Pollen Parent Effect on Outcrossing Rate, Yield, and Fruit Characteristics of 'Fuerte' Avocado

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Abstract. The effects of various pollen parents on outcrossing rates, yield, and fruit and seed weights were studied in a 'Fuerte' avocado (*Persea americana* Mill.). Isozyme analysis was used to identify the pollen parent of mature fruits. Cotyledons were assayed for five polymorphic enzyme systems: alcohol dehydrogenase, leucine aminopeptidase, malate dehydrogenase, phosphoglucotomutase, and triosephosphate isomerase. When sampling of fruits was done to a height of 2 m, percent of hybrids produced by 'Teague' and 'Topa-Topa' pollenizers was in the range of 30% to 40%. With 'Teague' as the pollenizer, 'Fuerte' yield increased by 30% in trees adjacent to the pollenizer. With 'Tops-Tops' as pollenizer, the yield was increased by 40% for trees adjacent to and at a distance from the pollenizer. 'Ettinger' trees planted at a distance of 30 to 50 m from 'Fuerte' were found to be the pollen parent of 2% to 14% of the progeny, thus supporting our previous conclusion regarding the high potency of 'Ettinger' as a pollen parent. 'Tops-Tops', 'Teague', and 'Ettinger' significantly increased fruit and seed weights of crossed compared with selfed 'Fuerte' fruits.

The synchronously dichogamous nature of the avocado flower and the existence of two flowering groups (A and B) promote cross-pollination (Bergh, 1977; Nirody, 1922; Stout, 1923). It has been assumed that interplanting of cultivars belonging to complementary flowering groups, whose blooming periods coincide, is a necessary and sufficient condition for successful pollination and fruit set (Gustafson and Bergh, 1966; Lee, 1974; Nirody, 1922; Papademetriou, 1976; Peterson, 1955). Indeed, the presence of complementary pollen parents was shown to increase avocado yields (Bergh, 1968; Bergh and Garber, 1964; Gazit, 1977; Gustafson and Bergh, 1966). However, it is well known that solid blocks of one cultivar can set consistently good crops (Davenport, 1986; Hodgson, 1947). The question as to whether interplanting of avocado cultivars is necessary for maximal production has thus far not been settled.

It became increasingly evident that different pollen parents, of the same flowering group and the same blooming period, may differ markedly from each other in their effect on fruit set and productivity (Bergh, 1967,

1975; Degani and Gazit, 1984; Gazit, 1977). Pollen donors may greatly influence the fruit set and survival of hand-pollinated young fruitlets (Argaman, 1983; Gafni, 1984; Gazit and Gafni, 1986). The use of isozyme techniques for parentage analysis of avocado fruitlets and fruits (Goldring et al., 1987; Torres, 1984; Vrecenar-Gadus and Ellstrand, 1985) had made possible the elucidation of the effect of the pollen donor on fruit set, abscission, and production (Degani et al., 1986, 1989; Goldring et al., 1987; Vrecenar-Gadus and Ellstrand, 1985).

Reliable information regarding the need for interplanting of pollen donors and the relative effectiveness of different pollen parents should be obtained from experimental orchards designed to explore the effect of various pollen parents on yields. We used such a 'Fuerte' orchard to study the effects of diverse pollen parents on outcrossing rates, yield, and fruit and seed characteristics using isozyme analysis.

The study was carried out with 'Fuerte'

fruits sampled from an 8-year-old avocado orchard in Kibbutz Daphna in the Hula valley of northern Israel. The trees were planted 6 × 7.5 m within and between rows, respectively. The 10-ha orchard was designed to study the effect of various pollen parents on 'Fuerte' yield. Rectangular pollination blocks were planted, each consisting of a central nucleus of two pollenizer trees surrounded by an inner belt of 10 'Fuerte' trees, an outer belt of 18 'Fuerte' trees, and a buffer belt of 26 'Fuerte' trees. The buffer belt was shared by several pollination blocks (Fig. 1). The five pollenizers and their flowering type were: 'Stewart' (A), 'Tova' (B), 'Teague' (B), 'Topa-Topa' (A), and 'Fuerte' (B). Four replicates were planted in a randomized block design, each consisting of the five pollenizers. 'Teague' and 'Topa-Topa' were chosen for this study because only their progeny could be readily identified by their heterozygosity for *Adh-2* (Table 1). The effect of 'Teague' and 'Topa-Topa' on 'Fuerte' outcrossing rate was determined in four replicated pollination blocks. In each block, at a height of up to 2 m, 50 fruit were randomly sampled from each of the following groups: the buffer belt trees, the outer belt trees, and the internal (facing the pollen parent) and external sides of the inner belt trees; in addition, 50 fruit were sampled from the top of the outer belt trees. Sampling was carried out at harvest time in Dec. 1985.

The orchard was surrounded by an 'Ettinger' (B) row planted as a windbreak; this 'Ettinger' row was separated from the orchard by a 7-m-wide road.

Extracts were prepared from the cotyledons of seed from each fruit (Torres, 1984) and analyzed for the enzyme systems: alcohol dehydrogenase (ADH) (EC 1.1.1.1) (Torres et al., 1978), leucine aminopeptidase (LAP) (EC 3.4.11.1) (Degani et al., 1986), malate dehydrogenase (MDH) (EC 1.1.1.37) (Degani and Gazit, 1984), phosphoglucotomutase (PGM) (EC 2.7.5.1) (Torres et al., 1978), and triosephosphate isomerase (TPI) (EC 5.3.1.1) (Goldring et al., 1987).

Effect of different pollen parents on hybrid percentage. The isozyme genotypes for the cultivars present in the Daphna orchard, as determined for the five enzymes systems used, are given in Table 1. 'Teague' and 'Topa-Topa' are heterozygous for *Adh-2* and 'Ettinger' for *Lap-2*, while 'Fuerte' is homozygous for both loci. Therefore, the pollen parent of 'Fuerte' cotyledons heterozygous for *Adh-2* is either 'Teague' or 'Topa-Topa';

Table 1. Flower group and isozyme genotypes of the six avocado cultivars present in the experimental orchard at Daphna, Israel.*

Cultivar	Flower group	<i>Adh-2</i>	<i>Lap-2</i>	<i>Pgm-1</i>	<i>Tpi-1</i>	<i>Mdh-1</i>
Fuerte	B	FF	FF	FS	FS	FS
Teague	B	FS	FF	SS	SS	FF
Topa-Topa	A	FS	FF	SS	SS	FS
Ettinger	B	FF	FS	FS	FS	SS
Stewart	A	FF	FF	FS	FF	FS
Tova	A	FF	FF	FF	FS	FS

*Abbreviations used refer to the relative mobilities of the isozyme coded for by the corresponding alleles: F = fast, S = slow. (See Torres et al., 1978).

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Table 2. Effect of various pollen parents on hybrid percentage in 'Fuerte' avocado fruits at several locations in the pollination blocks of 'Topa-Topa' and 'Teague'.

Location of trees	Calculated hybrid percentage ^a			
	Topa-Topa pollination blocks		Teague pollination blocks	
	Topa-Topa	Ettinger	Teague	Ettinger
Inner belt trees				
Internal side (<2 m height)	42 a	2 b	31 a	4 a
External side (<2 m height)	30 a	7 ab	12 b	4 a
Outer belt trees				
Lower part (<2 m height)	9 b	8 ab	6 c	14 a
Upper part (>2 m height)	29 a	9 ab	22 ab	11 a
Buffer belt trees	4 b	10 a	5 c	12 a

^aResults within a column followed by different letters differ significantly by Duncan's multiple range test, $P = 0.05$. Percentages are means of 200 (50×4) fruits taken from each location.

Table 3. Effect of pollen parents on 'Fuerte' yield in the Daphna orchard, 1985.

Pollination blocks ^a	Yield (kg/tree)	
	Location of trees	
	Inner belt	Outer belt
Teague	35.9 $\pm$ 0.9	26.0 $\pm$ 2.6
Topa-Topa	38.0 $\pm$ 9.6	38.5 $\pm$ 2.4
Fuerte	26.8 $\pm$ 4.2	29.6 $\pm$ 3.2

'Fuerte' cotyledons heterozygous for *Lap-2* are 'Ettinger' hybrids. Since only one half of the outcrosses can be definitely identified (FS offspring), the outcrossing rates are the observed rates multiplied by 2 (Table 2).

Since fruits from the upper parts of the tree canopy (up to 4 m) were difficult to reach and could not be properly sampled, most fruit sampling was done up to a height of 2 m. At this height, the percent of outcrossing in the pollination blocks of 'Topa-Topa' and 'Teague' was high in inner belt trees, especially on the side facing the pollen parent (internal side) (Table 2). With 'Topa-Topa' as a pollen parent, the percent of hybrids also was relatively high on the external side of the inner belt trees, was still noticeable in the outer belt trees, and decreased to a low value in the buffer belt trees. In contrast, when 'Teague' was the pollen parent, the percent of hybrids decreased markedly on the external side of the inner belt trees and was low in the outer and buffer belt trees. This pattern may have been the result of 'Teague' and 'Fuerte' belonging to the same flowering group, while 'Topa-Topa' belongs to the complementary flowering group (Ta-

ble 1). This assumption is consistent with earlier findings pointing to the advantage of using a pollen parent of a complementary flowering group in producing a high rate of outcrossing at large distances (Degani et al., 1989).

A pronounced difference was found in hybrid percentage between the lower and upper parts of the trees in the outer belt (Table 2). Compared to the lower part, hybrid percentage in the upper part was about three times greater with 'Topa-Topa' and about five times greater with 'Teague'. This difference points to the importance of adequate sampling from all parts of the trees.

'Ettinger' progeny was unequivocally identified since it was the only cultivar that was heterozygous for *Lap-2* (FS), while others were homozygous (FF). Although 'Ettinger' trees were located at a distance of 30 to 50 m from the buffer belt trees, they were more effective as a pollen donor than the much closer 'Teague' and 'Topa-Topa' trees (18.5 to 22.5 m away). This may have been due to the higher ratio of 'Ettinger' trees to pollinated 'Fuerte' trees, compared with the low ratio of two central pollenizer trees to buffer trees. It is also possible that fruitlets resulting from the 'Ettinger' pollen had a greater chance to survive. In this case, the massive abscission of fruitlets may transform a minor rate of pollination by 'Ettinger' to the observed 10% to 12% of 'Ettinger' hybrid fruits. It is possible that this mechanism might be responsible for significant hybrid production even in solid blocks of avocado, as was found by Vrecenar-Gadus and Ellstrand (1985).

In Dec. 1985, the 'Fuerte' fruits of the Daphna orchard were harvested and average

yields per tree in the inner and outer belt determined. 'Topa-Topa' appeared to be more effective than 'Teague' and 'Fuerte' as the pollen parent (Table 3).

'Teague' and 'Topa-Topa' cannot be considered as the best pollenizers for 'Fuerte' in the Hula Valley. Efforts should be directed to searching for other, more effective pollen parents for 'Fuerte' that will produce a higher hybrid percentage and higher yields. The use of isozymic techniques for parental analysis could shorten the time required to identify such pollenizers.

Effect of the pollen parents on seed and fruit weights. The effects on seed and fruit weights of the pollen parents 'Topa-Topa', 'Teague', 'Ettinger', and 'Fuerte' in the inner and outer belt of 'Teague' and 'Topa-Topa' pollination blocks are shown in Table 4. Selfed 'Fuerte' fruit consistently had the lowest fruit, seed, and pericarp weights, with a similar trend for fruit : seed ratio. 'Teague' and 'Topa-Topa' offspring were identified by their heterozygosity for *Adh-2*, and 'Ettinger' progeny by their heterozygosity for *Lap-2* (Table 1). Fruits were considered as 'Fuerte' selfs when they exhibited homozygosity for *Adh-2* (FF), as well as *Lap-2* (FF), and for *Tpi-1* (FF) or *Pgm-1* (FF), or for *Mdh-1* (SS) in 'Teague' pollination blocks. Identification of 'Fuerte' selfs is not conclusive, since homozygosity in the above mentioned isozyme systems does not exclude fruits that are 'Tova' and 'Stewart' progenies (Table 1). In addition, some of the fruits exhibiting homozygosity for *Lap-2* could actually be 'Ettinger' progeny, since a cross between a heterozygous ('Ettinger') and a homozygous ('Fuerte') plant is expected to yield heterozygous and homozygous offspring at a ratio of 1:1.

Out of 1600 fruits sampled in 'Teague' and 'Topa-Topa' pollination blocks, 221 were identified as progeny of 'Teague', 'Topa-Topa', or 'Ettinger'. In addition, 406 fruits were identified, with a high degree of certainty, as selfed 'Fuerte'. The individual identification of these fruits enabled us to determine the effect of pollen parents on seed and fruit weights.

To the best of our knowledge, the present study demonstrates for the first time the pollen parent's effect on avocado fruit and seed weights. The pollenizers 'Teague', 'Topa-Topa', and 'Ettinger' increased seed, fruit,

Table 4. Effect of pollen parents on fruit, seed, and pericarp weights in 'Fuerte' avocado.

Pollination blocks ^a	Pollen donor	Fruit identified (no.)	Fruit (g)	Seed (g)	Pericarp (g)	Seed : fruit wt ratio
Teague	Teague	62	266 a ^y	51 a	215 a	0.19 a
	Ettinger	30	263 a	45 b	218 a	0.17 b
	Fuerte	237	241 b	37 c	204 b	0.15 c
Topa-Topa	Topa-Topa	106	264 a	48 a	216 a	0.18 a
	Ettinger	23	251 a	40 b	211 a	0.16 b
	Fuerte	165	225 b	34 c	191 b	0.15 b

^aMeans of all fruits identified for a given pollen parent from four pollination blocks.

^yMeans within a column for each pollination block followed by different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

Fig. 1. Schematic map of two pollination blocks in the orchard at Daphna. 'Fuerte' trees (○); pollenizers (■, ▲).

and pericarp weights of 'Fuerte' fruits compared with selfed 'Fuerte' fruit (Table 4). The differences in fruit weight were not the result of different fruit loading, as fruits of different parentage were carried by the same trees. The effect of locations within the different belts was negligible and the mean values of the pollen donors adjusted for the location were almost identical to those of Table 4.

The lower fruit weight of selfed 'Fuerte' found in the pollination block of 'Topa-Topa', as compared to that found in the 'Teague' pollination block, is not surprising, in view of the higher fruit yield obtained in the 'Topa-Topa' pollination block.

The effect of pollen parents on seed weight may be important, especially with cultivars that tend to have a relatively large seed ('Fuerte'). 'Teague' and 'Topa-Topa' were responsible for an undesirable increase in seed percentage, up to values that may be unacceptable by consumers (Table 4).

The choice of a pollen parent may affect not only yield but also fruit and seed weights. These effects may be of economic importance. Thus, for avocado cultivars with small

fruits, such as 'Hass', it may be possible to use a pollenizer that increases fruit weight.

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