

Paternal parents enhance dispersal ability of their progeny in a wind-dispersed species, *Tecoma stans* L.

IN plants, as in animals, the participation of the maternal and paternal parent in reproduction is skewed with the maternal parent bearing a relatively larger investment cost¹⁻⁷. Under this scenario, it has been shown that the maternal and paternal parent would be in conflict with each other over the extent of resource allocation to their offspring^{1,3,4,8,9}. While the maternal parent would be selected to favour an optimal allocation of resources such that the marginal returns to her is maximized, the paternal parent would be selected to demand the maximum possible investments for their offspring^{1,3,10}. Uma Shaanker *et al.*¹ showed that such conflicts could potentially occur over a range of issues such as provision of resources in seed, number of seeds developing within a fruit (brood size), time of release from seed dormancy and seed and fruit dispersal¹¹⁻¹⁶. The conflict itself might be manifested proximately by the paternal parent by manipulating traits in the offspring. While paternal manipulation of offspring behaviour is well documented in animal systems, that in plants is poorly documented.

In this paper, we demonstrate the role of paternal parents in influencing the dispersal ability of their progeny in a wind-dispersed species, *Tecoma stans* L. We argue that the manipulation of offspring features is a manifestation of the conflict between the maternal and paternal parent over the dispersal efficiency of offspring. While maternal parent would seek to optimize the resource allocation to dispersal structures, the paternal parent would seek to increase the investments such that the fitness accrued through

increased dispersal distance is maximized.

The study was conducted on *Tecoma stans* L., (Bignoneaceae), a wind-dispersed shrub. We used the populations growing on the campus of the University of Agricultural Sciences, Bangalore, India. The fruit is a capsule containing 20–30 seeds bearing membranous wings; at maturity the capsule splits and the seeds are dispersed by wind¹⁷. A randomly selected plant was chosen as the ‘female’ parent and three other labelled plants from the population were chosen as pollen donors. Flowers on the female parent were emasculated in the evening and pollinated the following morning with either (a) pollen from the female parent (self-pollination), (b) pollen from the designated pollen donors, or (c) mixture of pollen grains from the three pollen donors. Care was exercised to ensure that abundant pollen grains were deposited on the stigma. The pollinated flowers were bagged and the fruits allowed to mature. At maturity the capsules from different pollination treatments were harvested, air-dried and the seeds collected (we failed to realize the mature capsules from the third donor cross because of premature abscission of the capsules). Weight of individual seed with the membranous wings was recorded and the surface area of the seed along with the wings was measured using a leaf area meter. Wing loading of the seed was computed as the ratio of surface area to weight of the entire seed^{1,18-24}. The membranous wings could not be extricated intact from the seeds and thus we could not arrive at separate estimates of the weight of seeds and their wings. As a

measure of the dispersal efficiency, the settling time of the seeds was determined by dropping the seeds from a height of 2.5 m in still air and then recording the time taken for the seeds to settle on the ground^{1,18,19,21,22}. The settling time is positively correlated with the horizontal dispersal distance^{1,18,19,21,22}.

The pollen donors and mixture of pollen donors were found to significantly influence the wing loading of seeds (Table 1 and Figure 1). While the selfed seeds had a wing loading of 10.83 mm²/mg, those sired by mixture of pollen donors had 16.28 mm²/mg. The settling time of the seeds was significantly positively correlated with the wing loading of the seeds, suggesting that seeds with a higher wing loading are likely to be dispersed to farther distances than those with low wing loading^{1,18,19,21-23} (Figure 2). The increased wing loading appears to be contributed by an increase in the surface area of the dispersal structure than due to a reduction in the seed mass; indeed the seed weights between most of the pollination treatments did not differ significantly (Tables 1 and 2). In other words, the increase in surface area of the seeds and their membranous wings caused by pollen donors appears to be due to a reallocation of the reproductive resources between the seeds and their wings. Such increased allocation to wings could reduce seedling vigour while enhancing the dispersal of seed.

The influence of pollen donors on F₀ seed properties is a well-documented phenomenon known as the ‘Xenia’ effect^{8,9,11,12,15,16,25,26}. In cotton, for instance, certain pollination treatments are

Table 1. Effect of pollination treatments on seed weight, seed surface area and wing loading in *Tecoma stans* (mean ± SE)*

Pollination treatment	N	Seed weight (mg)	Seed surface area (mm ²)	Wing loading (mm ² /mg)
F × F	203	8.24 ± 0.19	76.87 ± 1.96	10.83 ± 0.59
F × P ₁	325	7.19 ± 0.14	64.48 ± 1.12	10.63 ± 0.40
F × P ₂	80	7.74 ± 0.26	79.79 ± 1.21	13.16 ± 1.26
F × P ₁ + P ₂ + P ₃	157	8.18 ± 0.23	102.17 ± 1.62	16.28 ± 1.13

F: female parent; P₁, P₂, P₃ = pollen donors.

*All pair-wise comparison of means was analysed using Student's *t* test.

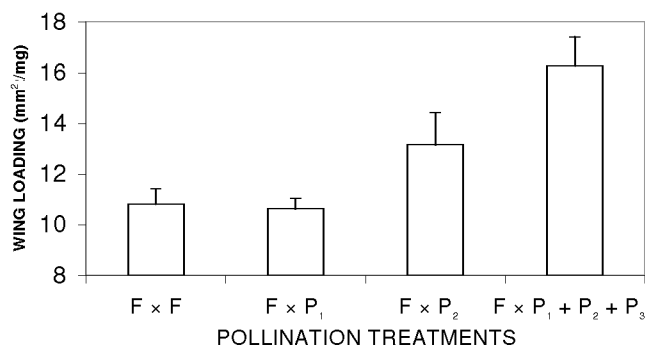


Figure 1. Effect of pollen donors on wing loading of seeds in *Tecoma stans*.

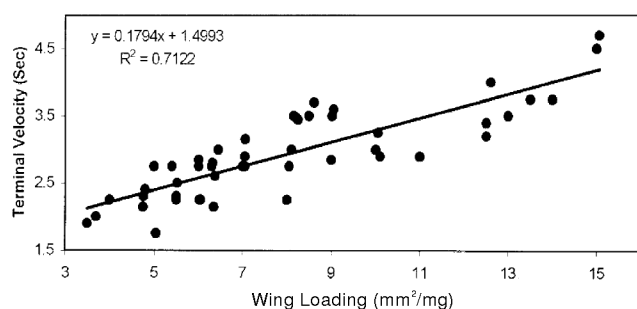


Figure 2. Relationship of wing loading of seeds with terminal settling velocity.

Table 2. Student's *t*-values for testing the differences among pollination treatments with respect to means of seed weight, seed surface area and wing loading*

Characters	Pollination treatments	F × P ₁	F × P ₂	F × P ₁ + P ₂ + P ₃
	Seed weight	F × F	4.43	1.41
	F × P ₁		1.74	3.83
	F × P ₂			1.19
Seed surface area	F × F	5.89	0.90	9.53
	F × P ₁		6.53	19.11
	F × P ₂			9.15
Wing loading	F × F	0.83	1.88	4.51
	F × P ₁		2.45	5.75
	F × P ₂			1.70

*Values in bold are significantly different at *p* = 0.05 level.

known to result in increased lint length, presumably leading to enhanced dispersal efficiency²⁵⁻³⁰. Such 'xenic' regulations by the pollen parents might, in fact, be a widespread feature to manipulate the offspring features and advance the interest of the paternal parent. However, it is intriguing to note that in this study, only one of the pollen donors used could elicit higher dispersal advantage and that the progeny from the mixture of pollen

donors behaved differently compared with pure (single) donor cross. Several earlier workers have indeed reported that the xenic effect in seeds is strongly controlled as an interaction between the male and female parents and that not all pollen parents need show the xenic effect^{9,13,31}. In *Mestha* for instance, Vasudeva¹³ had showed that the xenic effects were produced by the male parent AMC 40 only and not by HC 583. The different effects

of pollen donors when in mixture compared to in single pollen donor crosses have been earlier reported by Radha *et al.*³², in *Vigna unguiculata*. The pollen donors when in a mixture of genetically different pollen load yielded significantly different seed weights compared to when they were applied singly. They conjectured that, such pollen load-dependent behaviour of pollen grains could be best explained by yet undescribed interaction between the sibs and non-sibs within a legume pod. In other words, they argued that the seeds developing within a pod could distinguish between the sibs and non-sibs.

Though enhanced dispersal features may favour increased and similar dispersal distance of propagules in the self and crossed seeds, it need not translate into an equivalent fitness gain for both the parents. By enhancing the dispersal features, the male parent might gain more through increase in its individual fitness than the female parent, where the inclusive fitness of the parent could in fact decrease if increased dispersal were to be at the cost of reduction in some parameter of the fitness of the sibs. In fact, Uma Shaanker *et al.*¹ argued that while maternal parent would also benefit by enhanced dispersal, certain features such as packing cost of the seeds in fact can lead to a potential conflict between the maternal and paternal parent over the selection for dispersal features.

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B. MOHAN RAJU¹
K. N. GANESHAIAH^{2,3}
R. UMA SHAANKER^{1,3*}

Departments of ¹Crop Physiology and
²Genetics and Plant Breeding,
University of Agricultural Sciences,
GKVK Campus,
Bangalore 560 065, India
³Jawaharlal Nehru Centre for Advanced
Scientific Research, Jakkur,
Bangalore 560 065, India
*For correspondence
e-mail: rus@vsnl.com