Combining Ability Analysis in 10 Strawberry Genotypes Used in Breeding Cultivars for Tolerance to Verticillium Wilt

Agnieszka Masny¹ and Edward Żurawicz

Fruit Breeding Department, Research Institute of Horticulture, Konstytucji 3 Maja 1/3, 96-100 Skierniewice, Poland

Kris Pruski

Department of Plant and Animal Sciences, Dalhousie University, Truro, Nova Scotia B2N 5E3, Canada

Wiesław Mądry

Department of Experimental Design and Bioinformatics, Warsaw University of Life Sciences, Nowoursynowska 166, 02-787 Warsaw, Poland

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ABSTRACT. General combining ability (GCA) and specific combining ability (SCA) effects of 10 strawberry (*Fragaria ×ananassa*) cultivars (Darselect, Selvik, Elianny, Figaro, Sonata, Susy, Salsa, Albion, Charlotte, and Filon) for severity of verticillium wilt (*Verticillium dahliae*) were estimated. Progeny consisting of 45 F₁ full-sib families from the crosses made in a half diallel mating design according to the IV Griffing's method was evaluated in two field experiments conducted in 2009 and 2010 on a soil heavily infested with *V. dahliae* inoculum. Each hybrid family was represented by 60 seedlings (four replicates of 15 plants each). The analysis of variance revealed significant ($P < 0.01$) GCA and SCA effects of the parental cultivars for the verticillium wilt severity in plants. This suggests that genetic additive and non-additive effects are involved in the inheritance of strawberry tolerance to verticillium wilt. In 2009, a significant negative GCA effect ($P < 0.05$) for the verticillium wilt severity in plants was found in 'Selvik', 'Filon', and 'Sonata', indicating genetic transmission of tolerance from parents to the offspring. On the other hand, a significant ($P < 0.05$) and positive for the verticillium wilt severity GCA effect was found for 'Figaro' in 2009, indicating the transmission from this parent to its offspring relatively high susceptibility to the wilt. Only in one hybrid family, 'Albion' × 'Charlotte', was the SCA effect significantly positive ($P < 0.05$) for verticillium wilt severity in plants, whereas two other hybrid families—'Selvik' × 'Salsa' and 'Sonata' × 'Albion'—showed significantly negative SCA effects ($P < 0.05$). Three of 10 evaluated genotypes (i.e., 'Selvik', 'Filon', and 'Sonata') were found to be the most valuable parents to the strawberry breeding program for tolerance to verticillium wilt. The least suitable cultivar for this purpose was 'Figaro'.

Verticillium dahliae infects over 300 cultivated plants, including strawberry. The fungus destroys vascular tissues causing drought stress resembling foliar symptoms. The outer leaves wilt and turn brown and the inner wilt but remain bluish green. Brownish to bluish black streaks or blotches may also appear on the runners and/or petioles (Bielenin and Meszka, 2009; Meszka, 2013). New roots that grow from the infected crown are often dwarfed with blackened tips. Crowns when cut lengthwise may show blackening or browning of the vascular tissue. Daughter plants attached to the infected mother plants may also exhibit the disease symptoms [Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA), 2009]. Infected plants cannot balance their water intake. The fungus also releases toxins causing further damage to leaves (Király et al., 1977). In the case of severe infestation, strawberry plants die (Löckener, 1995).

V. dahliae overwinters in soil and plant debris as a dormant mycelium or black, speck-sized bodies (microsclerotia). Micro-

sclerotia can survive in soil for 12 to 14 years (Bielenin et al., 1998; Wilhelm, 1955). When suitable conditions occur (high humidity and temperature of 23 to 25 °C), these microsclerotia germinate by putting forth one or more thread-like hyphae (Domsch et al., 1980). These hyphae may penetrate the root hairs directly, but more infection can occur through breaks or wounds in rootlets caused by insects, cultivation or transplanting equipment, frost injury, or root-feeding nematodes (OMAFRA, 2009). The severity of infestation depends on susceptibility of the host-plant genotype, source of infection (Harris and Yang, 1996), and environmental factors such as humidity and temperature (Bielenin et al., 1998). According to Gallegos (2011), as low as five microsclerotia per gram of soil can reduce yield of commercial strawberries by 24% and 10 or more from 47% to 63%. Control of verticillium wilt is difficult as a result of wide presence of the fungus in soils (Borecki, 1987) and then high cost of its control. The use of healthy stock plant material and soil disinfection before transplanting are the most common approaches to the controlling the fungus control (Duniway, 2002; Meszka, 2013). Planting cultivars tolerant to verticillium wilt, or with low susceptibility, would be more desirable from economic and environmental points of view. Examples of the currently available germplasm include cultivars Pegasus, Pandora,

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¹Corresponding author. E-mail: Agnieszka.Masny@inhort.pl.

Calypso, Tango (Simpson et al., 1994), Senga Sengana, Elkat, Elianny, Vima Rina, Albion, Salsa, Evie II, Aga, Fara, Daroyal, Dukat, Filon, Salut, Vikat, Chandler, and Favette (Masny and Żurawicz, 2008, 2009a, 2009b). Shaw et al. (2005) state that plantations with susceptible cultivars can face up to 75% yield losses compared with 7% to 15% for tolerant or low susceptible. This makes expansion of strawberry breeding programs for tolerance to verticillium wilt a top priority to the small fruit industry. Although there are a number of tolerant strawberry cultivars available, none of them is fully resistant to *V. dahliae* (Bolda and Koike, 2013). Evaluation of candidate parental genotypes such as genetic indicators as general and specific combining ability for the resistance trait will undoubtedly significantly contribute to the efficacy of the breeding programs.

General combining ability of a parental genotype for the quantitative trait of interest describes the ability of that parent to pass the trait at some average level to its half-sib progeny (Baker, 1978; Griffing, 1956a, 1956b). Then, the GCA effect of a parent on a trait is a measure of the additive effect of the parent's genes on that trait within the gene pool of the parental forms taking part in the planned mating design (Griffing, 1956a, 1956b). GCA of the parents for a trait determines their overall usefulness, with respect to that trait, for creating new cultivars. The most valuable hybrid progeny in terms of quantitative traits can be obtained by crossing parents that exhibit favorable GCA effects for these traits (Masny et al., 2005, 2008, 2009; Yashiro et al., 2002; Żurawicz et al., 2006).

Specific combining ability of a pair of parents for the quantitative trait of interest is the genetic interaction of both parents on that trait, manifested in the full-sib progeny. Therefore, the SCA effect of two parents on a trait is a measure of their genetic interaction effect on that trait and is the result of the non-additive action (dominance and epistasis) of the parents' genes (Baker, 1978; Griffing, 1956a, 1956b).

Resistance to verticillium wilt is inherited polygenetically and depends on genetic additive effects and dominant effects (Bringhurst et al., 1968; Maas et al., 1989). However, so far combining abilities of strawberry germplasm for tolerance to verticillium wilt have not been comprehensively documented. Evaluation of the GCA and SCA effects of 10 strawberry genotypes used in breeding programs (Capocasa and

Mezzetti, 2012; Faedi et al., 2009) was the primary objective of this study.

Material and Methods

PLANT MATERIAL. F₁ seedlings belonging to 45 hybrid families obtained from crosses among 10 strawberry cultivars (Selvik, Elianny, Figaro, Sonata, Susy, Salsa, Albion, Filon, Darselect, and Charlotte) in a half diallel mating design according to the IV Griffing's method (Baker, 1978; Griffing, 1956b) were used in experiments. A brief description of crossed genotypes is in Table 1. Crossing was performed in the field in 2008 and 2009. Evaluation of diallelic progeny was carried out using 60 randomly selected plants from a larger seedling population of each hybrid family. Two separate field experiments—Expt. 1 (2009) and Expt. 2 (2010)—containing the same hybrid families with full-sib progenies were conducted at the Research Institute of Horticulture in Skierniewice, central Poland (lat. 51.959° N, long. 20.139° E). Each experiment was conducted during one season only. Both experiments were planted at the beginning of June 2009 and 2010, respectively, in standard, medium-fertile soil with *V. dahliae* inoculum averaging 4.8 fungus colonies per gram of soil. Both experiments were planted in a randomized block design with four replications and 15 plants per plot. Plant spacing was 0.25 × 1.1 m. Each year, 2700 seedlings (45 families × four replications × 15 plants) were evaluated. Plot management followed standard recommendations for commercial strawberry production in Poland (Żurawicz and Masny, 2005).

EVALUATION OF PLANT INFECTION BY *V. DAHLIAE*. Evaluation of verticillium wilt severity in strawberry plants in Expt. 1 was conducted three times (26 Aug., 28 Sept., and 28 Oct. 2009) and in the Expt. 2 twice (10 Sept. 2009 and 7 Oct. 2010). The severity of disease progress was described using a scale from 0 to 4, where 0 = tolerant plants [no visible symptoms of verticillium wilt (Fig. 1A)]; 1 = plants with low susceptibility to the pathogen [only a few older leaves wilted (Fig. 1B)]; 2 = medium susceptible plants [a number of wilted leaves, some of them already drying out (Fig. 1C)]; 3 = plants susceptible to the pathogen [most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms (Fig. 1D)]; 4 = very susceptible plants [either dead or dying, where only one middle leaf showing signs of growth (Fig. 1E)] (Masny

Table 1. Description of parental genotypes of strawberries used in crossing program (diallel cross mating design, Griffing's method IV) at Skierniewice, Poland, in 2009 and 2010.

Parental cultivar	Origin	Pedigree ^z	Ripening period ^y	Yield potential	Fruit size	Fruit firmness	Susceptibility to <i>Verticillium dahliae</i> ^z
Darselect	France	'Parker' × 'Elsanta'	JB early	Medium	Large	Very high	Low
Selvik	Poland	'Selva' × 'Vicoda'	JB late	High	Medium and large	High	Low
Elianny	Netherlands	—	JB early	Medium	Extra large	Medium	Low
Figaro	Netherlands	'Elsanta' × 'Pajaro'	JB mid-early	Medium	Medium and large	Very high	High
Sonata	Netherlands	'Elsanta' × 'Polka'	JB mid-early	Medium	Medium and large	High	Low
Susy	Netherlands	'Valeta' × 'Arking'	JB mid-late	Medium	Medium and large	High	High
Salsa	Netherlands	—	JB late	Very high	Medium and large	High	Tolerant
Filon	Poland	'Seal' × 'Selva'	JB mid-late	Very high	Medium and large	Medium	Low
Albion	USA	—	R ^y	High	Large	Very high	Low
Charlotte	France	'Mara des Bois' × 'CAL. 19'	R	Medium	Medium and large	High	—

^z— = lack of information in the literature.

^yJB = June-bearing cultivar; R = remontant cultivar.

Fig. 1. Ranking scale used for evaluation of verticillium wilt severity in strawberry plants: (A) plants with no symptoms (score = 0); (B) plants with only a few older leaves wilted (score = 1); (C) plants with a number of wilted leaves, some of them already drying out (score = 2); (D) plants with most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms (score = 3); (E) plants dead or dying where only one middle leaf showing signs of growth (score = 4).

and Żurawicz, 2008). Evaluations were performed separately for individual plants in each plot and the average value for per plot was calculated.

WEATHER CONDITIONS. In both years, weather conditions were monitored using meteo-station Methos Compact (Pessl Instruments, Werksweg-Weiz, Austria) located 5 km from research plots. Monitored variables included: temperature at 2 and 0.2 m aboveground, soil temperature at 5-cm depth, and precipitation (120 records per day for each variable). The average daily and monthly temperatures and rainfall were calculated.

STATISTICAL ANALYSIS. A two-stage analysis of variance of the means per plot was performed as described in Dossett et al. (2008) and Garretsen and Keuls (1978). Data were analyzed separately for each observation time as well as for the mean of the last observations in both years when verticillium wilt symptoms had been the most severe. In the first stage, the SAS PROC MIXED procedure (SAS Version 8; SAS Institute, Cary, NC) was used to perform the analysis of variance (ANOVA) of the data from the plots on the basis of a mixed ANOVA model for the randomized complete block design assuming the hybrid families to be a fixed factor, whereas the blocks were a random factor (Möhring and Piepho, 2009). After finding significant variation for the studied trait among the hybrid families, the second stage of the analysis involved performing a fixed model-based diallel ANOVA of family means (calculated across replications) together with estimating GCA and SCA effects as outlined by Griffing (1956b) for a half diallel complete mating design with parents treated as a fixed factor (Method IV,

Model 1). Further valuable methodological background and justification for these analyses is presented by Baker (1978) and their empirical use for fruit crops is illustrated by Dossett et al. (2008) and Giménez and Ballington (2002). This diallel analysis was conducted using the SAS PROC MIXED procedure (SAS Version 8). A detailed analysis of the significance of the GCA and SCA effects was made using a simultaneous test procedure based on the Bonferroni inequality (Garretsen and Keuls, 1978).

Results and Discussion

Weather conditions varied between years. In 2009, the month of June was considered very wet (147 mm rainfall), whereas summer months were dry [July (77 mm), August (73 mm), September (29 mm)]. More rainfall was recorded again in mid-October (83.4 mm). In 2010, on the other hand, June and July were dry (62 and 76 mm rainfall, respectively), August (100 mm) and September (123 mm) wet, and October very dry (3.8 mm).

The soil temperature during the summer months (June, July, and August) was 2 to 3 °C higher in 2010 than in 2009, but lower in September and October.

Because the 2009 season was dry (compared with 2010), the conditions were more favorable for the development of verticillium wilt diseases than in 2010. Heavy rainfall in June 2009 caused early appearance of verticillium symptoms and the pathogen's infection of vascular tissues of the strawberry seedlings. Followed by dry and sunny summer weather, severe symptoms of verticillium wilt appeared on leaves within 3 months.

Severity of symptoms increased with time progression (between the first, second, or third evaluation dates). According to Kronenberg and van der Giessen (1968), *V. dahliae* infection of young plants can be extremely quick and severe, resulting in premature death of plants susceptible to the pathogen within 3 months after planting. In their study, 70% to 85% of ‘Gorella’ plants died in the field just 3 months after planting. Although in 2010, the infection of young seedlings was less severe compared with 2009, the most affected were hybrids from crosses that included ‘Figaro’ as one of the parents (Fig. 2) in which parentage is ‘Elsanta’, a cultivar extremely susceptible to verticillium wilt. Variable responses of different strawberry cultivars to *V. dahliae* infection during different growing seasons were also reported by Shaw et al. (2005). Authors observed that independent of the year, the verticillium wilt severity in field-grown strawberry plants is stable for a particular genotype; even the interaction genotype × growing season has been highly significant. In our studies, disease symptoms became more pronounced with time reaching the highest level in October (Fig. 2).

Fig. 2. Degree of plant infection of 45 strawberry hybrid families by verticillium wilt observed at Skierniewice, Poland, in Oct. 2009 and 2010: 0 = plants with no symptoms; 1 = plants with only a few older leaves wilted; 2 = plants with a number of wilted leaves, some of them already drying out; 3 = plants with most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms; 4 = plants dead or dying where only one middle leaf showing signs of growth.

The nature of combining ability effects provides guidelines in identifying the better parents for use in crosses. Diallelic variance analyses of data have shown significant differences for the effects of GCA and SCA of strawberry parental genotypes for verticillium wilt severity at all evaluation times in both years ($P < 0.01$) (Table 2). Thus, genetic additive effects as well as non-additive play a significant role in displaying these traits in progeny. Estimated for detailed additive and non-additive effects, a description of inheritance of this particular trait GCA and SCA effects (S^2_{GCA}/S^2_{SCA}) was from 1.59 (7 Oct. 2010) to 7.68 (28 Oct. 2009). A relatively high (greater than 2) value of S^2_{GCA}/S^2_{SCA} indicates dominance of additive genetic effects over non-additive in genetic determination of the progeny quantitative trait coming from a gene pool of parental lines used for crossing (Baker, 1978; Griffing, 1956a, 1956b; Hortyński, 1987). This indicates a relatively high probability of showing this trait in the next generation based on the average from both parental forms. The resistance to verticillium wilt is inherited polygenetically and regulated by additive genetic effects and dominance effects (Bringhurst et al., 1968; Maas et al., 1989). Effects of dominance can be responsible for 50% of genetic variability for this trait (Shaw et al., 1996). The variance analysis of data on verticillium wilt severity for progeny of investigated strawberry families (Table 2) also clearly indicates the effects of weather conditions, where S^2_{GCA}/S^2_{SCA} drastically increases with the date of evaluation in 2009 (a year more favorable for *V. dahliae* infection) and decreases in 2010 (a year less favorable for infection).

Evaluation of GCA effects of 10 strawberry parental cultivars for the verticillium wilt severity in plants is shown in Table 3. The negative values of GCA effects indicate high plant tolerance to verticillium wilt, whereas the positive values of GCA effects indicate high susceptibility

Table 2. Analyses of variance for degree of plant infection by *Verticillium dahliae* for progeny families of 10 parental cultivars of strawberry (half diallel mating design, Griffing’s method IV) at Skierniewice, Poland, in 2009 and 2010.

		Mean squares (S ²) for degree of plant infection by <i>V. dahliae</i> ^y					
		2009			2010		
		Expt. 1			Expt. 2		
		Date of evaluation			Date of evaluation		
Source of variation ^z	df	26 Aug.	28 Sept.	28 Oct.	10 Sept.	7 Oct.	Avg 2009–10 ^x
GCA	9	0.337**	0.650**	0.639**	0.097**	0.049**	0.200**
SCA	35	0.086**	0.092**	0.083**	0.035**	0.031**	0.030**
Error	132	0.031	0.037	0.033	0.002	0.014	0.012
S ² _{GCA} /S ² _{SCA} ^w		3.92	7.07	7.68	2.74	1.59	6.60

^zGCA = general combining ability; SCA = specific combining ability.

^yRanking scale used for evaluation of verticillium wilt severity in strawberry plants: 0 = plants with no symptoms; 1 = plants with only a few older leaves wilted; 2 = plants with a number of wilted leaves, some of them already drying out; 3 = plants with most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms; 4 = plants dead or dying where only one middle leaf showing signs of growth.

^xAverage value for the observations made on 28 Oct. 2009 and 7 Oct. 2010.

^wQuotient of mean squares for general and specific combining ability effects.

**Significant at $P < 0.01$

Table 3. General combining ability effects of 10 strawberry parental cultivars for degree of plant infection by *Verticillium dahliae* (half diallel mating design, Griffing's method IV) at Skierniewice, Poland, in 2009 and 2010.

Parental cultivar	Evaluation of GCA effects for the degree of <i>V. dahliae</i> infection of strawberry plants ^z					
	2009			2010		Avg 2009–10 ^y
	Expt. 1		Expt. 2			
	Date of evaluation		Date of evaluation			
	26 Aug.	28 Sept.	28 Oct.	10 Sept.	7 Oct.	
Darselect	0.05	0.19*	0.19*	−0.05	−0.03	0.08
Selvik	−0.24*	−0.39*	−0.40*	0.25*	0.09	−0.15*
Elianny	−0.04	−0.10	−0.06	0.07*	0.00	−0.03
Figaro	0.31*	0.43*	0.42*	0.08*	0.13*	0.28*
Sonata	−0.18*	−0.16	−0.19*	−0.08*	−0.06	−0.12
Susy	0.24*	0.15	0.15	0.00	0.06	0.10
Salsa	0.06	0.08	0.05	0.02	0.04	0.04
Albion	0.06	0.17	0.15	−0.10*	−0.06	0.05
Charlotte	0.07	0.14	0.17	−0.08*	−0.08	0.05
Filon	−0.34*	−0.50*	−0.48*	−0.11*	−0.10	−0.29*
SE ($\hat{\sigma}_i$) ^x × 2.85	0.171	0.171	0.171	0.057	0.114	0.114

^zGCA = general combining ability. Ranking scale used for evaluation of verticillium wilt severity in strawberry plants: 0 = plants with no symptoms; 1 = plants with only a few older leaves wilted; 2 = plants with a number of wilted leaves, some of them already drying out; 3 = plants with most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms; 4 = plants dead or dying where only one middle leaf showing signs of growth.

^yAverage value for the observations made on 28 Oct. 2009 and 7 Oct. 2010.

^xSE of the estimates of GCA effects.

*Significant at $P < 0.05$ according to the Bonferroni procedure (Garretsen and Keuls, 1978).

to the disease. Low values for GCA effects of parental cultivars in both growing seasons indicate a significant interaction GCA × growing season that also was reported earlier by Shaw et al. (2005). Regrettably, a highly significant GCA × growing season interaction makes evaluation of parental forms very difficult for their suitability to the breeding program based on GCA.

In 2009, the highest significantly positive value ($P < 0.05$) for GCA effects for high verticillium wilt severity in plants was shown in cultivars Susy, Figaro, and Darselect (Table 3), whereas in 2010, it was shown in cultivars Figaro, Elianny, and Selvik. Positive GCA effect values for the trait are a disadvantage for breeding cultivars tolerant or low susceptible to verticillium wilt as a result of the possibility of high susceptibility to the disease in the F_1 generation of studied genotypes. Thus, these cultivars will not be suitable as parents for the breeding program although some of them are considered low susceptible to verticillium wilt. For example, ‘Susy’ was low susceptible to the disease in field studies, whereas in the greenhouse, under artificial inoculation with the pathogen, the cultivar showed typical symptoms of *V. dahliae* infection and was classified as medium susceptible to verticillium wilt (Olbricht and Hanke, 2008), similar to ‘Elianny’ (Dressler et al., 2010). As expected, ‘Figaro’ was not suitable as a parent for breeding verticillium wilt-tolerant plants because it showed high susceptibility to the disease similar to ‘Elsanta’, which is one of the parents of ‘Figaro’ (Masny and Żurawicz, 2009a).

Highly suitable for breeding verticillium wilt-tolerant cultivars were those having significant negative GCA effects. The lowest significant values of GCA effects were observed with a Polish cultivar, Filon. Low susceptibility of this cultivar to *V. dahliae* infection in field studies has been reported by Żurawicz and Masny (2005) as well as by Żebrowska (2011) for in vitro-grown material. It has also been reported that ‘Filon’ can be a valuable donor of other traits such as high yield and low susceptibility to strawberry leaf spot caused by *Mycosphaerella*

fragariae (Masny et al., 2008). Significantly negative GCA effects for verticillium wilt severity were also observed with ‘Sonata’. Similarly, another Polish cultivar, Selvik, has shown negative GCA effects at all three evaluation dates in 2009; so did French cultivar Charlotte and American (California) cultivar Albion at the first evaluation date (September) in 2010 (Table 3).

Data analysis of averages from both growing seasons indicates that cultivar Figaro passes high susceptibility to verticillium wilt to its progeny as it carries highly significant ($P < 0.05$) positive GCA effects for this trait. On the contrary, two Polish cultivars (Filon and Selvik) exhibited significantly negative GCA effects and thus are highly valuable for breeding strawberry cultivars low susceptible to verticillium wilt.

The significant SCA effects for strawberry characteristics often show up only in a few cross combinations and can either improve or degrade biological and agricultural value of the progeny (Hortyński, 1987; Masny et al., 2005, 2008; Spangelo et al., 1971; Żurawicz, 1990). Characteristics of parent cultivars with regard to the value of SCA effects for verticillium wilt severity in plants are presented in Table 4. Similar to the GCA effects, also the positive SCA effects for the trait indicate high susceptibility to the disease, whereas the negative values of SCA effects indicate low plant susceptibility to verticillium wilt. Surprisingly, significant favorable SCA effects for this trait evaluated for the hybrid family ‘Selvik’ × ‘Salsa’ predict high susceptibility to *V. dahliae* in offspring in 2009 and 2010 (Table 4). ‘Selvik’ and ‘Salsa’ showed low susceptibility to verticillium wilt in a 2-year field study. The soil in the field was heavily infected with *V. dahliae* (Masny and Żurawicz, 2009b). Individually, statistically significant favorable SCA effects for verticillium wilt severity in plants were observed for the following parent families: ‘Sonata’ × ‘Albion’, ‘Susy’ × ‘Charlotte’, ‘Selvik’ × ‘Elianny’, ‘Elianny’ × ‘Charlotte’, ‘Figaro’ × ‘Salsa’, ‘Figaro’ × ‘Albion’, ‘Susy’ × ‘Salsa’, and ‘Susy’ × ‘Filon’. The negative, statistically significant SCA effects for the trait were

Table 4. Significant estimates of specific combining ability effects of F₁ progeny of strawberry hybrid families for degree of plant infection by *Verticillium dahliae* (half diallel mating design, Griffing's method IV) at Skierniewice, Poland, in 2009 and 2010.

	Evaluation of SCA effects for the degree of <i>V. dahliae</i> infection of strawberry plants ^z					
	2009			2010		
	Expt. 1			Expt. 2		
Hybrid family	Date of evaluation			Date of evaluation		
	26 Aug.	28 Sept.	28 Oct.	10 Sept.	7 Oct.	Avg 2009–10 ^y
‘Selvik’ × ‘Elianny’	–0.21	–0.17	–0.12	0.20*	–0.03	–0.07
‘Selvik’ × ‘Susy’	–0.16	–0.01	0.03	–0.33*	–0.05	–0.01
‘Selvik’ × ‘Salsa’	0.54*	0.72*	0.68*	0.48*	0.22	0.45*
‘Selvik’ × ‘Filon’	–0.01	0.21	0.24	–0.15*	0.10	0.17
‘Elianny’ × ‘Susy’	0.45	0.43	0.29	–0.21*	–0.17	0.06
‘Elianny’ × ‘Salsa’	0.08	–0.03	0.05	–0.15*	–0.15	–0.05
‘Elianny’ × ‘Albion’	0.03	0.05	0.06	–0.24*	0.01	0.04
‘Elianny’ × ‘Charlotte’	–0.10	–0.11	0.04	0.41*	0.03	0.04
‘Elianny’ × ‘Filon’	–0.10	0.03	0.03	–0.09	0.36*	0.19
‘Figaro’ × ‘Salsa’	–0.13	–0.16	–0.13	0.14*	0.16	0.01
‘Figaro’ × ‘Albion’	0.19	0.28	0.12	0.16*	0.15	0.13
‘Figaro’ × ‘Charlotte’	–0.14	–0.23	–0.24	–0.27*	–0.16	–0.20
‘Sonata’ × ‘Susy’	–0.46	–0.34	–0.35	–0.18*	–0.16	–0.25
‘Sonata’ × ‘Albion’	0.67*	0.66*	0.75*	0.12	–0.08	0.34*
‘Susy’ × ‘Salsa’	–0.13	–0.12	–0.09	0.19*	0.23	0.07
‘Susy’ × ‘Charlotte’	0.52	0.45	0.36	0.05	–0.08	0.14
‘Susy’ × ‘Filon’	–0.09	–0.21	–0.23	0.35*	–0.06	–0.15
‘Salsa’ × ‘Filon’	0.07	0.11	0.14	–0.25*	–0.54*	–0.20
‘Albion’ × ‘Charlotte’	–0.80*	–0.72*	–0.54*	–0.12	–0.19	–0.37*
SE (s _{ij}) ^x × 3.33	0.500	0.566	0.533	0.133	0.333	0.333

^zSCA = specific combining ability. Ranking scale used for evaluation of verticillium wilt severity in strawberry plants: 0 = plants with no symptoms; 1 = plants with only a few older leaves wilted; 2 = plants with a number of wilted leaves, some of them already drying out; 3 = plants with most of the leaves wilted and/or drying out, where only a few youngest leaves showing no symptoms; 4 = plants dead or dying where only one middle leaf showing signs of growth.

^yAverage value for the observations made on 28 Oct. 2009 and 7 Oct. 2010.

^xSE of the estimates of SCA effects.

*Significant at $P < 0.05$ according to the Bonferroni procedure (Garretsen and Keuls, 1978).

found for the family 'Albion' × 'Charlotte' in 2009 and 2010 growing seasons (Table 4). In 2010, the significantly negative GCA effects were also evaluated for both parents indicating that the progeny of these two cultivars will be low susceptible to *V. dahliae* infection. Significant negative SCA effects for this trait were also evaluated for the following families: 'Salsa' × 'Filon' (for both dates in 2010), 'Selvik' × 'Susy', 'Selvik' × 'Filon', 'Elianny' × 'Susy', 'Elianny' × 'Salsa', 'Elianny' × 'Albion', 'Figaro' × 'Charlotte', 'Sonata' × 'Susy', and 'Susy' × 'Filon' (the negative significant SCA effects were only observed in a few individual dates). This indicates a good possibility for selection of valuable individuals with low susceptibility to verticillium wilt. The presence of four such individuals like 'Filon' and 'Selvik' among parent combinations shows that these cultivars have a high recombinant ability after a cross with a cultivar medium susceptible to verticillium wilt such as 'Susy' (Masny and Żurawicz, 2008).

Combining ability analyses indicate that strawberry cultivars used as parents in this study vary in their suitability for breeding of new cultivars tolerant or low susceptible to *V. dahliae* infection. The most valuable cultivars for such program are those with significantly negative GCA for verticillium wilt severity in plants as well as a parent combination having significantly negative SCA effects for this trait. These are two Polish cultivars, Filon and Selvik, as well as a Dutch cultivar, Sonata. Parent families 'Salsa' × 'Filon', 'Selvik' × 'Susy',

'Selvik' × 'Filon', 'Elianny' × 'Susy', 'Elianny' × 'Salsa', 'Elianny' × 'Albion', 'Figaro' × 'Charlotte', 'Sonata' × 'Susy', and 'Susy' × 'Filon' may also be suitable. The cultivar Figaro turned out to be unsuitable for breeding of strawberry plants low susceptible to verticillium wilt because significant positive GCA effects were observed for high verticillium wilt severity. It has also been concluded that additive and non-additive genetic effects play a significant role in inheritance of susceptibility to verticillium wilt in strawberry plants; however, genetic variability to this trait predominantly depends on the additive action of genes.

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