



Pre-dispersal seed predation and abortion in species of *Callisthene* and *Qualea* (Vochysiaceae) in a Neotropical savanna

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Received: 12 March, 2013. Accepted: 20 December, 2013

ABSTRACT

The ability of plants to generate fertile offspring is influenced by morpho-physiological and ecological factors. Hence, reproductive success is directly linked to factors affecting quantity and quality of their progeny. In the Cerrado (savanna) of Brazil, the Vochysiaceae is a widely distributed and ecologically important family. Factors affecting pre-dispersal seed predation and abortion were studied for populations of *Callisthene fasciculata*, *C. major*, *Qualea multiflora* and *Q. parviflora*. To characterize differences between genera, as well as among species, study areas, and individuals, we quantified pre-dispersal seed predation and abortion. Differences of seed abortion among the species were related to intrinsic reproductive features and not to area or other factors. In contrast, seed predation varied not only among species but also among areas and among individuals. Only *C. fasciculata* showed no seed predation. In *Qualea* species, insect predators were found inside the seeds; whereas predators of *Callisthene* species were outside seeds. In both genera, seed abortion correlated negatively with area size, as did pre-dispersal seed predation, which suggest seed abortion may be a counter-measure to avoid predation. Although seed abortion and predation reduced the progenies of the studied species, seed production did not differ from other Cerrado species.

Key words: Seed set, abortion, predation, beetles, Neotropics, savanna, Cerrado

Introduction

The ability of plants to generate fit, fertile offspring is influenced by intrinsic physiological processes, as well as by external biological and physical factors (Crawley 2000). A common phenomenon in the reproductive process of angiosperms is abortion (of the ovule or seed), which can affect the production of fruits and viable seeds (Wiens 1984; Kärkkäinen *et al.* 1999; Latta 2005; Porcher & Lande 2005). Many species allocate a great quantity of resources to flowers. Although most of those flowers will fail to develop into fruits, they might represent spare parts to be called upon in case of environmental stress, predation or disease. In addition, more flowers translates to increased pollen availability, attracting more pollinators and increasing pollen flow, thus allowing post-pollination gametophytic selection and selective abortion, which seems to improve fruit and seed quality (Janzen 1978; Stephenson 1981; Melser & Klinkhamer 2001).

Seed abortion is particularly common among self-incompatible species and woody perennials in particular, affecting more than 50% of the number of all ovules produced (Wiens 1984). Because mother plants have limited resources for production, protection and seed dispersal,

there are obligatory trade-offs among the size, quality and quantity of the seeds they produce (Haig & Westoby 1988). Therefore, seed abortion might result from parental resource allocation and competition among siblings (Bawa *et al.* 1989; Uma Shaanker & Ganeshiah 1997).

In addition to resource limitation and environmental stress, seed abortion and loss of mature seeds can be caused by pollen limitation and inbreeding (Wiens *et al.* 1987); breeding system incompatibility (Dhar *et al.* 2006); by genetic load (Wiens *et al.* 1987; Bawa *et al.* 1989; Porcher & Lande 2005); and by abnormalities during ovule ontogeny (Palser *et al.* 1990; Sedgley & Granger 1996). Therefore, seed abortion is the main mechanism of post-zygotic selection in plants, allowing resource allocation to be optimized and pre-dispersal seed predation to be avoided (Gribel & Gibbs 2002; Ward *et al.* 2005; Chacoff *et al.* 2008; Ghazoul & Satake 2009).

Seed production and survival are affected not only by brood selection, competition, and environmental factors but also by seed predators. Protein and nutrient content are usually higher in seeds than in vegetative tissues, and the seeds are, therefore, targeted by predators (Janzen 1971b; Mattson 1980; Willson 1983). There are two basic types of seed predation: pre-dispersal predation, which occurs

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while the seed is still attached to the mother plant; and post-dispersal predation, which occurs after separation from the mother plant but before the germination process begins (Janzen 1971b; 1978). The primary groups of seed predators include the larval instars and immature stages of Diptera, Coleoptera, Hymenoptera and Lepidoptera (Janzen 1970, 1971a; Ehrlén 1996; Crawley 2000; Spironello *et al.* 2004; Tuda *et al.* 2009). Pre-dispersal seed predation, the rate of which can be higher than 80% (in natural and cultivated areas alike), exerts enormous pressure on plant reproduction (Andersen 1988; Janzen 1970, 1971a; Zhang *et al.* 1997). In the typical scenario, adult female predators deposit their eggs inside developing ovaries or individual ovules; as the larvae and immature stages develop, they consume parts of the endosperm and embryo before the fruit or seed can mature (Ehrlén 1996; Barreto *et al.* 1999).

Seed abortion and predation are both considered determinants of the size and reproductive ecology of plant populations (Janzen 1971a, 1971b; Bradford & Smith 1977; Garcia *et al.* 2000; Leimu *et al.* 2002; Ghazoul & Satake 2009). Studies comparing populations in terms of the occurrence of abortion and predation can further understanding of the ecological consequences to plant reproduction and persistence (Bradford & Smith 1977; Ehrlén 1996; Pizo 1997; Crawley 2000; García *et al.* 2000, 2001; Steffan-Dewenter *et al.* 2001; Leimu *et al.* 2002; Baldissera & Ganade 2005; Marino *et al.* 2005; Figueiredo *et al.* 2008). In the Cerrado of Brazil, one of the most well-represented and characteristic families of woody plants is the Vochysiaceae, some species of which are among the most common and widespread in the Biome (Haridassan & Araújo 1988; Ratter *et al.* 1996; Apolinário & Schiavini 2002; Lopes *et al.* 2011). Vochysiaceae species are mostly self-incompatible, having been reported to feature fruit and seed abortion (Carmo-Oliveira 1998; Oliveira 1998). Seeds are wind-dispersed and recalcitrant in terms of germination, quickly losing their viability in storage (Boesewinkel & Venturelli 1987; Farnsworth 2000). Seed predation and its consequences for reproductive outcomes have not been studied in detail. In this context, the objective of this study was to quantify and compare the frequency of pre-dispersal seed predation and abortion in different populations of *Callisthene* and *Qualea* (Vochysiaceae) species within the Cerrado Biome, evaluating their consequences for the reproductive ability of the species. We hypothesized that these processes would be interrelated and would play a role in plant strategies to cope with predation.

Materials and methods

Species studied

The occurrence of pre-dispersal seed predation and abortion was studied for populations of *Callisthene fasciculata* Mart., *Callisthene major* Mart., *Qualea multiflora* Mart. and *Qualea parviflora* Mart. A brief description of

the main morphological and reproductive features of the plants is provided below.

Trees of the species *Callisthene fasciculata* are 5-8 m tall and occur on the shallow Entisols common to rocky basalt outcrops. These soils are relatively rich in nutrients and are associated with fragments of dry deciduous forest within the Cerrado Biome. The trees bloom for a short period in September and October when they are leafless, simultaneously dispersing the seeds from the previous year. The flowers are self-incompatible and bee-pollinated. The ovary is superior and trilocular, with two fully developed ovules per locus. The fruits are loculicidal capsules that open almost one year after flowering (Santos 1997).

Callisthene major is a tree that occurs in the areas of *cerradão* (woodland savanna) and semideciduous forests of the Cerrado Biome. Leaf flush and flowering occur between August and September. Flowers are also self-incompatible and pollinated by small social bees such as *Apis mellifera*. As in *C. fasciculata*, the ovary is superior and trilocular, with two fully developed ovules per locus. Fruits take nearly a year to mature, and seeds are wind-dispersed (Carmo-Oliveira 1998; Oliveira 1998).

Qualea multiflora is a shrub or small tree up to 6 m tall, occurring in open areas of *cerrado sensu stricto* in central Brazil. Flowering begins in October, just after the seed dispersal and leaf flushing in September, and continues until February. The flowers present a single stamen and superior ovary with up to six fully formed ovules per locus. It is self-incompatible and pollinated by large *Xylocopa* and *Centris* bees. Fruits are loculicidal capsules with winged seeds (Oliveira 1998).

Qualea parviflora is a species of tree that grows up to 8 m in height and is quite common in open areas of *cerrado sensu stricto*. Leaves are verticillate with extrafloral nectaries at the base of their petioles. The axillary inflorescences are produced from September to December. The flowers, which are self-incompatible and bee-pollinated, are smaller than are those of *Q. multiflora*, featuring a single lilac petal with a white nectar guide and a spurred calyx. Like those of *Q. multiflora*, the flowers of *Q. parviflora* present a single stamen and a superior trilocular ovary with six ovules per locus. The loculicidal capsule typically releases only two seeds per locus, one year after flowering (Oliveira 1998).

Study areas

For all four of the species studied, fruit were collected in seven different protected areas: six in the state of Minas Gerais—the *Clube Caça e Pesca Itororó de Uberlândia* (CCPIU, Itororó Hunting and Fishing Club of Uberlândia); the natural areas surrounding the Capim Branco II hydroelectric dam (CBII); Panga Ecological Station (PES); Glória Experimental Farm (GEF); Limoeiro Farm (LF); and Parque Nacional da Serra da Canastra (PARNASC, Serra da Canastra National Park)—and one in the state of Goiás—*Parque Estadual da Serra de Caldas Novas* (PESCAN, Serra de Caldas Novas State Park).

The CCPIU (18°59'S; 48°18'W), located 8 km south-east of the city of Uberlândia, comprises 127 ha of private ecological reserve dominated by *cerrado sensu stricto* and palm swamps (Appolinário & Schiavini 2002). Mature fruits of *Qualea multiflora* and *Q. parviflora* were collected from alongside the road that runs through the area.

Sampling at the CBII (18°35'S; 48°24'W) was done at km 131 of state road MG 223 in a fragment of semideciduous forest surrounded by coffee plantations and pastures. Fruits of *Callisthene fasciculata* were collected from trees within the forest, whereas *Qualea multiflora* fruits were obtained from isolated individuals at the forest edge.

The PES (19°10'S; 48°23'W) comprises 409.5 ha, located 30 km southeast of Uberlândia. It is one of the few protected areas in the "Triângulo Mineiro" (Minas Triangle) region (Cardoso *et al.* 2009) and features various vegetation formations characteristic of the Cerrado Biome (Schiavini & Araújo 1989). Fruits of *Qualea multiflora* and *Q. parviflora* were collected in an area of *cerrado sensu stricto*.

The GEF (18°56'S; 48°12'W) comprises an area of 685 ha within the city of Uberlândia. Although some of the GEF land is used for agricultural and cattle ranching experiments, the area also includes preserved forest fragments (Haridasan & Araújo 1988), from which we collected fruits and seeds of *Callisthene major*.

The LF (18°33'S; 48°28'W) is a private farm, located approximately 35 km southeast from Uberlândia, on state road MG 223. It presents an area of ≈3 ha, comprising a fragment of *cerrado* and a deciduous dry forest, both on a basalt outcrop (Santos 1997), from which we collected seeds of *Callisthene fasciculata* and *Qualea parviflora*.

The PARNASC (20°10'S; 46°33'W) is approximately 200 km east of Uberlândia, between the cities of Delfinópolis, São Roque de Minas and Sacramento. It comprises an area of 71,525 ha and features a great variety of vegetation formations, with high levels of endemism (Romero & Nakajima 1999). We collected fruits of *Callisthene major* near Rolinhos Waterfall, which is in the northeastern sector of the park.

The PESCAN (17°46'S; 48°40'W) is a area of 12,500 ha, located on a plateau (at 1043 m a.s.l.) between the cities of Caldas Novas and Rio Quente, in the state of Goiás (Almeida & Sarmiento 1998), approximately 200 km northwest of Uberlândia. Although the plateau presents a great variety of vegetation formations characteristic of the Cerrado Biome, it is dominated by *cerrado sensu stricto* (Lopes *et al.* 2011), from which we collected fruits of *Qualea multiflora* and *Q. parviflora*.

Voucher specimens were deposited in the Herbarium of the Federal University of Uberlândia (code, HUFU), in Uberlândia: *Callisthene fasciculata* (HUFU 55467-CBII; HUFU 55466-LF). *Callisthene major* (HUFU 45808-GEF; HUFU 55470-PARNASC). *Qualea multiflora* (HUFU 44918-CCPIU; HUFU 55469-CBII; HUFU 55468-PESCAN) and *Qualea parviflora* (HUFU 44919-CCPIU; HUFU 55464-LF; HUFU 55465-PESCAN).

Seed abortion and predation sampling

Fruits were collected between July and August of 2009, when all fruits were completely developed but before final maturation and dispersal. We collected fruits from at least five individuals per species in each of the seven populations evaluated. Due to the large volume of fruits collected, some were frozen for later analysis. We did not use any randomization procedure during collection, rather attempting to collect a similar number of fruits from each individual, although from different branches.

From each fruit, the seeds were removed and analyzed for the presence of embryos. The seeds containing embryos were stored in 70% ethanol. As previously mentioned, *Qualea* and *Callisthene* species present three pairs of ovules, resulting in a maximum of six seeds per fruit. Hence, the abortion rate was the number of missing viable seeds divided by six. This abortion rate was calculated for each population and individual using each fruit as a sampling unit.

The presence of endophagous insects or evidence of pre-dispersal seed predation was evaluated during fruit and seed abortion analyses. Seeds were dissected under stereomicroscopy in order to detect endophagous insect eggs, larvae or adults. The predation rate was calculated for embryo-containing seeds. Insect specimens were fixed in 70% ethanol for later identification.

Statistical analysis

To compare the frequency (rate) of aborted and predated seeds among areas and among individuals within each area, we used a generalized linear model with binary logistic distribution (Crawley 2007). The same procedure was used in comparing abortion and predation rates among *Callisthene fasciculata*, *C. major*, *Qualea multiflora* and *Q. parviflora*, as well as between the two genera. All analyses were conducted using the GLZM module of the Statistical Package for the Social Sciences, version 17.0 (SPSS, Inc., Chicago, IL, USA) with Type III test. To correlate abortion and predation rates for the populations of the two *Qualea* species, we calculated Spearman's correlation coefficient (r_s) using the SYSTAT[®] program, version 10.2 (Systat Software Inc., San Jose, CA, USA).

Results

Seed morphology and abortion

The proportion of aborted seeds per fruit greatly varied among individuals and populations but was markedly different between the two genera. In *Callisthene fasciculata*, embryo-less (aborted) seeds were thinner and darker than were embryo-containing seeds, although some aborted seeds showed a normal wing. We also found marked differences in *C. major*, in which embryo-containing seeds were larger and

had a fully developed wing. However, in both *Qualea* species, the size of aborted seeds did not differ greatly from that of viable seeds, and both showed wing development. The primary difference was the absence of the embryo itself, which was replaced by a resinous mass, although the seed integuments and other tissues developed as in the viable seeds.

Seed abortion rate

In all of the populations analyzed, we observed seed abortion—i.e., the development of seeds without embryos (Fig. 1). Species of *Callisthene* presented higher abortion rates than did those of *Qualea*. Abortion rates differed among areas and among species (Tab. 1), ranging from 22.3% in *Qualea multiflora* to 68.2% in *Callisthene fasciculata* and differing markedly between areas for the latter (Fig. 1). *Callisthene major* also presented high abortion rates (Fig. 1), although with no significant difference between areas (Tab. 1). Abortion rates for *Q. multiflora*, which were the lowest (only 20%), differed among areas and among individuals within areas (Fig. 1 and Tab. 1), whereas *Q. parviflora* presented abortion rates of 31.2–48.2% and also showed significant differences among areas and among individuals within areas (Fig. 1 and Tab. 1). Among the areas evaluated, the abortion rate was lowest in the LF.

For *Callisthene fasciculata*, half of the analyzed fruits (51.3%) presented five of the six possible seeds aborted in the CBII (Fig. 2), compared with only four of the six in the LF. For *C. major*, the abortion rates were similar among areas (Fig. 2), most fruits containing only three or four aborted seeds (74.70% in the PARNASC and 82.70% in the GEF). For the genus *Callisthene* as a whole, there were very few fruits with no aborted seeds (five for *C. fasciculata* and one for *C. major*). *Qualea multiflora* presented a larger number of fruits with few or no aborted seeds (Fig. 2), 21.5% of all *Q. multiflora* fruits presenting no aborted seeds. In *Q. parviflora*, the number of aborted seeds was higher and varied more widely, without a clear trend among areas and individuals (Fig. 2).

To compare the abortion rates for each species, we took into consideration the differences between individuals and populations. We found that seed abortion differed significantly among the four species studied (Tab. 2). The numbers of aborted seeds were significantly higher among *Callisthene* species than among *Qualea* species (Tab. 2), differing between *Q. multiflora* and *Q. parviflora* but not between *C. fasciculata* and *C. major*.

Pre-dispersal seed predation

The insect groups found inside fruits and seeds varied among the four tree species evaluated. Different forms of predation were observed for *Callisthene* and *Qualea*. Although it was not possible to identify predators to the species level, the general predation behavior was similar among morphospecies in each large group of insects.

We observed no seed predation in the fruits of *Callisthene fasciculata*. In *C. major*, predatory insects were found inside the fruits but not within the seeds. In that species, adult Curculionidae (Coleoptera), as depicted in Fig. 3A–C, preyed on seeds by drilling into the integuments in order to access the developed embryos. Thus, all seeds in the fruits of *C. major* were preyed upon by these insects. In contrast, the insects found in both *Qualea* species were only inside the seeds, causing damage to the embryos in their final developmental stage. Different instars of Buprestidae (Coleoptera) and Hymenoptera were found inside embryo-containing seeds at the cotyledon stage (Fig. 3D–F). The presence of immature stages and adults of both groups indicate that these insects complete their development inside the seeds, consuming the embryos and seed content when they are fully developed but before fruit maturation and seed dispersal. The presence of Buprestidae (Coleoptera) was much more common than was that of the Hymenoptera, which were probably parasitoids (Fig. 3G–N).

Pre-dispersal seed predation rate

As previously mentioned, there was no pre-dispersal seed predation in *Callisthene fasciculata* in either of the two areas in which it occurred (Fig. 1). There were populations of *C. major* and *Qualea multiflora* with and without predation, whereas there was evidence of seed predation in all sampled populations of *Q. parviflora* (Fig. 1 and Tab. 3). In *C. major*, predation occurred only in the PARNASC population. In *Q. multiflora*, predation rates were high only in the PES and PESCAN populations, and pairwise comparisons showed that those two populations differed from each other. All four populations of *Q. parviflora* presented relatively high seed predation rates. For the LF, PESCAN and PES, seed predation rates were $\approx 50\%$ and did not differ significantly among the three areas, being significantly different only for the CCPIU, where it was lower ($\approx 20\%$). Differences in the predation rate among populations were significant only for *Q. parviflora* (Tab. 4). Seed predation rates varied significantly among areas and individuals within species and genera (Tab. 4). However, unlike what was observed for abortion rates, the differences between genera and species were not significant.

Abortion and pre-dispersal seed predation for sympatric species of *Qualea*

Comparing the sympatric *Qualea* species, we found that the seed abortion rate varied mostly as a function of species, whereas the seed predation rate varied as a function of area and of species. For the seed abortion rate, there was no interaction between the factors area and species (Wald chi-square $[\chi^2]=4.36; p=0.113$). The areas sampled for two *Qualea* species (Fig. 4A) did not show significant differences in terms of the abortion rate ($\chi^2=2.17; p=0.339$), whereas the abortion rate did differ between those two species (Fig. 4B),

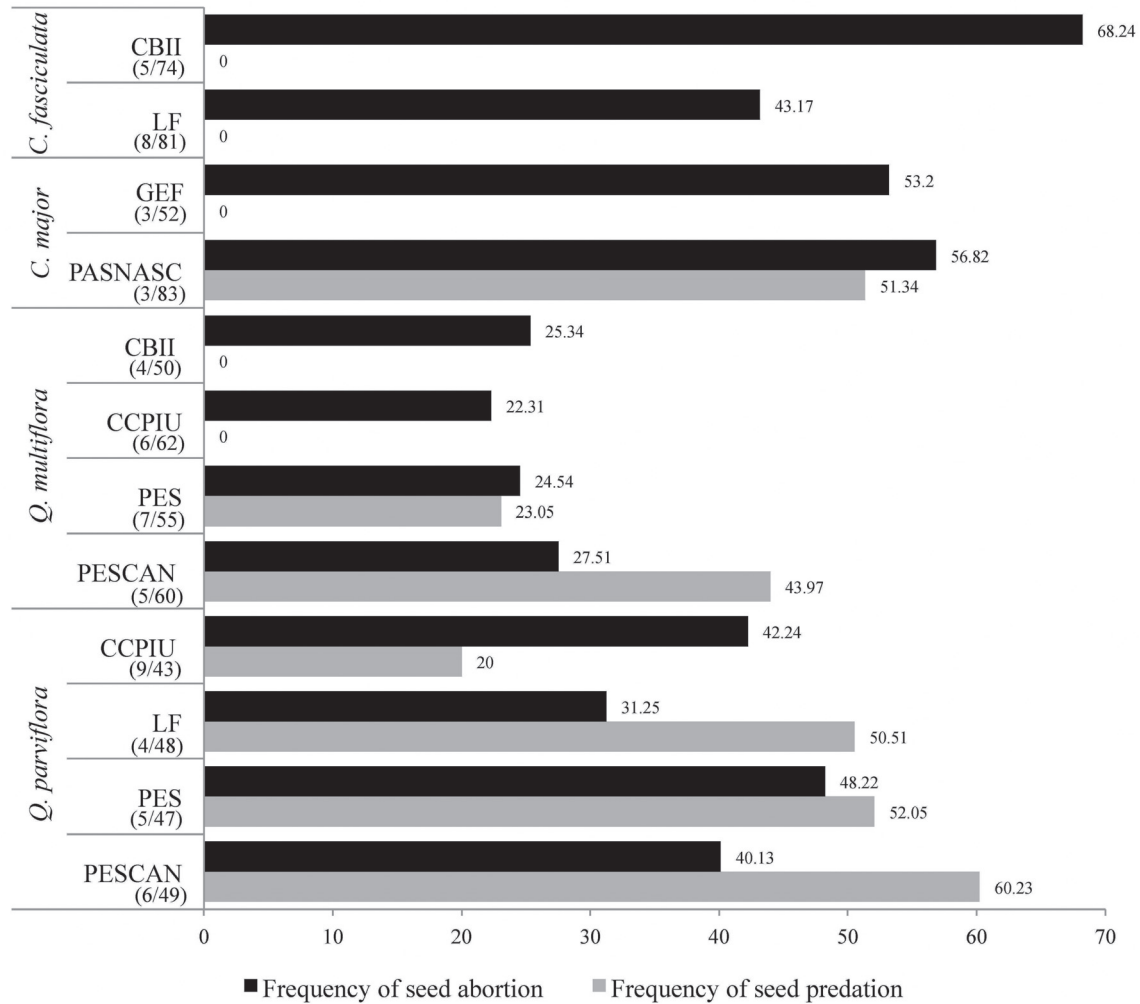


Figure 1. Rate (%) of seed abortion and seed predation for *Callisthene* and *Qualea* species in each studied area.*

CBI – natural areas surrounding the Capim Branco II hydroelectric dam; LF – Limoeiro farm; GEF – Glória Experimental Farm; PES – Panga Ecological Station; PARNASC – *Parque Nacional da Serra da Canastra* (Serra da Canastra National Park); CCPIU – *Clube Caça e Pesca Itororó de Uberlândia* (Itororó Hunting and Fishing Club of Uberlândia); and PESCAN – *Parque Estadual da Serra de Caldas Novas* (Serra de Caldas Novas State Park).

*For each species-area pair, the number of individuals/total number of fruits analyzed are shown in parentheses.

Table 1. Differences in seed abortion rate among the Vochysiaceae studied species. Values were derived from generalized linear models, with areas and individuals nested within areas as factors, the abortion rate being the dependent variable.

Species	Factor	df	χ^2	p
<i>Callisthene fasciculata</i>	Area	1	51.095	<0.001
	Individuals within areas	11	41.993	<0.001
<i>Callisthene major</i>	Areas	1	1.871	0.171
	Individuals within areas	4	2.566	0.633
<i>Qualea multiflora</i>	Areas	3	408.756	<0.001
	Individuals within areas	17	38.730	0.002
<i>Qualea parviflora</i>	Areas	3	1415.069	<0.001
	Individuals within areas	23	89.059	<0.001

χ^2 – Wald chi-square test.

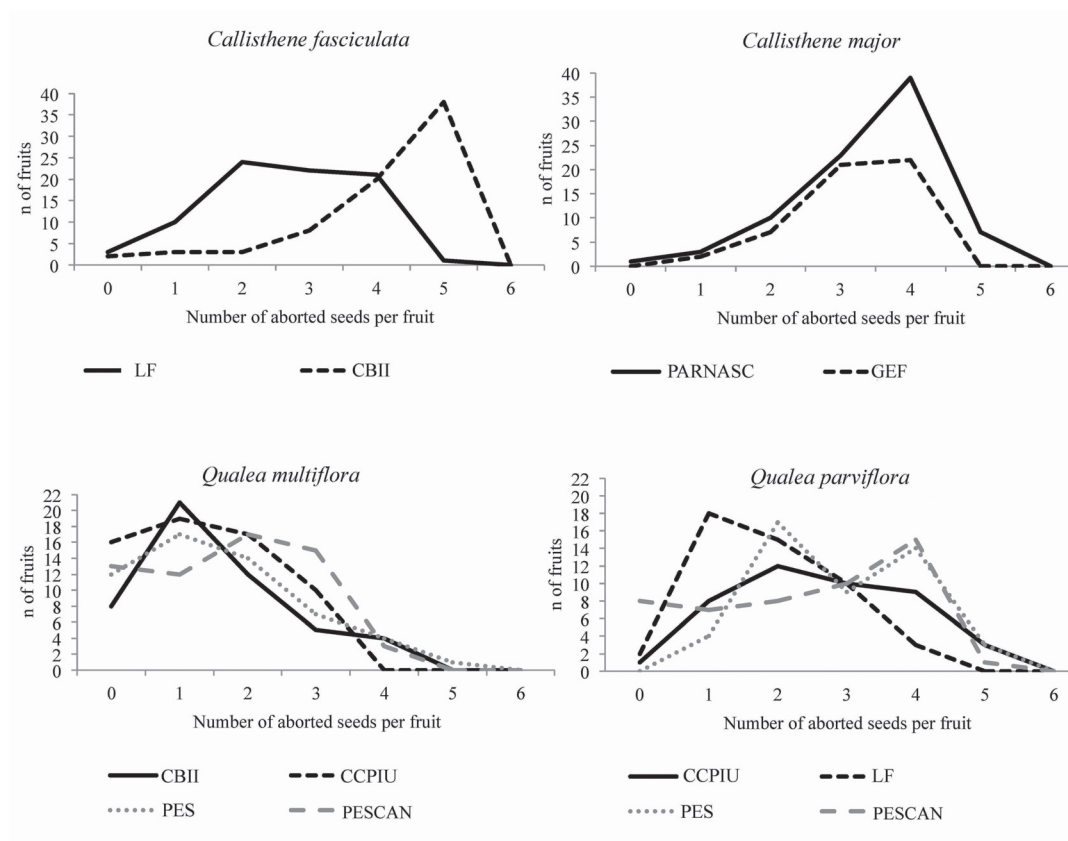


Figure 2. Frequency of fruits as a function of the number of aborted seeds in *Callisthene* and *Qualea* species, by area.

CBII – natural areas surrounding the Capim Branco II hydroelectric dam; LF – Limoeiro farm; GEF – Glória Experimental Farm; PES – Panga Ecological Station; PARNASC – *Parque Nacional da Serra da Canastra* (Serra da Canastra National Park); CCPIU – *Clube Caça e Pesca Itororó de Uberlândia* (Itororó Hunting and Fishing Club of Uberlândia); PESCAN – *Parque Estadual da Serra de Caldas Novas* (Serra de Caldas Novas State Park).

Table 2. Seed abortion rate among the four species studied and between the two genera (*Callisthene* and *Qualea*). Values were derived from generalized linear models results for each genus, the factors being species nested within genera, areas nested within species and individuals nested within areas.

Level	Factor	df	χ^2	p
Species	Species	3	183.976	<0.001
	Areas (species)	5	64.714	<0.001
	Individuals within areas	23	103.051	<0.001
Genus	Genus	1	121.657	<0.001
	Species (genera)	1	14.112	<0.001
	Areas (species)	3	49.232	<0.001
	Individuals within areas	23	112.677	<0.001

χ^2 – Wald chi-square test.

regardless of the area ($\chi^2=72.60$; $p<0.001$). These analyses showed that seed abortion seems to be characteristic of the species as a whole, without marked differences among areas or between populations (Fig. 4B).

In the seed predation analysis, we observed a significant influence on predation for the factors area ($\chi^2=5070.76$; $p<0.01$) and species ($\chi^2=5607.21$; $p<0.01$), with a significant interaction between the two factors ($\chi^2=4.94$; $p=0.026$) For

both *Qualea* species, seed predation rate was higher in the PESCAN than in the PES and CCPIU (Fig. 4C and 4D).

The fruits of *Qualea multiflora* presented lower rates of seed abortion and predation than did those of *Q. parviflora*, and there was a positive, albeit weak, correlation between seed abortion and seed predation for some *Q. multiflora* populations (Tab. 5). For *Q. parviflora*, the correlation between seed abortion and seed predation was strongest in

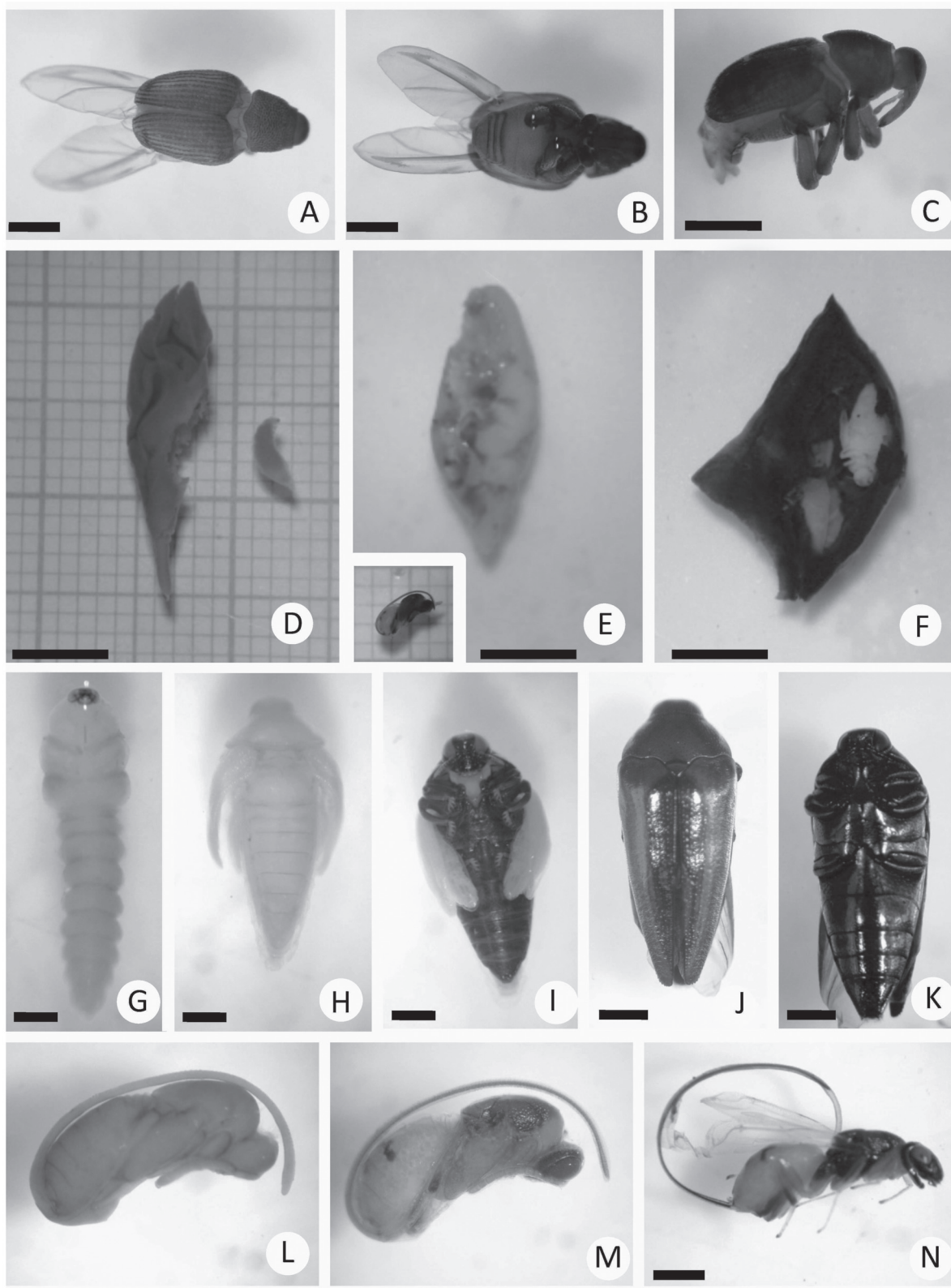


Figure 3. Diversity of insect predators found inside the Vochysiaceae studied seeds. A-C. Specimens of Curculionidae beetles (Coleoptera) removed from *Callisthene major* fruits collected in Serra de Caldas Novas State Park: A) dorsal view; B) ventral view; C) lateral view showing the rostrum (arrow). D-F. Embryos, seed predators and predated seeds of *Qualea multiflora*: D) an embryo at the cotyledon stage preyed upon by a larva; E) insect-damaged embryo and detail of an immature stage of Hymenoptera found inside a seed; F) cotyledon-stage embryo and an immature beetle (Coleoptera: Buprestidae). G-N. Specimens of predators and parasitoids found inside seeds of *Qualea* species: G-K) beetles (Coleoptera: Buprestidae) at different developmental stages; L-N) immature stages and an adult of a parasitoid Hymenoptera with a long ovipositor. Scale bars = 0.50 cm (A-F) and 1 mm (G-N).

Table 3. Pre-dispersal seed predation rates for the Vochysiaceae studied species. Values were derived from generalized linear models for areas and individuals nested within areas as factors, the frequency of seed predation being the dependent variable.

Species	Factor	df	χ^2	p
Callisthene major	Areas	1	0.000	1.000
	Individuals within areas	4	8.951	0.062
Qualea multiflora	Areas	3	0.000	1.000
	Individuals within areas	17	87.297	<0.001
Qualea parviflora	Areas	3	463.325	<0.001
	Individuals within areas	18	8933.539	<0.001

χ^2 – Wald chi-square test.

Table 4. Pre-dispersal seed predation rates for the genera *Callisthene* and *Qualea* (Vochysiaceae). Values were derived from generalized linear models for species, with areas nested within species and individuals nested within areas as factors, the frequency of seed predation being the dependent variable.

Level	Factor	df	χ^2	p
Species	Species	3	0.000	1.000
	Areas (species)	5	50.776	<0.001
	Individuals within areas	23	176.087	<0.001
Genus	Genus	1	0.000	1.000
	Species (genera)	1	0.000	1.000
	Areas (species)	3	21.683	<0.001
	Individuals within areas	18	99.176	<0.001

χ^2 – Wald chi-square statistics.

the PES population ($r_s=0.638$; $p<0.05$). These correlations suggest that predation is influenced by the number of viable seeds formed, the predation rate increasing in proportion to the number of viable seeds per fruit.

Qualea multiflora presented a significant correlation between the number of viable seeds and the predation rate only for the CBII, although the predation rate was very low and the correlation was weak ($r_s=0.373$; $p<0.05$). Abortion and predation both reduce the rate of development from ovule to seed, which is an indicator of reproductive efficacy (Tab. 6). Reproductive efficacy was highest for *Q. multiflora* and lowest for *Q. parviflora*, in which abortion and predation both contributed to reducing the number of ovules that developed into seeds.

Discussion

Seed abortion

We observed seed abortion in all species and populations, the seed abortion rate being above 50% in both of the *Callisthene* species studied, more than half of the ovule budget being expended during the process. Seed abortion rates of 20-60% have been described for other plant species (García *et al.* 2000; Allphin *et al.* 2002; López-Almansa *et al.* 2004; Teixeira *et al.* 2006), corroborating data showing that

seed abortion is especially common among self-incompatible trees and perennial trees (Sorensen 1982; Wiens 1984).

In the family Vochysiaceae, the seed abortion rate seems to be related to intrinsic features, given that it did not vary with time. A study carried out in 2007 showed similar abortion rates for *Callisthene fasciculata*, *C. major*, *Qualea multiflora* and *Q. parviflora* (64%, 73.7%, 19.61% and 39.10%, respectively; L. Custódio, unpublished data). In the present study, a greater proportion of the variation was explained by the taxa, species or genera than by the conditions of the area of occurrence. Among the sympatric *Qualea* species, the seed abortion rate was higher in *Q. parviflora*, regardless of the area. Hence, in the species studied, seed abortion is probably linked to morphological and physiological characteristics of the plants, which drive ovule ontogeny and resource allocation (Wiens 1984; Bawa *et al.* 1989; Uma-Shaanker & Ganeshiah 1997).

However, some variation between populations/areas did occur in *Callisthene fasciculata* and *Qualea parviflora*. Studies of other species have reported differences among populations in terms of the seed abortion rate, attributing those differences to the size and complexity of the populations, as well as to the quality of their environments (Nilsson & Wästljung 1987; García *et al.* 2000; Raimundéz-Urrutia 2008). The results of those studies suggest that such differences result in pollination limitation and disturbance, especially in self-incompatible species such as *C. fasciculata*

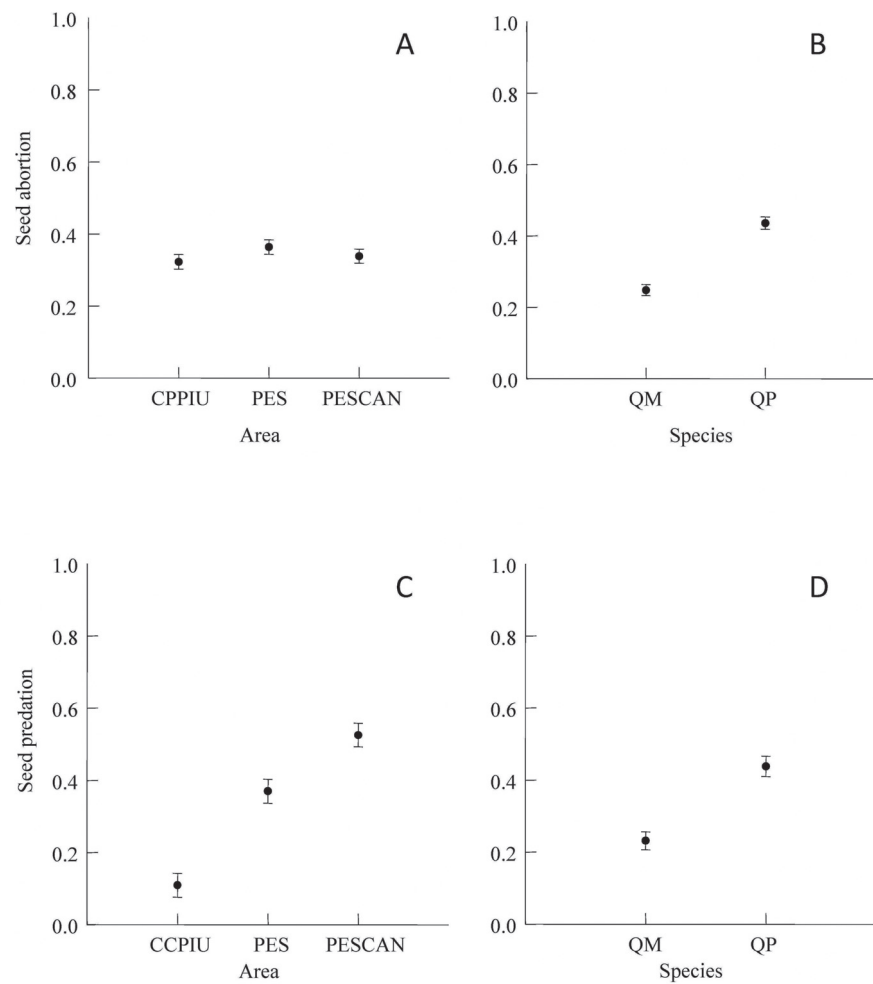


Figure 4. Rates of seed abortion and pre-dispersal seed predation for sympatric populations of *Qualea multiflora* (QM) and *Qualea parviflora* (QP). **A and B.** Seed abortion: **A**) no differences among areas (Wald's chi-square statistics [$\chi^2=2.17$; $p=0.339$]; **B**) significant differences between species ($\chi^2=72.60$; $p<0.001$). **C and D.** Seed predation: **C**) significant differences among areas ($\chi^2=5070.76$; $p<0.01$); **D**) significant differences between species ($\chi^2=5607.21$; $p<0.01$).

Results are expressed as mean and standard error.

CCPIU – *Clube Caça e Pesca Itororó de Uberlândia* (Itororó Hunting and Fishing Club of Uberlândia); PES – Panga Ecological Station; PESCAN – *Parque Estadual da Serra de Caldas Novas* (Serra de Caldas Novas State Park).

Table 5. Correlations between the number of viable seeds and the predation rate in *Qualea* species, by area.

Species	Area	n of fruits	Viable seeds per fruit	Insect-damaged seeds per fruit	r_s	p
			(mean±SD)	(mean±SD)		
<i>Qualea multiflora</i>	CCPIU	62	4.661±1.039	0.000±0.000	0.000	>0.05
	CBII	50	4.480±1.129	0.080±0.274	0.373	<0.05
	PES	55	4.418±1.272	1.018±1.557	0.053	>0.05
	PESCAN	60	4.283±1.209	1.883±1.678	0.122	>0.05
<i>Qualea parviflora</i>	CCPIU	43	3.372±1.273	0.674±1.128	0.034	>0.05
	LF	48	4.125±1.003	2.083±1.622	0.318	<0.05
	PES	47	3.106±1.127	1.617±1.278	0.638	<0.05
	PESCAN	49	3.592±1.513	2.163±1.712	0.537	<0.05

r_s – Spearman's correlation coefficient; CCPIU – *Clube Caça e Pesca Itororó de Uberlândia* (Itororó Hunting and Fishing Club of Uberlândia); CBII – natural areas surrounding the Capim Branco II hydroelectric dam; PES – Panga Ecological Station; PESCAN – *Parque Estadual da Serra de Caldas Novas* (Serra de Caldas Novas State Park); LF – Limoeiro farm.

Table 6. Seed loss due to abortion and predation, together with final seed production, in the Vochysiaceae species studied.

Species	Area	Seed abortion	Seed predation	Seed/ovule
		(%)	(%)	(%)
<i>Callisthene fasciculata</i>	CBII	68.24	0.00	31.76
	LF	43.82	0.00	56.18
<i>Callisthene major</i>	GEF	53.20	0.00	46.80
	PARNASC	56.82	51.34	18.27
	CBII	25.34	1.74	73.40
<i>Qualea multiflora</i>	CCPIU	22.31	0.00	77.68
	PES	24.54	23.05	56.67
	PESCAN	27.51	43.97	40.00
	CCPIU	42.24	20.00	44.96
<i>Qualea parviflora</i>	LF	31.25	50.51	34.03
	PES	48.22	52.05	24.82
	PESCAN	40.13	60.23	23.81

CBII – natural areas surrounding the Capim Branco II hydroelectric dam; LF – Limoeiro farm; GEF – Glória Experimental Farm; PARNASC – *Parque Nacional da Serra da Canastra* (Serra da Canastra National Park); CCPIU – *Clube Caça e Pesca Itororó de Uberlândia* (Itororó Hunting and Fishing Club of Uberlândia); PES – Panga Ecological Station; PESCAN – *Parque Estadual da Serra de Caldas Novas* (Serra de Caldas Novas State Park).

and *Q. parviflora*.

Pre-dispersal seed predation

There was a clear distinction between the main insect groups found inside fruits and seeds of the *Callisthene* and *Qualea* species studied. The Curculionidae beetles found in fruits of *C. major* represent the largest family of beetles (Coleoptera), with 62,000 species (McKenna *et al.* 2009). These beetles are common seed predators of native plants, especially palms and legumes (Spironello *et al.* 2004; Alves-Costa & Knogge 2005; Silva *et al.* 2007), as well as cultivated plants (Vilarinho 2007; Cícero 2007).

Most seed predators of *Qualea multiflora* and *Q. parviflora* were immature or adult Buprestidae beetles (Coleoptera) and micro-Hymenoptera. The Buprestidae also constitute a large group of Coleoptera, with some 15,000 species (Bellamy & Nelson 2002). Although the major Buprestidae species are wood-borers, some are seed predators (Carson & Holsinger 2010). Insect damage to seeds and embryos usually prevents them from developing and germinating (Bradford & Smith 1977; Zhang *et al.* 1997; Mickeliunas *et al.* 2006; Ribeiro *et al.* 2007).

The seed predation rate varied among the species studied, from null in *Callisthene fasciculata* to relatively high in *Qualea parviflora* and *C. major* (60.23 and 51.34%, respectively). For *Q. multiflora*, pre-dispersal seed predation showed marked population-specific differences in seed predation rates ranging from null to 43.97%. It is of note that seed predation was greatest in areas such as the PARNASC and PESCAN, which are larger and more well-preserved. Conservation status and area size can influence seed predators, because species richness and disturbance can affect

those specialized interactions (Janzen 1975; Ehrlén 1996; Pizo 1997; García *et al.* 2000; Baldissera & Ganade 2005).

Relationship between seed abortion and predation

Janzen (1971b; 1978) suggested that mother plants increase fruit and seed production as a strategy to satiate predators and guarantee a reliable seed supply, thereby ensuring germination and consequently recruitment. This satiation strategy is corroborated by various studies (Bradford & Smith 1977; Ehrlén 1996; Steffan-Dewenter *et al.* 2001; Raimundéz-Urrutia 2008), which have shown that, although predation intensity increases in parallel with seed availability, there are always some seeds that escape predation. There is another possible strategy that would involve selective abortion of fruits and seeds as a way to deter predation (Ghazoul & Satake 2009): seed and fruit abortion during development might be a strategy not only to adjust fruit and seed set to the physiological constraints of the mother plant but also to eliminate ovaries that had been preyed upon or parasitized. For the *Qualea* species studied here, there was a positive correlation between predation and the production of viable seeds. This might support the satiation hypothesis, although predation and seed production might both be linked simply to the better pollination observed at the sites that were larger and more well-preserved.

Our data on the *Callisthene* species studied here might support the idea that seed abortion acts as a counter strategy against predation, because those species showed high abortion rates and (mostly) low predation rates. It is conceivable that, if oviposition occurs early during fruit development, as it does in some Legume species (Janzen 1971a), abor-

tion would eliminate many of the ovules in which insects had oviposited, thus reducing the seed predation rate. To a certain extent, the same reasoning could be used for the two *Qualea* species studied here.

In general, the species studied are under pressure from a variety of factors, which limits their reproductive success. As self-incompatible species, they present relatively low rates of conversion from flowers to fruits under natural conditions (Santos 1997; Oliveira 1998), and we found that many of their fruits presented seed abortion. In addition, we found that some of their seeds did not fully develop, because of pre-dispersal predation. We would expect seed production to be a bottleneck in the reproductive process. Nevertheless, despite losses to abortion and pre-dispersal predation, seed production in the species studied was similar to that reported for other, phylogenetically unrelated, species in the Cerrado Biome (e.g. Oliveira & Silva 1993; Raimúndez-Urrutia 2008).

Acknowledgments

We thank the managers of the sampled areas for allowing us to collect fruits and seeds for this study. We are also grateful to Kleber del Claro, Larissa Nahas Domingues and Denise Lange, for their assistance in identifying the predatory insects; to Diana Salles Sampaio, for the comments and suggestions that helped us organize the data and text; and to the two anonymous reviewers, who suggested different approaches, which improved the manuscript. The study was funded by the *Fundação de Amparo à Pesquisa do Estado de Minas Gerais* (FAPEMIG, Research Grant no. CRA 2127/09) and by the Brazilian *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES, Master's scholarship to LNC).

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