

Differential rates of seed abortion among trees of *Dalbergia sissoo* : Role of post-dispersal sibling competition

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It has been suggested that production of a high frequency of few-seeded pods in most trees of *Dalbergia sissoo* is due to the enhanced dispersal efficiency and reduced sibling competition among the seeds of such pods. However, a few trees exhibit a relatively low seed abortion and hence, a relatively lower frequency of one- and two-seeded pods. Such reduced seed abortion in one such tree (T-9) is shown to be due the lack of establishment of a strong dominance by the early fertilized over the late fertilized ovules. Unlike in the pods of the normal trees, the early fertilized ovules in this tree do not inhibit the metabolic activity of the late fertilized ovules. We show that such reduced abortion in such trees is favoured due to reduced gains to the survivor in the few-seeded pods. While the dispersal advantage of the single-seeded over many-seeded pods in this tree remains the same as in others, the post-dispersal negative interactions among the seeds of a pod are significantly lesser in it than that in the pods of normal trees. We discuss these results in the context of sibling rivalry among, and inclusive fitness of, the seeds developing within the pods of *D. sissoo*.

IN certain multiovulated species where whole fruit or a part thereof is dispersed through wind or water, seed abortion occurs despite pollen and resource availability¹⁻³. Consequently, these species frequently exhibit a highly positively skewed distribution of seeds per fruit where the frequency of few-seeded fruits is more than that of the many-seeded fruits^{1,2}. Reduced seed number in fruits consequent to such intra-fruit abortion enhances the dispersal efficiency of the survivor owing to decreased wing loading of the pods⁴⁻⁶ and reduces post-dispersal competition among the sibs of a fruit for resources^{2,5,7}. Ganeshaiyah and Uma Shaanker¹ and Uma Shaanker *et al.*² have hence argued that such seed abortion has been selected in these species because it increases the dispersal advantage and reduces the post-dispersal sibling competition for the seeds that eventually survive in the fruits. They have also suggested that such intra-fruit seed abortion could hence be a manifestation of the fratricidal strategy of the developing seeds to eventually gain these advantages.

This argument predicts that the extent of intra-fruit seed abortion would be in proportion to the gain the eventual survivor in the pod accrues either through the increased dispersal advantage and/or through reduced post-dispersal sibling competition for resources. In other words, in situations where the dispersal advantage gained due to the reduced seediness of fruits is high, and/or when post-dispersal competition among the seeds of a fruit is intense, the extent of intra-fruit seed abortion and hence the extent of bias towards few-seeded pods is expected to be high. In this paper we offer evidence of this prediction.

System

Trees of *Dalbergia sissoo* bear indehiscent, flat pods that are dispersed through wind. Ganeshaiyah and Uma Shaanker¹ have shown that these pods exhibit a highly positively skewed frequency distribution of seed numbers in them with about 70–80% having one seed, 10–15% two and the rest with three or four seeds (Figure 1). Among these, the few-seeded (especially one-seeded)

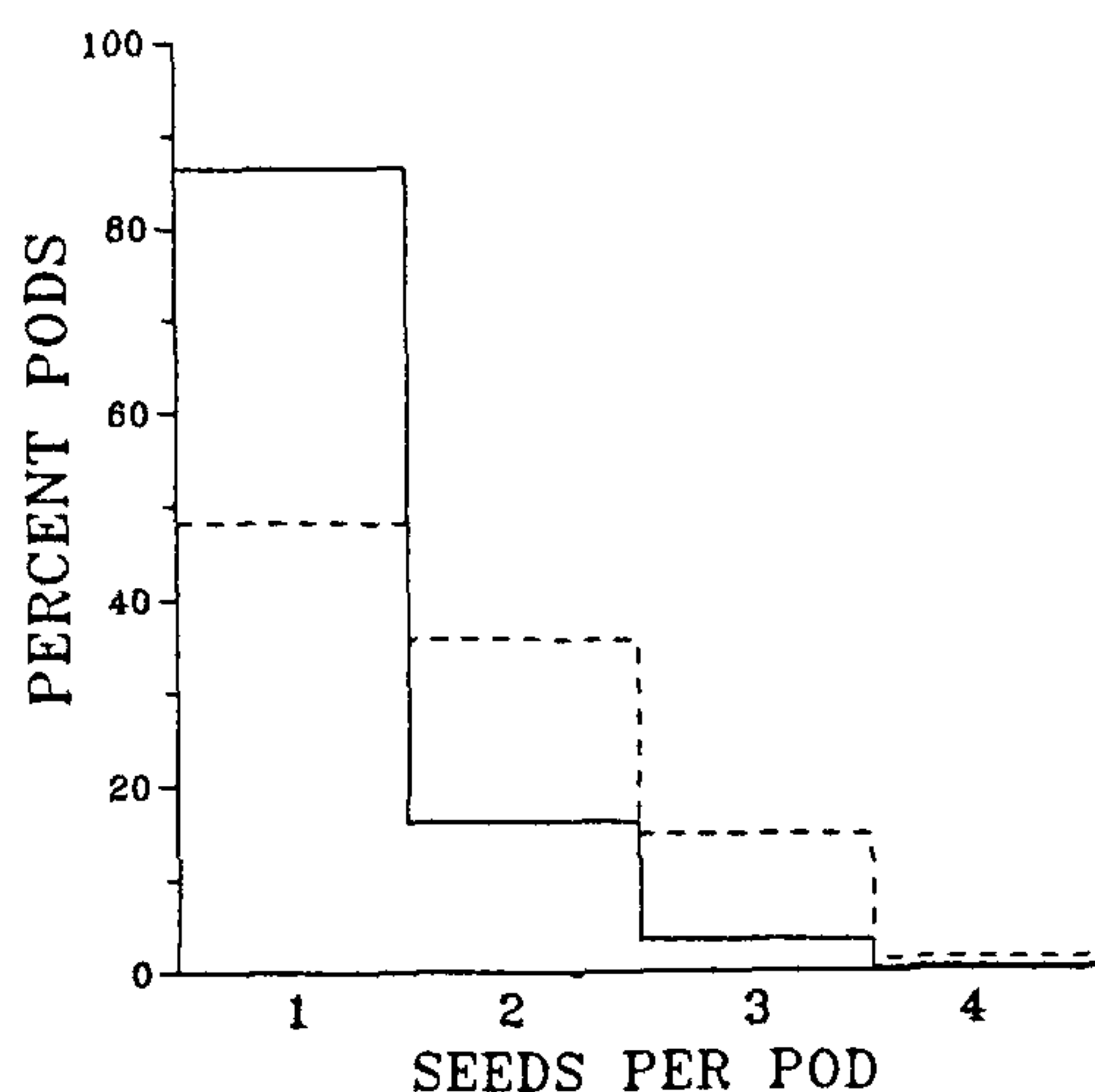


Figure 1. Frequency distribution of seeds per pod, data pooled from 10 trees (solid line; $n = 1465$ pods) are compared with the data on T-9 (dotted line; $n = 224$ pods). T-9 differed significantly (at 5%) from all other trees in frequency distribution (KS test)

†For correspondence.

Pods have an increased dispersal advantage owing to their reduced wing loading compared to many-seeded (two, three and four) pods. Ganeshiah and Uma Shaanker¹ have also shown that the formation of few-seeded pods is not due to pollen and resource limitation. Rather, such a high frequency of few-seeded pods is attributed to an intense intra-fruit abortion of ovules following their fertilization.

During these studies we observed that about 5% of the trees (7 out of the 150 trees examined) differ from the normal trees in that they bear less than the normal frequency ($\approx 70\%$) of single-seeded fruits. The present study compares the normal trees of *D. sissoo* with one of such trees (T-9) that exhibited unexpectedly low seed abortion and hence a relatively low frequency (50%) of single-seeded pods. We argue that the advantages to the survivor of the intra-fruit seed abortion in such trees should be less than those in other normal trees and that such relatively reduced gains to the survivor favour reduced intra-fruit abortion, resulting in an increased seed number per pod in these trees.

Mostly, two trees, viz. T-1 (representing the 'normal' trees) and T-9 (representing the 'deviant' trees), were sampled for studying different parameters. These two trees are located at Hebbal (old campus), University of Agricultural Sciences, Bangalore, and are separated by a distance of nearly 1 km; there were no noticeable differences in their growth environment nor in their gross morphological features. Whenever necessary data on other trees were also gathered.

Methods

Frequency distribution of seeds per pod

Mature pods from trees T-1 and T-9 were collected in two seasons and the seed numbers in them counted. The frequency distributions of the two trees were compared using the Kolmogorov-Smirnov (KS) test and their mean seeds per pod using the *t*-test.

Wing loading

Dry pods of T-1 and T-9 (Table 2 for sample size) were collected and dried further at 50°C for 3 days. Each pod was weighed and the pod surface area recorded using a Licor leaf area meter. The wing loading was computed as the ratio of weight to surface area of the pod.

Pattern of seed abortion

Our studies have shown that the subordinate ovules at the base of the pod are aborted because their metabolic

activity is highly suppressed by the dominant ovules at the stigmatic end. To examine this process, young pods aged 3 days after fertilization, in which abortion had not yet set in, were sampled for trees T-1 and T-9. From these pods the dominant (first two ovules from the stigmatic end) and subordinate ovules (the rest from the peduncular end) were excised and implanted in cavity slides containing 10 μ l of 25 μ Ci ¹⁴C sucrose and incubated for 12 h at 75% RH and 30°C. The ovules were then washed thoroughly in distilled water for 3 h, weighed and ground in Bray's solution and their radioactivity estimated by scintillation counter⁸.

Post-dispersal sibling competition

A set of two- and three-seeded dry pods of trees T-1 and T-9 were cut (see Table 4 for sample size) at the septa region and these segments (hereafter called 'separate') containing one seed each was sown at a density of 150 seeds/m² in sand beds. Another set of two- and three-seeded 'intact' pods were also sown at the same density. The emergence percentage of seeds after two weeks and seedling height and weight after a month were recorded for each seed.

Results

Differential seed set among trees

Most of the *D. sissoo* trees exhibit a highly positively skewed distribution of seeds per pod (Figure 1; pooled over 10 randomly selected trees). For clarity we have compared the data on a set of five trees with that of the unusual tree T-9 in Table 1 (see also Figure 1). Clearly, all the 'normal' trees bear 70–80% single-seeded pods while T-9 bears only 48% single-seeded pods. The average number of seeds per pod of the 'normal' trees is 1.23 ± 0.012 ($N = 10$ trees) with a skewness coefficient of 2.24; the mean number of seeds per pod in T-9 is

Table 1. Mean seed number, percentage pods with single seed and skewness coefficient of six trees of *D. sissoo*

	Trees						
	T-1	T-2	T-3	T-4	T-5	Pooled	T-9
Seeds/pod	1.18	1.18	1.16	1.35	1.21	1.23	1.69
SE (\pm)	0.025	0.038	0.025	0.044	0.036	0.012	0.051
Sample size (pods)	328	115	306	210	167	1465	224
Percentage pods with single seeds	84.45	82.60	87.25	71.42	81.43	86.55	48.2
Skewness coefficient	2.66	2.05	2.84	1.91	2.09	2.24	0.77

T-9 differed significantly (at 5%) from all other trees for the frequency distribution (KS test)

significantly higher ($\bar{x} = 1.69 \pm 0.051$; $P < 0.01$) with a skewness coefficient of 0.77.

Proximate causes of differential seed set

The increased seed set of T-9 cannot be attributed to the differences in the ovule numbers per ovary of the trees. The mean numbers of ovules per ovary for the two trees were similar ($\bar{x} = 4.57 \pm 0.104$ for T-1 and 4.59 ± 0.091 for T-9) and the frequency of ovules per ovary showed normal distribution for both trees (skewness coefficient of 0.326 for T-1 and 0.225 for T-9).

The extent of positive skewness for the frequency distribution of seed numbers per pod within each tree is consistent over seasons (Table 2), suggesting that these patterns may not be environmentally influenced and may rather be a consequence of certain internal regulation over seed set. Earlier studies^{1,8} have shown that poor seed set in *D. sissoo* is not due to pollen or resource limitation nor due to lack of fertilization of ovules. Thus, the increased seed set in T-9 cannot be attributed to elevated or enhanced pollen and/or resource status of the plant. The tree occurred within a few meters of T-1 and other trees that exhibited highly positive skew of seeds per pod and hence habitat differences could not be contributing to the enhanced seed set in its pods.

Reduced seed set in *Dalbergia* is shown to be a result of the establishment of dominance of the stigmatic ovules over those at the base owing to their head-start in fertilization^{1,8}. These dominant ovules apparently produce certain chemical(s) that inhibit the metabolic activity of the subordinate ovules at the base, hindering their development^{1,8}. Consequently, the ovules at the base are starved and are eventually aborted. In this context, the relatively reduced seed abortion in T-9 could be due to reduced dominance established by the stigmatic over peduncular ovules. The ¹⁴C sucrose uptake activity of the stigmatic ovules is almost equal to that of peduncular ovules in T-9 (ratio = 0.98; Table 3)

while it was always more than unity in T-1. In other words, in T-9 the basal and stigmatic ovules are equally metabolically active; the stigmatic ovules do not establish dominance in this tree as they do in T-1. Such a lack of dominance allows the developing ovules (embryos) at the base to be metabolically active over a long period during the initial stages of development, resulting in their better survival, establishment and maturation to seed. It is, however, not clear if such a lack of dominance is due to enhanced synchrony in the sequence of fertilization of ovules in T-9 compared to other trees.

Adaptive basis of differential seed abortion

Trees did not differ in wing loading of the pods (Table 2); wing loading of the single-seeded pods of both the trees are equal and less compared to their respective two- and three-seeded pods. Thus, the dispersal advantage of single-seeded pods over many-seeded pods is expected to favour abortion in T-9 also to the same extent as it would in T-1 and other normal trees.

The seedlings emerging from 'separated' seeds of two- and three-seeded pods of T-1 weighed significantly more and grew taller compared to those of the 'intact' pods (Table 4), suggesting that there is an intense post-dispersal interaction among the seeds of a pod of this tree. However, in T-9 the 'separated' and 'intact' seeds of both two- and three-seeded pods did not differ in their seedling height and weight, suggesting a lack of negative interactions among the seeds of the pod in T-9. Thus, the extent of post-dispersal sibling competition is very less among the seeds of a pod in T-9 compared to those of T-1. In other words, the gains to the surviving offspring by aborting the sibs in the pods are less in T-9 compared to those in T-1 and this might select for reduced abortion in the former tree. These differences between the trees in the post-dispersal interactions among the seeds of their pods could not be attributed to the differences in the weights of seeds; the two trees showed similar seed weights (Table 5).

Table 2. Frequency distribution of seeds per pod and wing loading in T-1 and T-9

Seeds per pod	T-1				T-9			
	Percentage pods		Wing loading* (g cm ⁻²)		Percentage pods		Wing loading* (g cm ⁻²)	
	Season 1	Season 2	n	$\bar{x} \pm SE$	Season 1	Season 2	n	$\bar{x} \pm SE$
1	84.45	83.67	20	16.33 ± 0.32 ^a	48.21	49.20	30	16.43 ± 0.27 ^a
2	13.41	12.92	20	18.52 ± 0.36 ^b	35.71	33.58	40	18.09 ± 0.17 ^b
3	1.82	2.72	6	20.25 ± 1.05 ^c	14.73	14.62	24	18.86 ± 0.25 ^c
4	0.30	0.68	—	—	1.33	2.56	—	—
Sample size	328	147			224	390		

T-1 Season 1: 3 March 1990; Season 2: 12 March 1992 (KS test between seasons for T-1: $D_{max} = 1.28$; NS).

T-9 Season 1: 21 March 1992; Season 2: 27 October 1992 (KS test between seasons for T-9: $D_{max} = 1.23$; NS).

KS test between the T-1 and T-9 for data pooled over seasons within each tree: $D_{max} = 0.35$, $P = 0.0001$.

*The wing loading values were compared within each tree; mean values with different superscripts differ significantly at 5%.

Table 3. ^{14}C sucrose uptake by stigmatic (stig) and peduncular (ped) ovules in two trees of *Dalbergia* three days after fertilization

Tree	Experiment 1			Experiment 2			Mean ratio
	<i>n</i>	cpm/ovule	Ratio (stig/ped)	<i>n</i>	cpm/ovule	Ratio (stig/ped)	
T-1							
Stigma	3	287.50	1.75	3	255.80	2.07	1.91
Peduncle	3	164.40		3	123.40		
T-9							
Stigma	3	198.80	0.98	3	133.80	0.98	0.98
Peduncle	3	200.90		3	136.00		

n = no. of replications; each replication had 20 ovules.

Experiments 1 and 2 refer to two sets of experiments conducted on two different days.

Table 4. Effect of seed number per pod on post-dispersal seedling competition in two trees

	Mean germination (% \pm SE)*				Mean seedling height (cm \pm SE) [†]				Mean seedling dry wt (g \pm SE) [‡]	
	<i>n</i>	Intact	<i>n</i>	Separate	<i>n</i>	Intact	<i>n</i>	Separate	Intact	Separate
T-1										
2-seeded pods	80	52.50 \pm 5.62 ^a	80	52.50 \pm 5.62 ^a	42	43.45 \pm 3.30 ^a	42	57.45 \pm 4.07 ^b	3.28 \pm 0.46 ^a	6.08 \pm 1.80 ^b
3-seeded pods	60	43.33 \pm 6.45 ^a	60	43.33 \pm 6.45 ^a	26	43.81 \pm 4.11 ^a	26	79.60 \pm 7.48 ^b	2.93 \pm 0.51 ^a	14.33 \pm 0.51 ^b
T-9										
2-seeded pods	40	92.50 \pm 4.22 ^a	40	67.50 \pm 7.50 ^b	37	44.16 \pm 2.33 ^a	27	46.04 \pm 2.58 ^a	2.18 \pm 0.23 ^a	2.53 \pm 0.27 ^a
3-seeded pods	30	63.33 \pm 8.96 ^a	30	60.00 \pm 9.11 ^a	18	42.72 \pm 2.88 ^a	19	39.05 \pm 2.62 ^a	1.81 \pm 0.30 ^a	1.45 \pm 0.22 ^a

n = number of seeds

*Mean values with similar superscripts within each row are not significantly different for mean seed germination

[†]Mean values with similar superscripts within each row are not significantly different for mean seedling height

[‡]Mean values with similar superscripts within each row are not significantly different for mean seedling dry weight.

Table 5. Seed weights in mg (\pm SE) of two- and three-seeded pods of the two trees

Trees	<i>n</i>	Position of the seed in the pod from the stigma		
		1	2	3
Two-seeded pods				
T-1	50	22.14 \pm 0.17	20.78 \pm 0.17	
T-9	40	21.80 \pm 0.33	21.53 \pm 0.44	
Three-seeded pods				
T-1	11	21.09 \pm 0.42	18.18 \pm 0.42	18.09 \pm 0.61
T-9	20	19.80 \pm 0.54	20.95 \pm 0.59	19.35 \pm 0.37

n = number of pods

Discussion

The results support the prediction that the abortion of the seeds in the pods of *D. sissoo* is in proportion to the gain the survivor accrues. In T-1 the seeds surviving following intra-fruit seed abortion derive increased dispersal advantage and also avoid the post-dispersal competition or negative interactions in their growth by other sibs of the pod. Selection thus favours the offspring to

be the lone survivors and hence it is argued that they resort to abort the other offspring of the pod (interpreted as 'fratricide' by Uma Shaanker *et al.*²). But in T-9, though the surviving offspring of the few-seeded pods gain dispersal advantage, they do not seem to suffer from the post-dispersal negative interactions from the sibs of the pod, at least during the early stages of the growth and establishment of the seedlings. Thus, the effective (cumulative) sibling competition among the members of the same fruit is much less in this tree than in others. Consequently, offspring in T-9 are selected to abort their sibs to a lesser degree than those in T-1. Such reduced fratricide among developing seeds results in a lower frequency of single-seeded pods. It would be worthwhile, however, to examine the heritability of this trait in tree T-9 as a test of the above argument. We have embarked on a long-term monitoring of the seed number per pod of progenies of tree T-9.

The process underlying the existence (in T-1), or lack (in T-9), of such post-dispersal negative interactions among the growing seeds of a pod is not clear. It certainly is not due to any differences in the seed weights and is probably due to genotypic differences

in their pattern of post-dispersal interactions. It is likely that in 'intact' pods of T-1 the germinating seeds diffuse out growth-retardant(s) to other seeds through the xylem vessels connecting them in the dry pod so as to reduce the competition for resources and space at later stages. The diffusion of such chemicals might be hindered or blocked in the vessels in T-9, probably by the physical barriers developed during the late stages of pod maturation. Such a phenomenon could have been selected as a maternal counterstrategy so as to avoid competition or any negative interactions among her offspring and thus to increase her own inclusive fitness.

At the same time, the possibility that the extent of intra-fruit seed abortion and post-dispersal negative interactions is linked to the genetic relatedness among the offspring cannot be ruled out. Uma Shaanker *et al.*² have argued that offspring-driven seed abortion could be reduced when the sibs in a pod are highly genetically related. Though this leads to increased number of seeds per pod, and hence the survivors suffering a loss in dispersal advantage, their inclusive fitness could still be enhanced through the genetically related sibs that survive with them in the pod. That there is a reduced dominance hierarchy among the developing seeds in T-9 (indicating reduced 'fratricide') is suggestive of increased genetic relatedness among them. How such differences in the genetic relatedness arise among trees is not immediately clear but could be a consequence of the differences in their levels of outbreeding.

Finally, the differences in the extent of seed abortion between the trees T-1 and T-9 could merely emerge from the underlying differences in the sink-drawing ability (SDA) of their ovules as predicted by Ganeshiah and Uma Shaanker^{9,10}. They have shown that starting

with identical ovules, differential development (asymmetry), and in extreme cases abortion, of ovules could arise through a process of 'self-organized' flow of resources wherein, purely due to a random drift (flow) of resources to one of the ovules and their subsequent autocatalytic positive feedback, a dominance hierarchy sets in; the extent of asymmetry was shown to be nonlinearly related to the SDA of the ovules^{9,10}. Accordingly, they^{9,10} predicted that species/individuals with higher SDA would exhibit a higher extent of asymmetry or seed abortion. In this context, it is likely that the observed differences in seed abortion between trees T-1 and T-9 is due to their differences in SDA *per se*.

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