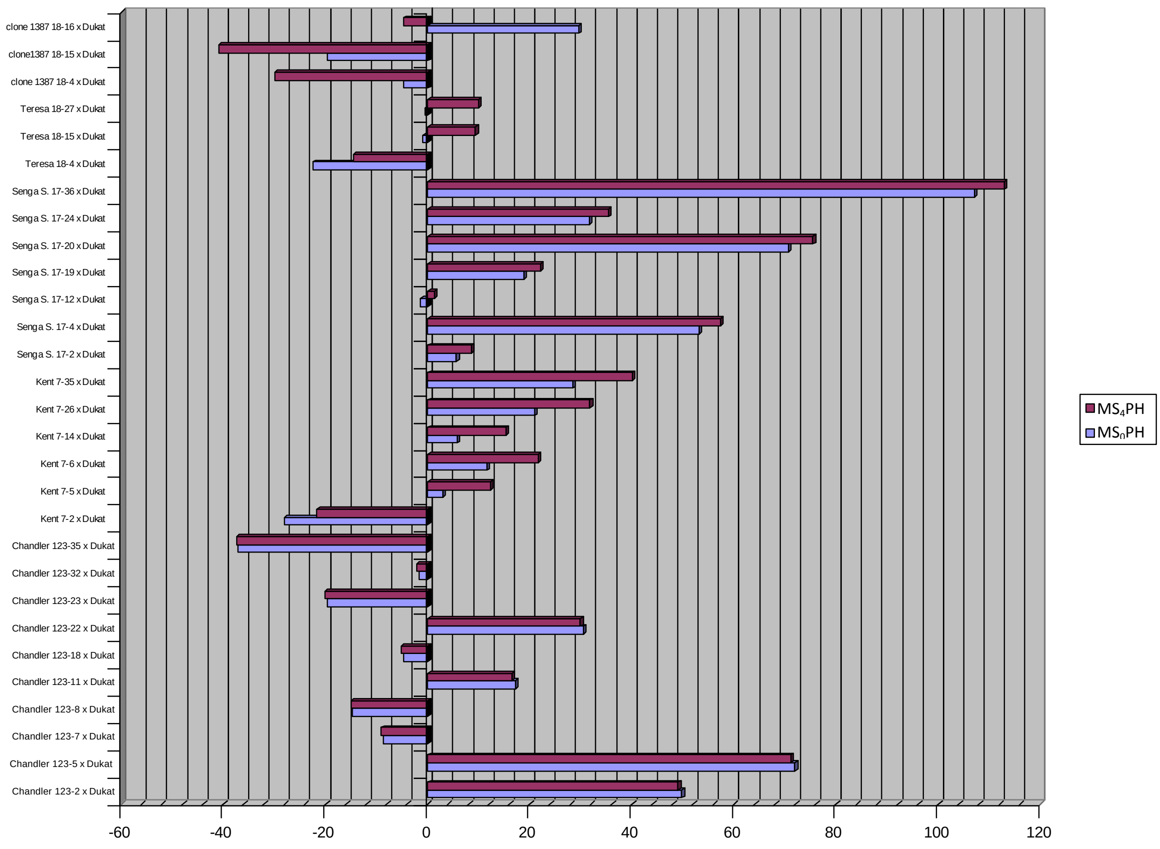
MS_4PH
MS_0PH

e)



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Senga S. 17-2 x Dukat
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Chandler 123-18 x Dukat
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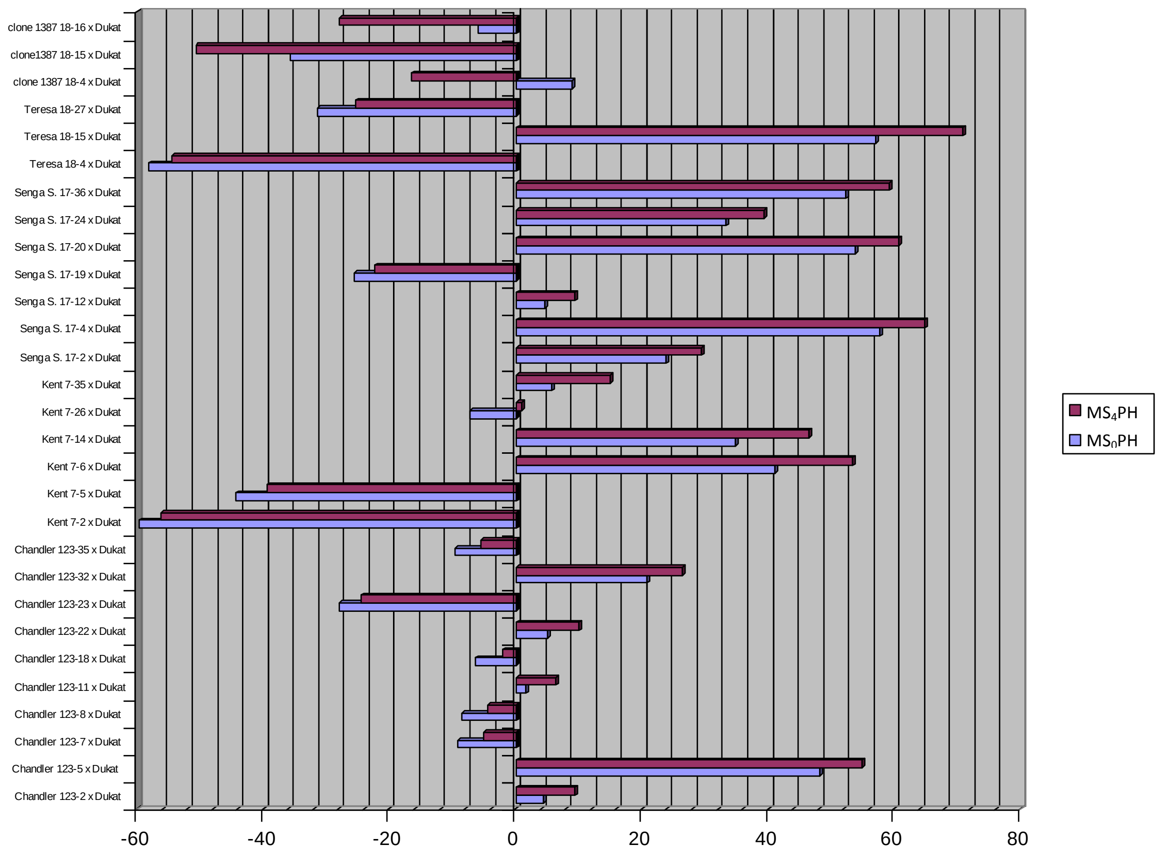
120
MS4PH
MSnPH

f)



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Kent 7-2 x Dukat
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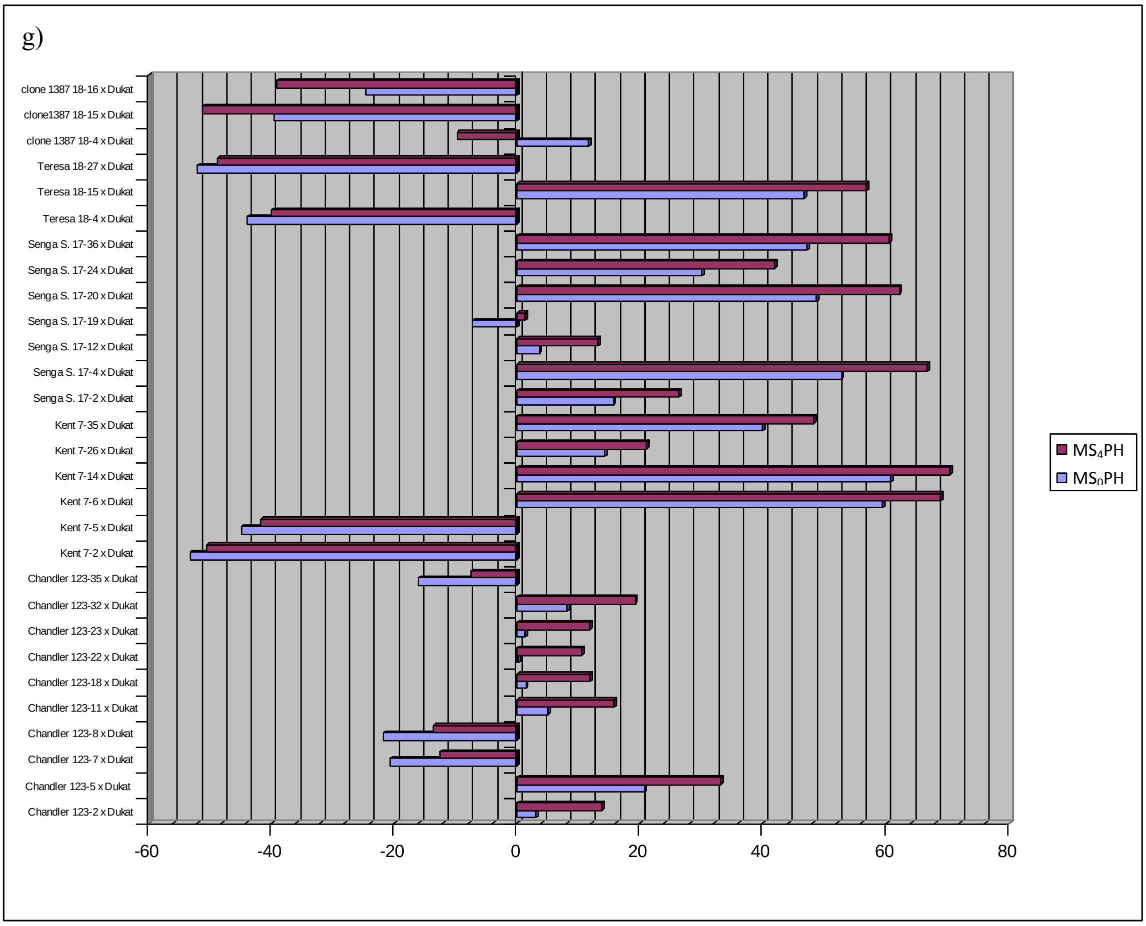
MS4PH
MSnPH



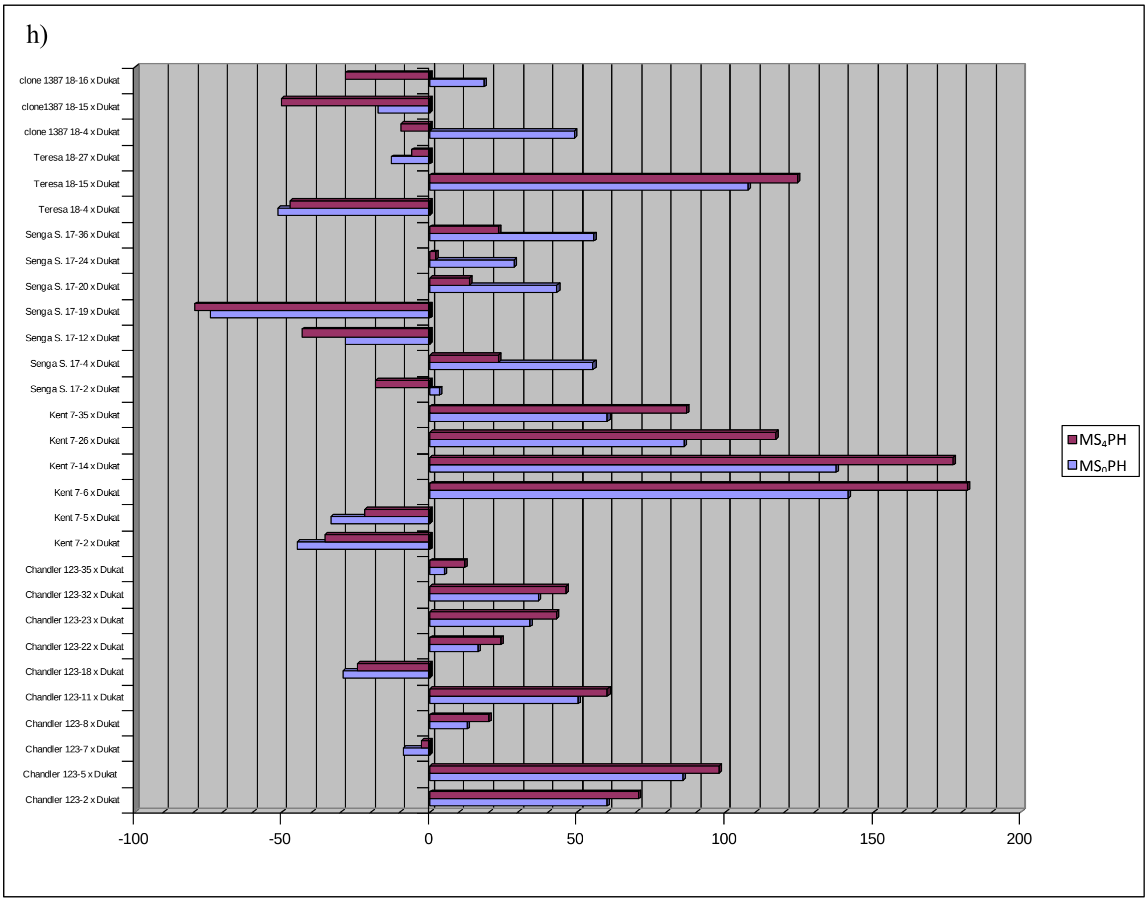


Fig. 2. Mid parent heterosis (%) for: (a) number of inflorescences, (b) number of flowers per inflorescence, (c) fruit yield per plant, (d) fruit number per plant, (e) average fruit weight, (f) number of leaves, (g) weight of leaves, (h) number of runners per plant. MS_4PH – Mid S_4 parent heterosis; MS_0PH – Mid S_0 parent heterosis

CONCLUSIONS

Consequently, the present study demonstrated the existence of a wide range of variations for most of the characteristics among strawberry genotypes, providing the opportunity for genetic gain through selection and hybridization. Previously obtained data on phytochemicals properties and agronomic value of the test genotypes indicated that 'Senga Sengana' 17 inbred lines were donors of most of the positive traits, whereas 'Kent' 7 was the best donor of soluble solids, acidity and dry matter [Kaczmarska et al. 2016] and could be used as a parent in breeding programs. Therefore, breeding of inbred lines in octoploid strawberry can be achieved if individuals showing inbreeding depression are eliminated and vigorous individuals are selected. Crossings between these lines may result in a strong heterosis of F_1 hybrids.

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