

Table 3. Mean seedling root rot ratings and percentage of seedlings showing symptoms for 17 red raspberry progenies planted in 1975 and rated in 1977.

Seed parent	Pollen parent							
	Newburgh		WSU 458 ^x		WSU 460 ^x		Glen Clova	
	Rating ^z	%	Rating	%	Rating	%	Rating	%
Latham	0.5 a ^y	25	0.5 a	29	0.5 a	30	1.6 abc	50
Newburgh			1.1 ab	40	2.4 bcd	55	4.4 ef	83
WSU 458 ^x					2.9 cd	62	5.1 fg	92
Sumner			2.1 bcd	49	2.9 cd	61	5.2 fg	90
WSU 460 ^x							5.8 g	80
Meeker	2.0 bcd	63	2.1 bcd	53	3.2de	73	6.3 g	90

^z0-9 rating scale, 0 = no symptoms, 9 = death; % refers to % hills showing symptoms.

^yMean separation by Duncan's multiple range test, 5% level.

^x'Newburgh' × 'Sumner' seedlings from the Washington State University breeding program.

Although it is not possible to trace the original source of resistance exhibited by 'Latham', its parent, 'King', was known for its ability to thrive on poorly drained clay soils (6). 'Latham' is the source of resistance found in 'Chief' and 'Sumner'. 'Taylor', a 'Newman' × 'Lloyd George' seedling, probably received its resistance from 'Newman' because 'Lloyd George' is extremely susceptible. 'Newman' originated from mixed open-pollinated seed of 'Herbert', 'King', 'Louden', 'Cuthbert' and 'Eaton' (6). 'WSU 458' may have derived its resistance from both its parents, 'Newburgh' and 'Sumner'.

The high heritability estimates for root rot resistance suggest that considerable additive genetic variance exists and that the mating of parents based on their phenotypes will result in rapid genetic gain.

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Variation in Stability of Cytoplasmic-genic Male Sterility in *Capsicum annuum* L.¹

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Abstract. Several cytoplasmic-genic male-sterile (partially fertile) cultivars were developed in pepper. Three cultivars demonstrated different levels of male sterility; male sterility stability of 'Bikura' was reliable for hybrid seed production.

Cytoplasmic-genic male sterility in *Capsicum annuum* was originally documented by Peterson (6). Inheritance was suggested primarily due to a single recessive gene interacting with S-type cytoplasm. In his material, Peterson demonstrated variation in anther morphology and in production of pollen grains which could be related to the different cultivars used in the crosses. In addition, the character was found to be highly sensitive to fluctuating growth conditions, particularly tempera-

tures. Novak et al. (5), working with Peterson's source of male sterility and broader genetic material, found digenic inheritance; they also noted variable degrees of sterility from complete male-sterility to partial fertility. According to Pochard (7), Novak (5), Hirose (3) and Horner (4), abnormal development in Peterson's source of male sterility occurs in premeiotic stages, but the final breakdown stage is postmeiotic. Shifriess and Frankel (8) found S-type cytoplasm following intraspecific crosses in *C. annuum*, probably identical to that found by Peterson (6). Since these previous studies indicated lack of stability of cytoplasmic genic male sterility, the character was not utilized in breeding F₁ hybrids, while genic male sterility is already in commercial use (2). The present paper reports variation in level of male sterility among and within male sterile cultivars and its bearing on future F₁ seed production, utilizing cytoplasmic-

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genic male sterility.

Materials and Methods

The original cytoplasmic genic male sterility induced by Shifriss and Frankel (8) was incorporated during 6 to 8 backcross generations into several sweet pepper cultivars. Male-sterile versions of the cultivars 'Bikura', 'Yellow-Yolo-Y' (yellow-fruited mutant from 'Yolo-Y') and 'Zohar' were used as maternal parents-A lines (S)*msms*. Simultaneously, a restorer gene *Ms* from 'Jalapeno' was incorporated into the original S-type male steriles followed by 7 backcross generations to 'Yolo-Y' and to 'Maor'. Heterozygous (S)*MSms* plants were selfed and homozygous paternal parents (lines (S)*MSMS*) of 'Yolo-Y' and 'Maor' were isolated.

During the summer seasons of 1975, 1976 and 1977 the following experiments were carried out in the open field:

1975 experiment. 'Bikura' (S) *msms* line was exposed to natural pollination with (S) *MSMS* 'Yolo-Y'.

1976 experiment. 'Zohar' (S)*msms* line was exposed to natural pollination with (S)*MSMS* 'Yolo-Y'.

1977 experiment. 'Zohar' and 'Yellow-Yolo-Y', both (S) *msms* lines, were exposed to natural pollination in the same plot with a common pollinator, 'Maor' (S)*MSMS*.

In these experiments hundreds of male sterile and male fertile plants were planted in a 1:1 ratio and in separate rows 50 cm apart in the beginning of May. In the 1975 experiment there were 2 seed harvests at a 1 month interval, corresponding to fruit set under different periods of anthesis. In subsequent experiments all mature fruits were harvested in a single harvest and the seed bulked.

Identification of hybrids vs. progenies produced by selfing in maternal male sterile plants. The male sterile cultivars used in the present experiments contain recessive marker genes, whereas the pollinator C lines contain the corresponding dominant alleles. Hence progenies that showed the recessive traits were considered to result from selfing in male sterile plants. 'Bikura' and 'Zohar' male sterile lines carry the recessive erect fruit character (*pp*) while the pollinators 'Yolo-Y' and 'Maor' carry the dominant pendent trait (*PP*). Both maternal lines have other plant and fruit characteristics which could be recovered in selfed progenies. 'Yellow-Yolo-Y' male sterile has the recessive yellow fruit color at maturity (*yy*) while the pollinator cultivars have the dominant allele for red fruit color (*YY*).

Greenhouse and growth chamber experiments. Male sterile plants from the cultivars 'Bikura', 'Yolo-Y' and 'Zohar' were grown in a greenhouse during 1976. Night temperature during winter was maintained at 15°C and maximal day temperatures during summer months reached 38°-40°. Weekly microscopic observations with 1% aceto carmin-dye were made on pollen production in male-sterile plants. In addition, flowering male sterile plants were transferred for a 50-day period during winter from a greenhouse to a growth chamber in which the 12-hr day-temperature was 32°C and the night temperature was 25°. Light intensity of 54 klx was measured above the plant level.

Results and Discussion

During 6 to 8 backcross generations using S-type male-sterile and male-fertile mother plants, a single gene inheritance for male sterility was repeatedly confirmed. This was the case when all previously mentioned cultivars were used in the crosses. Progeny classification was rather simple when based on morphological difference, i.e., small shrunken undehisced anthers at early anthesis vs. normal anthers of fertile individuals. However, under common growing conditions in the field, all previously mentioned male sterile cultivars could produce different amounts of normal pollen grains. Hence, terminology must be revised and the present cytoplasmic-genic male steriles are actually partial fertile. In the 1975 field experiment 'Bikura' was found to be a promising cultivar by providing a stable male-sterile

phenotype (Table 1). Less than 1% selfing is highly satisfactory, from the seed production point of view. This male-sterile cultivar demonstrated its stability during the flowering period of July-August (judged from 2 seed harvests made during August-September). Further field experiments with 'Bikura' male sterile line (Shifriss, unpublished) corroborated the 1975 findings. 'Zohar' was unstable during 1976 and 1977, as shown by a high rate of selfing (Table 1) that makes it unreliable as a seed parent for hybrids. Alternatively, cultivars with this rate of fertility restoration could be considered for utilization as paternal C lines. 'Yellow-Yolo-Y' male sterile shows a level of instability between the 2 cultivars mentioned above (Table 1). This cultivar is important since it is of the large-fruited 'Bell'-type.

Generally, following natural pollination, 'Yellow-Yolo-Y' male sterile produced atypically flat fruits, due to small amounts of seeds (F_1 and selfed ones). A few exceptional normal fruits which had a larger number of seeds were obtained. However, an individual large fruit, such as in acc. 7155, did not result from an extra amount of outcrossing but from an increase in selfing (Table 1). This high percentage of selfing in individual flowers vs. 14% in bulked seeds demonstrates the intraplant instability in this cultivar. Results of greenhouse studies indicated the following: (a) Flowers of male-sterile (partially fertile) cultivars produced both aborted and normal pollen grains throughout the year, but in different quantities and proportions; (b) An increase in male sterility (percent of aborted pollen grains) with the approach of the hot season was noticed in all cultivars; (c) 'Bikura' and 'Yolo-Y' demonstrated a higher level of male sterility than 'Zohar' and the difference between these 2 groups was great during March-April; such inter-cultivar differences are in complete agreement with field performance; (d) Degree of male sterility was unaffected by plant age.

Flowering under exceptionally high temperatures (32°/25°C) in a growth chamber resulted in flower bud abscission. However, flowering was restored at the same temperatures 1 month later.

The chamber conditions affected meiosis in both control and male-sterile plants, but in different ways. The control 'Maor' was relatively resistant to the high temperatures of 32/25°C, since pollen abortion occurred only after 30 days of exposure. In plants of the male sterility genotype, pollen breakdown occurred much earlier, i.e. during 1-3 weeks of exposure (Table 2). In addition, male sterility expression in 'Maor' was typified by a normal quantity of pollen grains but a low percentage of normal ones. Hence one could assume that pollen abortion in the control 'Maor' occurred after meiosis. In 'Bikura' and 'Zohar' male sterile individuals, meiosis was blocked, resulting in zero or a negligible amount of pollen grains, both

Table 1. Amount of selfing by natural pollination in maternal plants which are phenotypically male sterile.

Year	Cultivar	Total plants	Individuals resulting from selfing	
			No.	%
1975	Bikura (S) <i>msms</i>			
	1st harvest	~1200	1	0.08
	2nd harvest	897	1	0.1
1976	Zohar (S) <i>msms</i>	246	70	28
1977	Zohar (S) <i>msms</i>	64	18	28
	Yellow-Yolo Y (S) <i>msms</i>			
	7152*	27	2	7
	7153*	59	5	8
	7155*	29	18	62
	7156 (bulk)~	85	12	14

*Each line represents progeny from a single fruit of different (S)*msms* plants.

Table 2. Male sterility levels of individual flowers during exposure of plants to stress conditions (32^o/25^oC day/night temperatures).

Cultivar	Plant code	Male sterility level ^z										
		Days in growth chamber										
		0	2	4	6	18	22	30	36	37	44	49
Bikura (male sterile (S) <i>msms</i>)	77-92-3	1++	2++	1++	0				0	0	0	
			3++		0					0	0	
			3++		0							
			1++		0							
			1++									
Zohar (male sterile (S) <i>msms</i>)	79-93-1	1++	3+++	0				1+	1+			
		3++	3++	3++					1+			
	77-93-3	0						1+	0			
									1+			
77-93-4	3++				1+	1+						
	2++				0	0						
Maor (control)							3+++		3+		3+	

^zFrom 0-3 (normal quantity of pollen grains per flower); from low (+) to high (+++) percentage of normal pollen grains per flower.

aborted and normal (Table 2).

Pollen abortion in normal pepper was found by Hirose (3) to depend on increasing daily mean temperatures. In addition, the magnitude of pollen abortion was correlated with temperatures prevailing during the 2-3 weeks preanthesis stage.

During the middle of August (hottest month) 50-80% pollen abortion was recorded in 'Zairaityuzisi' (3). Hence, stabilizing male sterility in cytoplasmic male-sterile individuals may be possible, provided superoptimal field temperatures prevail during a certain preanthesis period.

In the present studies single gene segregation for structural differences between anthers of normal and male sterile (partially fertile) plants was indicated. However, the intercultural variation in levels of male sterility, i.e., amount and quality of pollen grains in 'Bikura' vs. 'Zohar' (Table 2), suggests additional genes with accumulative effects.

The common phenomenon of mixed aborted and normal pollen grains in the present material appears similar to the nuclear cytoplasmic male-sterility in alfalfa (1). In alfalfa, lack of pollen dehiscence was associated with a low percentage of normal pollen grains and not with total number of pollen grains. This point is different in cytoplasmic male sterile pepper since lack of anther dehiscence under normal or stress conditions (Table 2) is associated with a decrease in total number of pollen grains.

According to Barnes and Garboucheva (1), cytoplasmic nuclear male sterility in alfalfa is caused by a chemical system that has a threshold concentration for each level of sterility. Similarly, in pepper, a gradient of concentrations modified by temperatures may explain the variation in pollen production.

We conclude that cultivars with male sterility stability, like that of 'Bikura', can serve as A lines using natural cross pollination in hybrid seed production. In unstable cultivars typified by intraplant variation, further progress towards utilization of

cytoplasmic genic male sterility may be achieved through the following breeding procedures: (a) selection for higher level of male sterility through maintainer plants; (b) incorporation of seedling marker genes into maternal male sterile cultivars for early elimination of progenies resulting from selfing; and (c) sampling environmental conditions that produce the highest level of male sterility.

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