Pollen Parent Effect on the Selective Abscission of 'Mauritius' and 'Floridian' Lychee Fruitlets

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Abstract. Fruit produced by adjacent blocks of 'Mauritius' and 'Floridian' lychee (*Litchi chinensis* Sonn.) were sampled at four different stages of development and the embryos were analyzed for pollen parentage by phosphoglucose isomerase (PGI; EC 5.3.1.9) isozyme system. Hybrid percentage increased significantly from ≈ 5 weeks after fruit set to maturity as follows: from 29.5% to 76.3% in 'Mauritius' and from 74.2% to 92.5% in 'Floridian'. These findings clearly indicate selective abscission of selfed fruitlets. In 'Mauritius', yield was not related to the distance from the pollenizer block or hybrid percentage. In 'Floridian', yield of trees adjacent to the 'Mauritius' pollenizer was higher by 36% than that of trees at a distance of 24 m. The correlation between 'Floridian' yield and hybrid percentage tended toward significance ($r = 0.64$, $P = 0.08$). In addition, in both cultivars, fruit and seed weights were affected by the pollen parent: outcrossed fruit were heavier and contained heavier seeds than selfed ones.

Lychee appears to be self-compatible since monocultivar lychee blocks are capable of producing large crops in different regions of the world (Campbell and Malo, 1968; Chandler, 1958; Joubert, 1986; McConchie and Batten, 1989; Menzel and Simpson, 1990; Popenoe, 1920). However, using the phosphoglucose isomerase (PGI) isozyme system for parentage analysis in lychee, a significant correlation has been found between hybrid percentage and yield in a 'Floridian' block bordering a large 'Mauritius' block in Israel. Furthermore, cross-pollination was found to have a significant effect on fruit and seed weight. Outcrossed fruit were heavier and contained heavier seeds than selfed fruit (Stern et al., 1993).

Two distinct abscission waves of female flowers and/or fruitlets have been observed in 'Mauritius' and 'Floridian' lychee (Stern, 1992; Stern et al., 1994). At the end of the first wave, which lasted for $\gg 4$ weeks, only 4% to 10% of the 'Mauritius' female flowers set fruit. After a lull of ≈ 1 week, a second abscission wave began, at the end of which half of the fruitlets had survived. There was essentially no further fruit drop until harvest.

In this study we identified the pollen parent of fruitlets and fruit of 'Mauritius' and 'Floridian' and determined its effect on the abscission tendency of its progeny. For this purpose we followed the percentage of hybrids vs. selfs during fruit development using PGI isozymes as genetic markers.

Materials and Methods

Plant material. The study was carried out in a 12-year-old commercial lychee orchard in Kefar Hitim, located in the Lower Galilee. The orchard consisted of 10 rows, each containing 28 trees planted 6×6 m apart. The first five trees at the western end of each row were 'Floridian', the other 23, 'Mauritius'. The timing of the various flowering stages (male, female, and pseudohermaphrodite) was monitored every other day.

From May to July 1991, fruitlets and fruit were sampled at the following developmental stages: 1) before the start of the second wave of fruitlet abscission (fruitlet weight ≈ 1.5 g); 2) at the

beginning of the second wave of fruitlet abscission (fruitlet weight ≈ 2 g); 3) at the peak of the second wave of fruitlet abscission (fruitlet weight ≈ 3.5 g); 4) at harvest time (fruit weights ≈ 18 g and ≈ 19 g for 'Floridian' and 'Mauritius', respectively).

At stage 1, 'Mauritius' and 'Floridian' fruitlets were sampled from trees adjacent to their respective outcrossing pollen parent (pollenizer), on the side facing the pollenizer and on the opposite side. 'Mauritius' fruitlets were also sampled at two distances from the pollenizer — 16 trees away (96 m) and 22 trees away (132 m); 'Floridian' fruitlets were also sampled at a distance of 4 trees (24 m) from the pollenizer. Fruitlets were sampled in quadruplicate at each distance, using two trees as the replicate. Several hundred fruitlets were picked and scored for the presence of embryo and/or endosperm to obtain, for each distance, 80 fruitlets (20 per replicate) for the isozymic analysis. Trees at the borders of the orchard were not sampled. At harvest (stage 4), 80 fruit were sampled per distance from the same trees.

The distances for sampling fruitlets at stages 2 and 3 (Table 1) were chosen on the basis of the hybrid percentage found at the first sampling stage (Tables 2 and 3). For 'Mauritius', the opposite side of trees adjacent to the pollenizer (29.5% hybrids) was chosen, since in the more distant trees the outcrossing rate was very low. For 'Floridian', the fourth row from the pollenizer was chosen, since at this distance the outcrossing rate at stage 1 was not too high (74.2%), thus providing a convenient range for following the rate of hybrid formation during fruit development.

Isozyme analysis. Fruit and their seeds, and fruitlets were weighed before the isozyme analysis. Fruitlets were cut and the presence of discernible embryo and/or endosperm was determined. In young fruitlets, liquid endosperm was drawn with a micropipette and analyzed for PGI. In older fruitlets, the embryo and/or the endosperm were analyzed. In mature fruit, only the embryo was present and analyzed (Stern et al., 1993).

Results

Flowering phenology. Flowering data for 'Mauritius' and 'Floridian' are presented in Fig. 1. Within cultivars, some overlap occurred between the female bloom and the two pollen-releasing blooms (male and pseudohermaphrodite). Partial overlap occurred between the 'Mauritius' female bloom and the 'Floridian' male (M.) bloom, and full overlap occurred between the 'Floridian' female bloom and the 'Mauritius' pseudohermaphrodite (M.) bloom.

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Fig. 1. Flowering phenology of 'Mauritius' and 'Floridian' (Kefar Hitim, 1991.). Male flowering (M₁), female flowering (F), pseudohermaphroditic flowering (M₂). The peak of flowering is represented by the center of the rhombus; its edges represent the start and termination of flowering.

Table 1. Percentage of 'Mauritius' and 'Floridian' hybrid fruit at different stages of fruit development'.

Sampling stage	Sampling date		Fruit with embryo and/or endosperm (%)		Hybrids (%)	
	Mauritius	Floridian	Mauritius	Floridian	Mauritius	Floridian
Before start of 2nd abscission wave	26 May	5 June	100	49	29.5 a [*]	74.2 a
Start of 2nd abscission wave	2 June	10 June	100	71	35.2 ab	77.8 ab
Peak of the 2nd abscission wave	12 June	16 June	100	80	55.6 b	84.8 ab
Harvest	10 July	28 July	100	100	76.3 c	92.5 b

^{*}'Mauritius' fruit were sampled from the opposite side of trees adjacent to 'Floridian' trees. 'Floridian' fruit were sampled in the fourth row from 'Mauritius' trees.

^{*}Results (in columns) followed by different letters are significantly different by *t* test, *P* = 0.01. For each cultivar, 80 fruitlets or fruit were isozymically analyzed for each distance.

Presence of embryo and endosperm. The percentage of fruitlets containing embryo and/or endosperm was determined (Table 1). A marked and significant difference was found between the two cultivars. In 'Mauritius', no fruitlets without embryo and/or endosperm were found; whereas, in 'Floridian', the percentage of fruitlets with empty seeds was 51% before the start of the second abscission wave, 20% at the peak of this wave, and none at maturity (Table 1).

Hybrid percentage during fruit development. Percentage of hybrids was determined at the four stages of fruit development (Table 1). In both cultivars the rate of hybrids increased consistently and significantly with time. In 'Mauritius', the increase was rapid from the start of the second abscission wave to its peak. During this short 17-day period, hybrid percentage increased by 88%. This suggests that in 'Mauritius' most of the fruitlets that dropped during this period originated from self-pollination. The selective drop of selfed 'Mauritius' fruitlets continued beyond the abscission peak; thus, the rate of hybrids increased to 76% at harvest. In 'Floridian', similar behavior was observed, but the increase in hybrid percentage between sampling dates was smaller because of the initial high rate of hybrids (74.2%).

Effect of distance from the outcrossing pollen parent on hybrid percentage. The distance dependence of the effect of each pollen parent on hybrid percentage was determined at early fruit development (5-week-old fruitlets) and at fruit maturity (Tables 2 and 3). Percentage of hybrids in 'Mauritius' was determined at four distances from 'Floridian': in adjacent trees on the side facing 'Floridian' and on the opposite side, at 96 m and at 132 m. Percentage of hybrids in 'Floridian' was determined at three distances from 'Mauritius': on both sides of the adjacent trees and at 24 m.

In trees adjacent to those of the pollenizers, no significant difference was found between hybrid percentages on the facing

and opposite sides. In both cultivars, hybrid percentage increased from fruit set to maturity at all distances examined. In 'Mauritius', a pronounced decrease of hybrid percentage with increasing distance from the pollenizer was observed (Table 2). A similar trend was found for 'Floridian' (Table 3).

The effect of the outcrossing pollen parent on yield. In 'Mauritius', the yield per tree was not affected by proximity to 'Floridian'. Yield was uniform throughout the orchard, even though the rate of hybrids decreased from a value of 80% in trees adjacent to 'Floridian' to a value of 59% in the trees most distant from the pollenizer (Table 2). In contrast, 'Floridian' yield was affected by the distance from the pollenizer. Yield of 'Floridian' trees adjacent to 'Mauritius' was higher by 36% than that in the more distant trees (Table 3). The correlation between yield and hybrid percentage in this cultivar tended toward significance (*r* = 0.64, *P* = 0.08).

The effect of pollen parent on fruit and seed weight. In both cultivars, a clear and consistent correlation was found between pollen source and the weights of fruit and seeds (Table 4). Fruit originating from cross-pollination were heavier and contained heavier seeds than their corresponding selfed fruit. In 'Mauritius', the differences in the weights of fruit and seeds between hybrids and selfed fruit were significant; whereas, in 'Floridian', these differences were not significant, due to the very low number of selfed fruit found (*n* = 11).

Discussion

The effect of pollen parent on lychee fruitlet survival was elucidated by determining the percentage of hybrids and selfs at four stages of fruit development. Our findings (Tables 1–3) clearly show selective fruitlet abscission in 'Mauritius' and 'Floridian'

Table 2. Outcrossing rate and yield in 'Mauritius' in relation to the distance from 'Floridian'.

Tree (no.)	Distance from Floridian (m)	Hybrids %		Yield (kg/tree)
		5-Week-old fruitlets	Mature fruit	
1	6-Facing side	31.4 a A ^z	82.5 a B	
	6-Opposite side	29.5 a A	76.3 a B	45.1 a ^y
16	96	3.4 b A	20.0 b B	42.0 a
22	132	1.3 b A	5.0 b B	45.9 a

^zResults within columns followed by different lowercase letters differ significantly by Tukey's test, $F^* = 0.05$; results within rows followed by different uppercase letters differ significantly by ANOVA F test, $P = 0.001$.

^yAverage of both sides.

Table 3. Outcrossing rate and yield in 'Floridian' in relation to the distance from 'Mauritius'.

Tree (no.)	Distance from Floridian (m)	Hybrids (%)		Yield (kg/tree)
		5-Week-old fruitlets	Mature fruit	
1	6-Facing side	90.0 a A ^z	98.8 a B	
	6-Opposite side	84.5 ab A	95.0 ab B	32.8 a ^y
4	24	74.2 b A	92.5 b B	24.1 b

^zResults within columns followed by different lowercase letters differ significantly by Tukey's test, $P = 0.05$; results within rows followed by different uppercase letters differ significantly by ANOVA F test, $P = 0.001$.

^yAverage of both sides.

lychee. In both cultivars, selfed fruitlets abscised at a much higher rate than outcrossed ones. The advantage of hybrids apparently derives from the fact that selfed progeny often have less vigorous embryo than outcrossed progeny due to inbreeding depression (Charlesworth and Charlesworth, 1987; Sedgley and Griffin, 1989). Selective fruitlet abscission has been reported for other crops (Degani et al., 1986; 1989; Stephenson, 1981; Stephenson and Winsor, 1986).

In both cultivars, hybrid percentage consistently decreased with increasing distance from the pollenizer block (Tables 2 and 3). In 'Mauritius', the decrease was much more pronounced compared to our findings from the previous year in the same plot (Stern et al., 1993). This difference might be due to the fact that the overlapping period between the 'Mauritius' female bloom and 'Floridian' M₁ bloom was shorter in 1991 than in 1990 (Fig. 2) (Stern et al., 1993). Consequently, in 1991, the rate of cross-pollination at great distances from the pollenizer block was scant. The overlapping period between 'Floridian' bloom and the effective 'Mauritius' M₂ bloom was perfect in 1991 (Fig. 2) and much better than that found in 1990 (Stern et al., 1993). This is probably the reason for the higher percentage of hybrids found in the 'Floridian' block at all distances in 1991.

In 'Mauritius', yield was not related to the distance from the pollenizer block or hybrid percentage in either of the two consecutive years (Table 2) (Stern et al., 1993). On the other hand, during both years, yield of 'Floridian' trees adjacent to the pollenizer was considerably higher (36% to 40%) than that of trees 24 m away. In 'Floridian', correlation between yield and hybrid percentage was significant in 1990 and tended toward significance in the present study (Table 3) (Stern et al., 1993). 'Mauritius' and 'Floridian' apparently exhibit different responses to self vs. cross-pollination. In both cultivars there is an inherent advantage to cross-pollination: outcrossed fruitlets exhibit better survival rates and are heavier and contain heavier seeds than selfed ones (Tables 1 and 4). It seems that outcrossed fruitlets have a better chance of

Table 4. Fruit and seed weight in selfed and outcrossed 'Mauritius' and 'Floridian' fruit.

Fruit type	Fruit (no.)	Fruit (g)	Seed (g)	Seed (%)
<i>Mauritius</i>				
Selfed	173	18.4 a ^z	3.3 a	17.9 a
Outcrossed	147	19.6 b	3.7 b	18.9 a
<i>Floridian</i>				
Selfed	11	17.1 a	3.4 a	19.9 a
Outcrossed	228	19.3 a	3.9 a	20.0 a

^zResults within columns followed by different letters differ significantly by Tukey's test, $P = 0.05$.

outcompeting selfed fruitlets on tree resources. However, in 'Mauritius', enough selfed fruitlets reached maturity, thus, fruit yield was determined by the tree's capacity to bear fruit. In 'Floridian', on the other hand, most of the selfed fruitlets tended to abscise. This might be due to the fact that 'Floridian' selfed fruitlets, unlike 'Mauritius' selfed fruitlets, tend to undergo embryo degeneration; all 5-week-old fruitlets of 'Mauritius' had embryo and/or endosperm, whereas about half of the corresponding 'Floridian' fruitlets had none (Table 1). Most fruitlets with aborted embryos abscised and all of them were eliminated at maturity (Table 1). Apparently, inbreeding depression at the early embryo stage is much more debilitating in 'Floridian' than in 'Mauritius'. Similar variability among cultivars should be expected in other self-compatible species.

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