Components of Fecundity and Abortion in a Tropical Tree, *Dahlstedtia pentaphylla* (Leguminosae)

Simone de Pádua Teixeira[1*]**, Rodrigo Augusto Santinelo Pereira**[2] **and Neusa Taroda Ranga**[3]

[1]*Departamento de Ciências Farmacêuticas; FCFRP; Universidade de São Paulo; Av. do Café, s/n; 14040-903; spadua@fcfrp.usp.br; Ribeirão Preto - SP - Brasil.* [2]*Departamento de Biologia; FCCLRP; Universidade de São Paulo; Av. Bandeirantes, 3900; 14040-901;Ribeirão Preto - SP - Brasil.* [3]*Departamento de Zoologia e Botânica; IBILCE; Universidade Estadual Paulista; 15054-000; São José do Rio Preto - SP - Brasil*

ABSTRACT

Studies were conducted on pollination and patterns of fruit and seed production to assess the potential factors causing high fruit and seed abortion in Dahlstedtia pentaphylla (Leguminosae) through analyses of relationships between flower position in the inflorescence and ovules and seeds within ovaries and fruits, and flower, fruit and seed abortion. No differences were found in pollination and fruit set as a function of inflorescence position. There was no relationship, neither between degenerating ovules and their position within the ovary, nor between developing seed and fruit position. Maternal resource limitation related to fruits and embryos, due to the high cost of fruit production and seed maturation, was one of the factors that led to a high abortion rate in D. pentaphylla.

Key words: Abortion, Atlantic Rainforest, *Dahlstedtia pentaphylla,* Leguminosae, reproduction

INTRODUCTION

In the majority of flowering plants, few of the ovules result in viable seeds. Some ovules do not develop due to the lack of fertilization and for those that are fertilized, embryos may be aborted during embryogenesis (Sedgley, 1980; Bawa and Webb, 1984). The occurrence of abortion is not exclusive of the legumes, but this family offers convenient opportunities for abortion studies because of the linear arrangement of ovules within the ovary, which permits the study of gradients of seed formation within fruits (Hossaert and Valéro, 1988). Several factors can lead to flower and fruit abortion (Lloyd, 1980; Stephenson, 1981; Bawa and Webb, 1984). Among these are quantity of pollen grains deposited on the stigmas (Mogensen,

1975) and ovule competition for the resources required for seed development (Lloyd, 1980). Such competition combined with resource limitation, could lead to the selective abortion of ovules and seeds (Hossaert and Valéro, 1988).

Abortion of embryos that occur farthest from the stigma is the most common pattern found in legumes (Bawa and Buckley, 1989). In this case, ovules farthest from the stigma could be the last to be fertilized just because of their position. Even if the genetic traits and capacities of pollen grains were kept constant and similar amongst all the pollen grains fertilizing a flower, the ovule that is fertilized first will have a head start in drawing resource. Such a head start could play a highly significant role in that ovule becoming the dominant embryo and result in the other ovules

---

[*] Author for correspondence

being starved to death or not get enough resource to develop into large seeds. If basal ovules have a spatial advantage (Horovitz et al., 1976; Heering, 1994) the stigmatic ovules could have a similar advantage of being the first to be fertilized and establish a stronger resource sink. Such strong resource sink in first fertilized ovule at the stigmatic end leading to a high frequency of pods with stigmatic seeds has been shown in many different species (Lee and Bazzaz, 1982, Hossaert and Valéro, 1988, Arathi et al., 1999).

These arguments were tested in the present study in the neotropical legume species *Dahlstedtia pentaphylla* (Taub.) Burk. Representatives of this species have been registered from Brazil, especially in the Atlantic Rainforest (Geesink, 1981), but in a low density, as revealed by a phytosociological study from the Southeastern Atlantic Forest (Guilherme et al., 2004), suggesting that *D. pentaphylla* was a rare species. Preliminary observations showed that fruit and seed sets were low in spite of the production of numerous flowers. Moreover, many fruit and seed were aborted. The components of fecundity (pollination and patterns of fruit and seed production) were examined in *D. pentaphylla* to assess the potential factors causing high fruit and seed abortion in its representatives. The following questions were addressed: Does pollen deposition vary among flowers located in different positions of the inflorescence? Are ovule fertilization and seed development dependent on positions within the ovary and fruit? Are positional patterns correlated to the distribution patterns of maternal resources or to pollen performance?

MATERIAL AND METHODS

Study species
Representatives of *D. pentaphylla* are shrubs or small trees (3-4m), with self-compatible (Teixeira et al., 2001), hummingbird-pollinated flowers. The number of flowers per inflorescence ranged between eight and 35, and flowers last two or three days. Anthesis begins basally in the inflorescence, characterizing acropetal maturation. These plants have been recorded from Brazilian Atlantic Forest, but only in eastern São Paulo, Paraná and Santa Catarina States. They occur in moist habitats, inside the forest, as isolated plants, with no large populations. Only a few individuals have been found in flower (7 of 90 plants) and fruit (2 of 90 plants)

throughout a six-year period of field observations (1993-1995 and 1996-2000). Most of them showed vegetative propagation (Teixeira and Ranga, 2004). Because flowering and fruiting were rare events in the species natural habitat, this study was carried out on cultivated plants in Campinas (22°54'S, 47°03'W) and Piracicaba (22°43'S, 47°38'W), São Paulo State, Brazil. Vouchers are in the Herbarium of Universidade Estadual de Campinas (UEC), under numbers S. P. Teixeira s/n° (UEC 89076, 109265, 109535 and 109536) and N. M. Ivanauskas 83.

Fruit and seed set
All flowers from four plants cultivated in Campinas were marked in August 1998 (open pollination) and the developing fruits were counted one, two and four months later, because previous observations showed that it took five months for fruits to mature. In August 2000, this experiment was repeated on five plants from Campinas. The number of ovules per ovary in 18 flowers per plant (four plants) and the number of seeds per fruit in 11, 12 and 49 fruits collected from three plants (total of 72 fruits) were counted. The length and maximum width of eight mature fruits and 10 mature seeds were measured for two plants. It was not possible to measure more samples because only a few fruits and seeds reached maturity.

Flower position vs. pollen deposition and fruit set
Open-pollinated flowers were collected two days after anthesis and were assigned to three categories, according to their position in the inflorescence: apical, median and basal. Three flowers per position were utilized on nine inflorescences from three individuals. Germinating pollen grains, stained with acetocarmine, were counted on each stigma, with the use of a compound microscope. All developing fruits on three plants were scored and the number of fruits per position in the inflorescence axis on each plant was counted (apical, median and basal).

Within-ovary position vs. degenerating ovules
Ovaries from 10 flowers from each of five plants were collected after 72h (open pollination). Ovules within the ovary were cleared in Herr's Fluid (Herr, 1971) and examined to verify the position of degenerating ovules using Nomarski Differential Interference Contrast (DIC). Ovules

that emitted fluorescence indicated the presence of callose and were considered degenerated (Vishnyakova, 1991). A period of 72h was required for callose deposition to occur in ovular maternal tissues, which indicated abortion of both fertilized and unfertilized ovules (Teixeira et al., 2001). For simplicity, both fertilized and unfertilized ovules were called ovules in the results.

Within-fruit position vs. seed abortion
Developing fruits, with nearly 5.5 cm length, were collected and the position of aborted or developing seeds was examined (10 fruits per plant, from 10 plants).

Data Analyses
Pollination and fruiting patterns in relation to position in the inflorescence was analyzed by ANOVA (Zar, 1996). A partially nested ANOVA were performed with plant and position as fixed, crossed factors and inflorescence, a random factor, nested within plant. To calculate *F*-ratios, plant MS was tested against inflorescence nested within plant MS, and position MS was tested against position x inflorescence within plant MS. This latter interaction was tested against the error.

Counts (pollen grain and fruit number) were square root transformed in order to make variances independent from means and to correct departures from normality (Zar, 1996). In these analyses the residuals showed no obvious patterns, and plots of the ranked residuals against the standard normal deviates were close to straight lines, supporting the assumption of normal errors.

Relationships between a degenerating ovule and its position within the ovary and a developing seed and its position within the fruit were analyzed by logistic regression (Hosmer and Lemeshow, 1989), with each ovule or seed as an observation. Plant identity was included as a co-variate in the model to control the confounding effects of between-plant variation. Frequencies in each position were also tested for independence using a Chi-square test (Zar, 1996) in case a relationship between position and ovule or seed was not monotonic. All quantitative variables are presented by means ± standard error throughout the test.

RESULTS

The mean number of flowers (Fig. 1) was much higher than the number of developing fruits per plant (Table 1). After four months of observation, all fruits were aborted (Table 1; note that the fruit took five months to mature). The mean number of ovules per ovary (5.8 ± 0.1, n=54 from 3 plants; Fig. 2) was greater than the number of seeds per fruit (1.2 ± 0.05, n=72 from 3 plants). Fruits were one, two or three-seeded, but the majority were one-seeded (One-seeded: 86.1%, two-seeded: 12.5%, three-seeded: 1.4%; n=72 fruits from 3 plants). The sizes observed for mature seed and fruit revealed that the seed was large compared to the fruit. The maximum length and width of the fruit (Fig. 3) were 10.1 cm ± 1.3 and 4.0 cm ± 0.5 (n=8), respectively. The maximum length and width of the seed (Fig. 4) were 2.3 cm ± 0.4 and 4.0 cm ± 0.2 (n=10), respectively.

Figures 1-4 - Fotographs of inflorescence (1), open carpel (2), fruits (3) and seed (4) of *Dahlstedtia pentaphylla*.

Teixeira, S. P. et al.

Table 1 - Number of flowers and fruits (mean ± standard error) per plant of *Dahlstedtia pentaphylla* in 1998 (n=4 plants) and of fruits in 2000 (n=5 plants).

Year	Flowers	Fruits		
		After 1 month	After 2 months	After 4 months
1998	530.3±139.6	12.0±6.4	5.5±2.3	0
2000	-	14.4±9.0	5.3±1.1	0

No significant differences were found in the number of germinating pollen grains of apical, median and basal flowers of the inflorescences ($F_{2, 16}$=0.848, P=0.446; Table 2). Nor there were significant differences in the number of fruit produced on apical, median or basal positions in the inflorescences ($F_{2, 98}$=0,753, P=0.473; Table 2).

Between plants, were found no significant differences in the number of germinating pollen grains ($F_{2, 6}$=2.655, P=0.149), but there were significant differences in the number of fruit produced ($F_{2, 47}$=3.209, P=0.049).

Table 2 - Number (mean ± standard error) of pollen grains recorded on the stigmas (3 inflorescences per plant; 3 plants; n=18 flowers per position) and number of fruits produced (3 plants; n=50 observations per position) according to inflorescence position of *Dahlstedtia pentaphylla*.

Position	Pollen grains	Fruit
apical	30.2 ± 7.9	0.5 ± 0.1
median	30.3 ± 4.9	0.7 ± 0.1
basal	38.0 ± 5.4	0.6 ± 0.1

Out of 310 ovules analyzed from five plants, between 47.6 to 100% were degenerating, as indicated by callose in the inner and outer integuments (Table 3a). The proportion of degenerating ovules was slightly higher in the basal position in the ovary (Fig. 5a). However, data analyses by the logistic regression (Table 4a) and by the test of independence for callose deposition in maternal ovular tissues (Pearson χ^2_5=2.471; prob.=0.781) showed no significantly relationship between callose deposition and ovule position within the ovary. Of the 253 seeds analyzed, between 34 to 76.4% were aborted (Table 3b), as

evidenced by dark coloration, tissue retraction and reduced size compared with developing seeds. The fourth position in the fruit showed a higher proportion of developing seeds (non-aborted) whereas the sixth position, which were closer to peduncle, showed lower proportion of developing seed (Fig. 5b). However, there was no significant relationship between developing seeds and their position within a fruit as determined by the logistic regression (Table 4b) and by the test of independence (Pearson χ^2_5=3.050; prob.=0.550).

Table 3 - Percentage of degenerating ovules and aborted seeds per plant of *Dahlstedtia pentaphylla*. N=number of ovules and seeds analyzed per plant.

Plant	(a) degenerating ovules		(b) aborted seeds	
	n	%	n	%
1	21	47.6	75	58.7
2	89	100	25	40.0
3	97	100	55	76.4
4	76	93.4	50	34.0
5	27	51.9	48	58.4

Table 4 - Results of the logistic regressions used to explain the probability of ovule degeneration and seed abortion in *Dahlstedtia pentaphylla*. χ2 value corresponds to the change in deviance caused by the removal of the factor from the full model. The factor "Plant" was included in the model as co-variate to control the confounding effects of between-plant variations.

Factor tested	(a) ovule degeneration			(b) seed abortion		
	χ^2	d.f.	prob.	χ^2	d.f.	prob.
Plant	88.726	4	$<10^{-3}$	22.339	4	$<10^{-3}$
Position	0.022	1	0.882	0.215	1	0.883
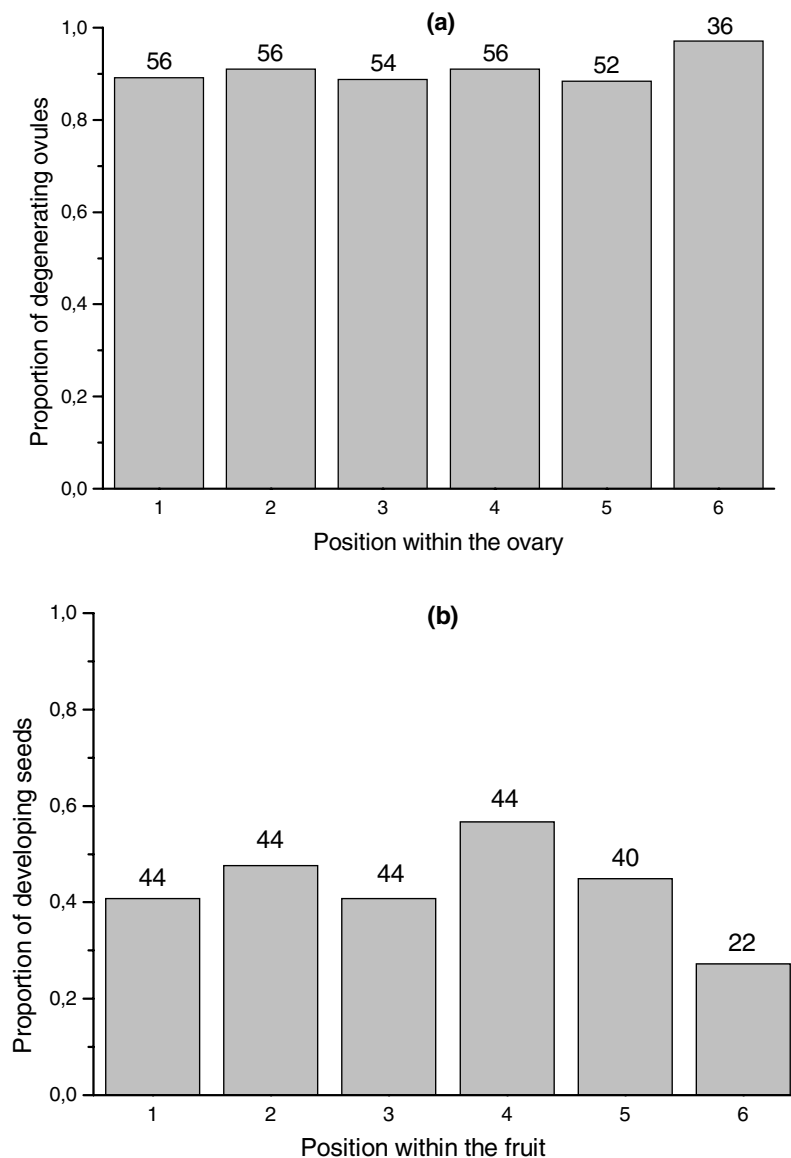
Figure 5 - Proportion of (a) degenerating ovules at different positions within ovaries and (b) developing seeds at different positions within fruits in *Dahlstedtia pentaphylla*. Position 1 is the closest to the style and 6 is closest to the flower peduncle. Sample sizes are given above the bars.

Significant differences between plants were detected in the probability of both ovule degeneration and seed abortion in *D. pentaphylla*, as shown by the significant change in deviance caused by the removal of the factor "plant" (Table 4).

DISCUSSION

In *D. pentaphylla* both fruit and seed set are extremely low. As the abortion pattern of embryos inside the fruit is quite different from that of fruits in plants (Bawa et al., 1989), the abortion in this species should be focused at two levels: why do flowers not set fruits? and why do ovules not set seeds?

Fruit abortion
Since significant differences were not found in fruit formation and pollen deposition with respect to the position within an inflorescence in *D. pentaphylla*, the hypothesis relating fruit abortion to the order of flower opening in the inflorescence (Stephenson, 1980) is unlikely. This hypothesis predicted that in the case of acropetal maturation (found in the majority of legumes, including *D. pentaphylla*), flowers basally located on the inflorescence would be pollinated first and their fruits would have more chances to survive, acquiring the available resources before the fruits that began to develop late (Stephenson, 1980). The lack of significant differences in pollen deposition related to flower position in the inflorescence indicated that either pollinator visits were random within the inflorescence or the absence of pollinators in the study area and a high degree of autonomous self-pollinations (S. P. Teixeira, unpublished data).
Fruit abortion due to selection according to the cost of fruiting and seed maturation seemed more probable, because of the high number of fruits aborted early in the development of *D. pentaphylla*, before the substantial increase in fruit and seed mass. According to Nakamura and Stanton (1987), aborted fruits (or seeds) contained few of the maternal resources allocated to reproduction. Fruit and seed costs might be high in *D. pentaphylla*: seeds were large, exendospermic, cotyledons were well-developed and photosynthetic, filling all the seed cavity, and seed germination required seed coat rupture by the embryo itself (S. P. Teixeira, unpublished data). Moreover, as a result of the high rates of ovule and

seed abortion, nearly 85% of the fruits were one-seeded, rejecting the hypothesis that fruits with more seeds would be selected in relation to the others (Lee and Bazzaz, 1982; Nakamura, 1986; Bawa et al., 1989).
Since seed abortion occurred randomly in *D. pentaphylla*, its single-seeded fruits were not the result of the position-dependent seed abortion as reported to *Pongamia pinnata* (Arathi et al., 1999, see also Lee and Bazzaz, 1982 for a discussion on multi-seeded pods). Also, the observed pattern in *D. pentaphylla* may not be explained by fitness advantage in dispersal distance of single-seeded wing fruits as tested in *Platypodium elegans* (Augspurger, 1986), given that *D. pentaphylla* has indehiscent but no wing fruits. Moreover, no evidences for animal dispersal were found in the literature or in the field observations. Few mature fruits fall and remain for long time in the soil until seeds are liberate. Then dispersal distance seems to be short anyway.
Predation is another factor involved in fruit abortion (Lee and Bazzaz, 1982; Augspurger, 1986; Arista et al., 1999). Although there have been observations of ants disturbing the calyx and basal stamen tube where nectar is released in *D. pentaphylla*, these injuries do not prevent fruit development, and are observed only in the persistent calyx of developing fruits. Injuries to fruits were not observed.

Seed abortion
Abortion, related to the ovule and seed position, occurred randomly. As no relationships were found in ovule degeneration or seed development and their positions within the ovary or fruit, the hypotheses of temporal (Jaranowsky, 1962), spatial (Horovitz et al., 1976) and parental (Janzen, 1977; Niesenbaum, 1999) advantages, confirmed in other legume species, seemed to be unlikely for *D. pentaphylla*. The apical ovules (stigmatic position) of *D. pentaphylla* did not significantly set more seeds than the others, despite being fertilized first. Besides, the embryo sac viability is high, and flowers can last two or more days on the plant (Teixeira et al., 2001), which means that the basally positioned ovules also have chances to be fertilized. Basal seeds (peduncle position) within the fruits showed the same development probability as the others, which differed from the results of Horovitz et al. (1976) for *Lupinus* and *Medicago* species. According to these authors, those seeds closer the maternal

nutrition have more chances to complete development.

Present results showed that on average about 30 pollen grains were deposited onto stigmas and that the average ovary contained about six ovules. Thus, pollen deposition was about five-fold greater than the number of ovules and the quantity of pollen deposited was also unlikely to limit seed set. Further, no temporal differences in pollen tube growth after self- and cross-pollination (Teixeira et al., 2001), or anomalies in the pollen grain development (Teixeira et al., 2002) have been observed and fruits form after autonomous self-pollination (S. P. Teixeira, unpublished data). If not, the autonomous self-pollination would indicate that quality of pollen may be limiting. Therefore, these data suggested that fertilization and seed development in *D. pentaphylla* did not depend on pollen performance and pollen donor to originate more vigorous embryos. Alternatively, the high ratios of ovule and seed abortion occurring randomly in *D. pentaphylla* could be explained by the hypothesis of (a) maternal resource limitations; (b) genetic conflicts among the endosperm, maternal tissues and embryos within a fruit (kin-selection hypothesis); and/or high inbreeding depression (genetic load hypothesis).

According to the kin-selection theory (Westoby and Rice, 1982; Queller, 1983), the endosperm, maternal tissues and embryos within a fruit share genes in different proportions, and conflicts occur among them. Because maternal tissue and endosperm (double fertilization) share more genes with the maternal plant, the latter thus controls the amount of resources provided to a developing embryo. On the other hand, an embryo (and the paternal plant) can increase its fitness, at the expense of fitnesses of maternal plant and other embryos, by obtaining a greater share of maternal resources. To deal with greedy fathers and progeny, selection has favored maternal control over resources to maximize her fitness, by restricting resources to individual embryos and by aborting certain embryos. Such control is possible because maternal tissues (integuments) control the amount of resources allocated to each embryo. Thus, if the embryo development was considered individually (Queller, 1983), mother-plants would be selected to control resource distribution to the embryos inside a fruit, according to their resource sink and not to their position within the fruit. This pattern has been anatomically confirmed in *D.*

pentaphylla; the first changes in aborting ovules and seeds occur in the maternal tissues, and the abortion in offspring tissues occurs later (Teixeira et al., 2001).

The genetic load hypothesis predicted that aborted embryos were intrinsically non-viable, and would not develop even if the dominant embryo was destroyed experimentally, a consequence of high inbreeding depression and high levels of self-pollination (Bawa et al., 1989). In *D. pentaphylla*, 91% of the analyzed ovules showed signs of degeneration (callose deposition) and 56% of seeds were aborted at the early stages of development. During this study, all fruits produced were also aborted and no seedlings were observed near the mother-plant. Such results were very similar to those found in the endangered *Dedeckera eurekensis* (Polygonaceae) (Wiens et al., 1989). However, no anomalies were found at the stages of embryogenesis of *D. pentaphylla* (Teixeira et al., 2001). There was no histological evidence indicating inbreeding depression, as found in *Dedeckera eurekensis* (Wiens et al., 1989). Studies on genetics and experimental embryology would be important to evaluate if, besides maternal resource limitation, the genetic load due to recessive lethals is acting in *D. pentaphylla*.

ACKNOWLEDGMENTS

RESUMO

Este trabalho estudou o efeito dos componentes de fecundidade na reprodução de *Dahlstedtia pentaphylla*, leguminosa neotropical com baixa produção de frutos e sementes. Para tal, foram analisadas as relações das posições das flores na inflorescência e dos óvulos/sementes no ovário/fruto ao aborto de frutos e sementes. Não

ocorreram diferenças na deposição de pólen em flores e na formação de frutos em função da posição na inflorescência. Não se encontrou também relação entre aborto de óvulos/sementes e sua posição no ovário/fruto. A limitação dos recursos maternos aos frutos e aos embriões, devido ao alto custo de formação de frutos e maturação das sementes, foi um dos fatores responsáveis pelas altas taxas de aborto nesta espécie.

REFERENCES

Arathi, H. S.; Ganeshaiah, K. N.; Shaanker, R. U. and Hegde, S. G. (1999), Seed abortion in *Pongamia pinnata* (Fabaceae). *Am. J. Bo.*, **86**, 659-662.

Arista, M.; Ortiz, P. L. and Talavera, S. (1999), Apical pattern of fruit production in the racemes of *Ceratonia siliqua* (Leguminosae: Caesalpinioideae): role of pollinators. *Am. J. Bot.*, **86**, 1708-1716.

Augspurger, C. K. (1986), Double- and single-seeded indehiscent legumes of *Platypodium elegans*: consequences for wind dispersal and seedling growth and survival. *Biotropica*, **18**, 45-50.

Bawa, K. S. and Buckley, D. P. (1989), Seed: ovule ratios, selective seed abortion, and mating systems in Leguminosae. *Monogr. Syst. Bot.*, **29**, 243-262.

Bawa, K. S.; Hedge, S. G.; Ganeshaiah, K. N. and Shaanker, R. U. (1989), Embryo and seed abortion in plants. *Nature*, **342**, 625.

Bawa, K. S. and Webb, C. J. (1984), Flower, fruit, and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *Am. J. Bot.*, **71**, 736-751.

Geesink, R. (1981), Tephrosieae (Benth.) Huch. In: Polhill, R. M. and Raven, P. H. (Eds). *Advances in Legume Systematics*. Kew: Royal Botanic Gardens. pp. 245-260.

Guilherme, F. A. G.; Morellato, L. P. C. and Assis, M. A. (2004), Horizontal and vertical tree community structure in a lowland atlantic rain forest, southeastern Brazil. *Braz. J. Bot.*, **27**, 725-737.

Heering, J. H. (1994), The reproductive biology of three perennial *Sesbania* species (Leguminosae). *Euphytica*, **74**, 143-148.

Herr Jr., J. M. (1971), A new clearing-squash technique for the study of ovule development in Angiosperms. *Am. J. Bot.*, **58**, 785-790.

Horovitz, A.; Meiri, L. and Beiles, A. (1976), Effects of ovule positions in fabaceous flowers on set and outcrossing rates. *Bot. Gaz.*, **137**, 250-254.

Hosmer, D. W. and Lemeshow, S. (1989), *Applied logistic regression*. New York: Wiley.

Hossaert, M. and Valéro, M. (1988), Effect of ovule position in the pod on patterns of seed formation in two species of *Lathyrus* (Leguminosae, Papilionoideae). *Am. J. Bot.*, **75**, 1714-1731.

Janzen, D. H. (1977), A note on optimal mate selection by plants. *Am. Nat.*, **11**, 365-371.

Jaranowsky, J. (1962), Fertilization and embryo development in cases of autogamy. *Gen. Pol.*, **3**, 209-242.

Lee, T. D. and Bazzaz, F. A. (1982), Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology*, **63**, 1363-1373.

Lee, T. D. (1986), Maternal regulation of fecundity: non-random ovule abortion in *Cassia fasciculata*. *Oecologia*, **68**, 459-465.

Lloyd, D. G. (1980), Sexual strategies in plants. 1. An hypothesis of serial adjustement of maternal investment during one reproductive session. *New Phytol.*, **86**, 69-79.

Mogensen, H. L. (1975), Ovule abortion in *Quercus* (Fagaceae). *Am. J. Bot.*, **62**, 160-165.

Nakamura, R. R. (1986), Maternal investment and fruit abortion in *Phaseolus vulgaris. Am. J. Bot.*, **73**, 1049-1057.

Nakamura, R. R. and Stanton, M. L. (1987), Cryptic seed abortion and the estimation of ovule fertilization. *Can. J. Bot.*, **65**, 2463-2465.

Niesenbaum, R. A. (1999), The effects of pollen load size and donor diversity on pollen performance, selective abortion, and progeny vigor in *Mirabilis jalapa* (Nyctaginaceae). *Am. J. Bot.*, **86**, 261-268.

Queller, D. C. (1983), Kin selection and conflict in seed maturation. *J. Theor. Biol.*, **100**, 153-172.

Sedgley, M. (1980) Anatomical investigation of abscissed avocado flowers and fruitlets. *Ann. Bot.*, **46**, 771-777.

Stephenson, A. G. (1980), Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology*, **61**, 57-64.

Stephenson, A. G. (1981), Flower and fruit abortion: proximate causes and ultimate functions. *Ann. Rev. Ecol. Evol. Syst.*, **12**, 253-279.

Teixeira, S. P.; Prakash, N. and Ranga, N. T. (2001), Ovule and early seed development related to seed abortion in *Dahlstedtia pinnata* and *D. pentaphylla* (Leguminosae, Papilionoideae). *Phytomorphology*, **51**, 41-50.

Teixeira, S. P.; Forni-Martins, E. R. and Ranga, N. T. (2002), Development and cytology of pollen in *Dahlstedtia* Malme (Leguminosae: Papilionoideae). *Bot. J. Linn. Soc.*, **138**, 461-471.

Teixeira, S. P. and Ranga, N. T. (2004), Biosystematics of the genus *Dahlstedtia* Malme (Leguminosae, Papilionoideae, Millettieae). *Braz. J. Bot.*, **27**, 37-45.

Vishnyakova, M. A. (1991), Callose as an indicator of sterile ovules. *Phytomorphology*, **41**, 245-252.

Westoby, M. and Rice, B. (1982), Evolution of the seed plants and inclusive fitness of plant tissues. *Evolution*, **36**, 713-724.

Wiens, D.; King, E. J.; Nickrent, D. L.; Calvin, C. L. and Vivrette, N. L. (1989), Embryo and seed abortion in plants. *Nature*, **342**, 626.

Zar, J. H. (1996), *Biostatistical analysis*. 3rd ed. New Jersey: Prentice Hall.