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The Inheritance of Parthenocarpy in Oregon T5-4 Tomato

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Abstract. **The inheritance of a tendency to set parthenocarpic fruit in tomato (*Lycopersicon esculentum* Mill.) line Oregon T5-4 (T5) was studied in the field in crosses with 3 normal, seeded cultivars. F_1, F_2, and backcross data indicated that the parthenocarpic tendency in T5 is recessive. F_2 data fit a 9 seeded : 7 seedless ratio, indicating that normal seediness requires 2 complimentary dominant genes. Parthenocarpic plants were earlier than seeded plants. Early ripening in T5 crosses resulted in most instances from a reduced period of time from first flower to first ripe fruit, and not from early flowering. The F_2 from a cross of T5 with 'Severianin', an unrelated parthenocarpic cultivar, approached a theoretical 27 seeded : 37 seedless for 3 complimentary gene pairs and demonstrated that parthenocarpic tendency is determined by different factors in these 2 parents.**

Some early maturing lines of tomatoes developed at Oregon Station Univ. produce parthenocarpic (seedless) fruit at the beginning of the summer, then normal, seeded fruit for the rest of the season. 'Oregon 11' (3) and 'Gold Nugget' (4) usually produce 50–70% seedless fruit in western Oregon, while 'Oregon Cherry' (1) may have 5% seedless fruit and Oregon T5-4 (T5) (2) about 30%. This characteristic is apparently temperature-dependent—parthenocarpic fruit are produced early in the season because temperatures are low. These lines and cultivars generally produce seeded fruit in the greenhouse. Seedlessness in tomatoes is considered to be a desirable quality characteristic, and, in these lines, appears to be generally related to earliness.

Tomato lines or cultivars with heritable tendency for parthenocarpic fruit set have been reported (2, 3, 6, 8, 11, 17, 20, 21). Specific cultivars have been described as setting parthenocarpic fruit when exposed to high day and night temperatures (6, 10), or low night temperatures (16). 'Severianin' (11) was reported to set seedless fruit without pollination. By contrast, preliminary evidence suggests that Oregon T5 requires pollination for seedless fruit set.

Several researchers have studied the relationship between earliness and parthenocarpy. Marre and Murneck (12) concluded that fruit with many seeds have increased metabolic activity, which accelerates cell enlargement and fruit development. However, Rylski (18) found no relationship between the number of seeds per fruit and the number of days required for fruit ripening of seeded, naturally seedless, and growth regulator-induced seedless tomatoes. Several other researchers (5, 7, 9, 10), studying F_2 progenies from crosses between parthenocarpic and nonparthenocarpic tomato cultivars, found that the parthenocarpic genotypes were earlier than normal genotypes. Scott and George (19), working with several different parthenocarpic genotypes, found that the relationship between parthenocarpy and earliness was different for different genotypes.

Soressi and Salamini (20) found that parthenocarpy in their material (derived from a chemically induced mutation), was due to a single recessive gene, *pat*. Plants carrying *pat* were high-yielding, early, and had small fruit (20–42 g). Philouze and Maisonnueve (14) found parthenocarpy in the Russian cultivar Severianin, obtained from interspecific hybridization, was due to a single recessive gene (*pat-2*), nonallelic to *pat*. The same authors (15) found that parthenocarpy in the German line 75/59 developed by Reiman-Phillip is controlled by several recessive genes other than *pat* and *pat-2*.

The purpose of this study was to determine the inheritance of a parthenocarpic tendency in Oregon T5, a small-fruited line released as germplasm in 1978, and to determine the relationship between parthenocarpy and earliness in this line.

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Table 1. Ratios of seeded (S) and parthenocarpic (P)[z] plants tested for fit to the 9:7 dihybrid ratio, 1979.

		Number of transplanted plants					Number of direct-seeded plants				
		Observed		Expected			Observed		Expected		
Cross	Generation[y]	S	P	S	P	χ^{2x}	S	P	S	P	χ^2
T5 x 'Saladmaster'	Pp	0	40				0	29			
	Ps	36	0				25	0			
	F_1	120	0				39	0			
	F_2	112	87	112	87	0.0	129	72	113	88	4.8*
	F_2R	126	72	111	87	4.1*					
	BCP	11	70	20	61	5.0*	7	35	10	32	1.1
	BCs	142	1				58	3			
T5 x 'Willamette'	Pp	0	40				0	29			
	Ps	40	0				19	0			
	F_1	79	0				40	1			
	F_2	104	94	111	87	1.0	117	74	107	84	1.7
	F_2R	137	61	111	87	13.0**					
	BCp	5	94	25	74	20.0**	4	43	12	35	6.0*
	BCs	117	0				42	0			
T5 x 'Starshot'	Pp	0	40				0	29			
	Ps	37	0				27	0			
	F_1	75	1				21	0			
	F_2	105	92	111	86	0.6	103	65	94	74	1.5
	F_2R	125	71	110	86	4.2*					
	BCp	18	131	37	112	12.6**	5	47	13	39	5.8*
	BCs	47	0				60	10			

[z]Parthenocarpic (P) plants are those having seedless fruit at any time during the season.
[y]Ps = seeded parent, Pp = parthenocarpic parent, BCs = F_1 x seeded parent, BCp = F_1 x parthenocarpic parent, F_2R = reciprocal F_2.
[x]F_2 tested for fit to 9 S:7 P ratio; BC_p tested for fit to 1 S : 3 P ratio.
*,**Significant at 0.05 and 0.01 probability levels, respectively.

Table 2. Comparison of population means[z] for total number of seedless days, and transplants and direct-seeded plants combined, 1979.

	Mean total no. seedless days		
Population[y]	T5 x Saladmaster	T5 x Willamette	T5 x Starshot
Ps	0.0 a	0.0 a	0.0 a
F_1	0.0 ab	0.1 ab	0.0 ab
BCs	0.6 abc	0.2 abc	1.3 abc
F_2R	6.2 d	4.8 d	6.1 d
F_2	6.9 de	7.8 de	7.4 de
BCp	17.6 f	25.1 f	18.8 f
Pp	34.1 g	34.1 g	34.1 g

[z]Duncan's multiple range test; means followed by the same letter are not different at 0.05 probability level.
[y]Ps = seedy parent, Pp = parthenocarpic parent, BCs = F_1 x seedy parent, BCp = F_1 x parthenocarpic parent, F_2R = reciprocal F_2.

Materials and Methods

T5, the parthenocarpic parent in this study, originated from complex parentage (2). It bears abundant small (2.5 to 5-cm in diameter) pink fruit and is extremely early.

The field study made in 1979 involved crosses of an F_7 subline of T5 (T5-4-3-2-1), which was more uniform and produced a higher proportion of parthenocarpic fruit than the original Oregon T5-4. Normal parents were 'Saladmaster', 'Starshot', and 'Willamette'. Populations tested were parthenocarpic parent, T5 (Pp), normal seeded parent (Ps), F_1, F_2, backcross F_1 x parthenocarpic parent (BCp), and backcross F_1 x normal parent (BCs). Reciprocals were grown separately but were combined in data analysis if heterogeneity χ^2 tests were not significant.

Both transplanted and direct-seeded plants were observed. Transplants were seeded in the greenhouse 3 Apr. and set in the field 24 May, 46 cm apart in rows 1.8 m apart. Direct-seeded plots were planted 23 May and thinned to about the same spacing. Fertilizer was banded at the rate of 67.4N–90P–56K $kg \cdot ha^{-1}$. Sprinkler irrigation was applied as necessary for normal growth.

Populations were replicated 4 times in a randomized block design. In the transplant test, there were 10 plants of each population in each replication, except for the F_2, which included 50 plants each of the reciprocals in each replication. In the direct-seeded planting, which was separate from the transplanted plot area, problems in germination reduced total populations.

Individual plant data were taken at 2- or 3-day intervals. Flowering date was considered to be the day the first flower opened. First ripe fruit was the day the first normal-size fruit was at edible stage. The first ripe fruit on each plant was examined within 2 or 3 days of its ripening date for the presence of seeds. Thereafter, each plant was checked once each week to determine whether ripening fruits were seeded, until 23 Sept., when ripe fruit of all plants were seeded. For a qualitative expression of parthenocarpic tendency, plants were classified as parthenocarpic if seedlessness was found in ripe fruit at any time before 23 Sept. For quantitative expression, the total number of seedless days was determined by combining the initial seedless period after the first ripe fruit date and any subsequent periods during which the plant reverted back to ripening seedless fruit.

In 1980, F_2 seeds of an additional cross, T5 x 'Severianin', were direct-seeded to determine if parthenocarpy in T5 is controlled by the same genetic system as reported for 'Severianin' (14).

Table 3. Correlation of number of seedless days with maturity in F_2 populations, 1979.

Cross	Planting method[z]	n	Correlated variable[y]	Correlation coefficient
T5 x Starshot	TP	393	First flower	0.01
			First ripe fruit	−0.12*
			First flower to first ripe fruit	−0.14**
	DS	168	First flower	0.02
			First ripe fruit	−0.45**
			First flower to first ripe fruit	−0.45**
T5 x Saladmaster	TP	397	First flower	−0.02
			First ripe fruit	−0.22**
			First flower to first ripe fruit	−0.19**
	DS	201	First flower	−0.11
			First ripe fruit	−0.47**
			First flower to first ripe fruit	−0.43**
T5 x Willamette	TP	396	First flower	−0.16**
			First ripe fruit	−0.29**
			First flower to first ripe fruit	−0.13**
	DS	191	First flower	−0.27**
			First ripe fruit	−0.57**
			First flower to first ripe fruit	−0.50**

[z]TP = transplants, DS = direct-seeded plants.
[y]Number of days.
*,**Significant at 0.05 and 0.01 probability levels, respectively.

Results and Discussion

All of the T5 plants bore seedless first-ripe fruit, and no seedless fruit were found in 'Saladmaster', 'Willamette', or 'Starshot' (Table 1). Of the total of 374 F_1 plants, all were seeded except for one plant in T5 x 'Starshot' transplants and one plant in T5 x 'Willamette' direct-seeded, which were considered to be possible seed mixtures.

F_2 progenies of all 3 crosses in both transplant and direct-seeded plots tended to fit ratios of 9 S : 7 P. F_2 and F_2 reciprocal (F_2R) differed significantly in transplants for each cross and are shown separately in Table 1. In each instance, the F_2 fit the 9:7 ratio closely, while the F_2R differed from the 9:7 at 5% or 1% probability with an excess of seeded plants. It is noted that in the reciprocals tending not to fit the 9 S : 7 P ratio, the seeded parent was female, suggesting a maternal effect that reduced the expression of parthenocarpy in the transplants, but not under the slightly different environment in which the direct-seeded plants set fruit. In the direct-seeded planting, reciprocal F_2 progenies were not different and were combined. Only the F_2 ratio for T5 x 'Saladmaster' failed to fit the 9 S : 7 P, and this ratio was very close. In general, the F_2 ratios indicated that normal seediness was controlled by 2 complimentary dominant genes.

Backcrosses to the parthenocarpic parent approached or fit the expected 1 S : 3 P ratio, except for the transplants of T5 x 'Willamette' and T5 x 'Starshot'. It appears that modifiers from the seeded parent prevent full expression of parthenocarpy in these backcrosses. BCs progenies were generally all seeded, except for T5 x 'Starshot' direct-seeded, which included 10/60 parthenocarpic plants.

Similar results were obtained when parthenocarpy was treated as a quantitative character, expressed as total number of seedless days. Duncan's multiple range test was used to test differences among population means (Table 2). In all 3 crosses, the F_1 and BCs means for total number of seedless days were not significantly different from the mean of the seeded parent (Ps), indicating again that the inheritance of parthenocarpy in T5 is recessive. The F_2 means were biased strongly toward the mean of Ps, but significantly different from it in all instances. The BCp means were intermediate between those of the F_2 and Pp, and statistically different from each.

Relation of parthenocarpy to earliness. There were consistent significant negative correlations (Table 3) between number of seedless days and days to first ripe fruit, indicating that parthenocarpic fruit ripened earlier than seeded fruit. There was usually no relationship between seedless first ripe fruit and days to first flower, but there were exceptions in both the transplanted and direct-seeded F_2 of T5 x 'Willamette', in which plants with seedless first ripe fruit flowered earlier than those with seeded fruit. A strong association was indicated between parthenocarpy and the number of days from first flower to first ripe fruit in all 3 crosses and for both planting methods. Significant negative correlations, ranging from −0.14 to −0.50, were obtained for number of seedless days vs. the interval from first flower to first ripe fruit. In every instance, the ripening period from flowering to ripe fruit was shorter for the plants bearing parthenocarpic fruit than for the plants bearing normal fruit. These data suggest that plants bearing parthenocarpic fruit are early, not because they flower earlier, but because the length of the ripening period is shorter than for plants bearing seeded fruit. Apparently, physiological conditions associated with parthenocarpy cause early ripening. Scott and George (19), however, found that seed formation in itself was not a rate-limiting factor in tomato maturation with parthenocarpic genotypes. It may also be that plants that do not have the genetic capacity to set parthenocarpic fruit will not set fruit at all for a period of time in the spring when temperatures are cool.

T5 x 'Severianin'. The first ripe fruit were seedless in 100% of the T5 and 'Severianin' plants. In the F_2, 66% of the plants had seedless first fruit. This ratio of 123 S : 239 P approaches an expected ratio of 153 S : 209 P derived from the theoretical ratio of 27:37 for 3 complimentary gene pairs. The χ^2 value of 9.7 is significant at the 1% probability level.

If parthenocarpy in T5 and 'Severianin' is controlled by the same recessive gene, then the F_2 of T5 x 'Severianin' would have only parthenocarpic fruit. The results under the conditions of these studies indicate this is not the case. It appears that parthenocarpy in T5 is controlled by the recessive alleles of 2 complimentary gene pairs, and that these loci also interact in a complimentary manner with the gene *pat-2* in 'Severianin'.

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Estimates of Heritabilities and Genetic Variances of Three Yield and Five Quality Traits in Three Fresh-market Cucumber Populations

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Additional index words. *Cucumis sativus*, quantitative genetics, vegetable breeding, selection methods, gain from selection

Abstract. **Variance components for 3 fruit yield and 5 fruit quality traits in 3 cucumber (*Cucumis sativus* L.) populations were estimated using a North Carolina Design I analysis. Three populations were studied (elite, medium base, and wide base), having been formed by intercrossing lines to produce 3 levels of genetic diversity. Families were evaluated in 1.5 × 1.5 m plots using once-over harvest at the stage of 15% oversized fruits. Heritabilities based on full-sib family selection for fruit yield ranged from 0.03 to 0.25, and for the fruit quality traits 0.00 to 0.30. The wide base population would be best for long-term selection for the traits studied, because it had the highest predicted means for all traits except percentage of culls, fruit shape, and overall performance after 15 cycles of full-sib family selection.**

Since the introduction of North Carolina Designs I, II, and III by Comstock and Robinson (1, 2) in 1948, these designs have been used by many plant breeders for estimating genetic variance components in plant populations. The N.C. Design I has been used successfully in obtaining estimates of genetic variance components for pickling cucumber populations. McCreight et al. (5) used a N.C. Design I to estimate the half-sib heritability of reducing sugars in cucumber. Expected gains per cycle of selection, based on half-sib progeny testing and half-sib testing, were 0.42 and 0.21 mg reducing sugar per g of fruit tissue, respectively. Smith et al. (8) estimated the variance components for 3 fruit yield and 5 fruit quality traits, and number of days to harvest in a monoecious pickling cucumber

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