Effects of the seed predator *Acanthoscelides schrankiae* on viability of its host plant *Mimosa bimucronata*

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ABSTRACT

Seeds of *Mimosa bimucronata* are heavily infested (pre-dispersal predation) by the bruchid beetle *Acanthoscelides schrankiae* in Brazil. In this study, firstly we set up experiments to assess seed germination under seven and six different light and temperature regimes, respectively, and then we evaluated the ability of seeds to germinate after predation. We tested the hypothesis that the non-predated seeds from infested fruits may respond differently when set for germination than those seeds of non-infested fruits. We also hypothesized that predation may increase the production of unviable seeds. Seeds under 18 hours of light presented the highest percentage of germination, and the alternating temperature 20-30 ºC was considered as optimum for germination (abnormal seedlings were not considered as a successful germination). Germination of seeds from non-infested fruits was significantly higher than germination of non-predated seeds from infested fruits, and predation also caused a significant increase in the proportion of dead seeds. Our results also show a positive correlation between proportions of unviable seeds and predated seeds. These results demonstrated that seeds of *M. bimucronata* are strongly affected by predation because predated seeds did not germinate and non-predated seeds had their viability reduced when located in infested fruits, supporting our hypothesis.

Key terms: *Acanthoscelides schrankiae*, Bruchidae, germination, *Mimosa bimucronata*, seed predation.

INTRODUCTION

Herbivory is defined as the consumption of plants by animals, and encompasses different types of interactions. For example, seed and seedling herbivory are predatory interactions because herbivores kill individuals in the population (Strauss and Zangerl, 2002), and animals that feed mainly or exclusively on seeds are termed granivores (Hulme and Benkman, 2002). Granivory can be extremely important for limiting the size of plant populations (top-down effects) because high mortality rates are expected when predation is severe, decreasing seedling densities in future generations (Crawley, 1992; Hulme, 1998; Crawley, 1997; Gurevitch et al., 2002). Therefore, granivores play a crucial role on regeneration, colonization ability, and spatial distribution of plants (Louda et al., 1990; Myster and Pickett, 1993; Hulme, 1997; Castro et al., 1999; Forget et al., 1999; Picó and Retana, 2000).

Among the most important seed predators are the insects, mainly those from Coleoptera, Diptera, Lepidoptera, and Hemiptera orders (Janzen, 1971). Bruchid (Coleoptera) beetles (62 genera worldwide) are seed-eating insects (larval stage) that feed in the seeds of about 34 plant families, and many species are of considerable economic importance, inflicting damages on cultivated plants (Cardona, 1989; Baier and Webster, 1992; Nápoles, 2002). As most bruchids are host specific, they naturally regulate plant populations by killing their seeds, giving no options for plants to disperse (Janzen, 1975; Southgate, 1979; Nápoles, 2002). The bruchid beetle

Acanthoscelides schrankiae (Horn) feeds in the seeds of twelve plant species (10 *Mimosa*, 1 *Acacia*, and 1 *Schrankia*) even though there are new host plants to be discovered, mainly in tropical areas (Nápoles, 2002), and this species can be found in Bahamas, Ecuador, the United States, Mexico, the Dominican Republic, Venezuela, and Brazil (JR Nápoles, personal communication). Very little is known about this bruchid beetle as information in the literature is rather scant (Johnson, 1983, 1990; Silva et al., 2007) and the effects of predation on seed germination by this bruchid are still unknown.

Mimosa bimucronata (DC.) Kuntze (Fabaceae: Mimosoideae) is an endemic perennial tree (or shrub) from Brazil, Paraguay, Argentina, and Uruguay (Burkart, 1959), reaching around 10 m high with intense ramification of branches. This plant grows along wetlands and riverbanks, and on the shore of lakes, where few individuals can form dense aggregations (Lorenzi, 2000). *Mimosa bimucronata* is an important agent for restoration of degraded areas, and produces good quality wood for charcoal utilization (Reitz et al., 1983; Marchiori, 1993). However, *M. bimucronata* is also an important weed when dense populations grow in pasture areas (Lorenzi, 2000) because its large branches with thorns can hamper cattle from accessing water and fresh grass. Moreover, only a few grasses can grow below the canopy of these plants due to shading, which causes loss of areas for grass management. Most *M. bimucronata* seeds (located in craspedium fruits) have a semi-permeable seed coat and scarification (mechanical or chemical) increases the speed of germination (Ferreira et al., 1992; Ribas et al., 1996). Low humidity usually decreases their germination potential (Ferreira, 1976; Ferreira and Callegari-Jacques, 1980), and either hot water at 80ºC (Ribas et al., 1996) or sulphuric acid application for 10 minutes (Fowler and Carpanezzi, 1998) are satisfactory methods to increase the performance of seed germination. Despite the economic importance of *M. bimucronata*, little is

known about its biology, ecology, and associated organisms. Thus, as their seeds are heavily infested by *A. schrankiae* in Brazil it is worthwhile to understand the effects of seed predation on germination.

As *A. schrankiae* kills *M. bimucronata* seeds during consumption not allowing germination (see Results), we tested the hypothesis that the non-predated seeds from infested fruits may respond differently than those seeds of non-infested fruits when set for germination because differences in resource allocation may occur. Therefore, dry weights and water contents of non-predated seeds from infested and non-infested fruits were compared. As differences in seed germination between infested and non-infested fruits were expected, we investigated whether predation by *A. schrankiae* reduces seed quality by increasing the proportion of unviable seeds in *M. bimucronata* plants. Although there are some studies focused on seed technology of *M. bimucronata*, regional differences in seed germination are usually expected (Cruz et al., 2003; Schütz and Rave, 2003). Thus, as there are no published studies focusing on seed germination of this plant species in our locality (state of São Paulo, city of Botucatu), we finally set up experiments to assess seed germination under seven and six different light and temperature regimes, respectively, so as to determine the best environmental conditions for seed germination.

MATERIAL AND METHODS

Study site and collection of fruits

Seeds of *M. bimucronata* were randomly collected from twenty plants selected for their uniform size, located in the city of Botucatu-SP (Brazil), at the Faculdade de Ciências Agrárias of the Universidade Estadual Paulista – Unesp (22° 50' 52" S; 48° 25' 46" W). The climate in the area is typically mesotherm of dry winter (Koeppen – Cwb) (Carvalho et al., 1983), and all plants grow by a lake, surrounded mainly by grasses. After collection, all

fruits were exposed to fresh air in a shady environment for drying. After drying, fruits were separated in two groups (A and B) to set up the experiments. Fruits from groups A and B were arranged to evaluate the effects of light and temperature on seed germination, and the effects of seed predation on germination, respectively.

Effects of light and temperature on seed germination

Firstly, the infested and non-infested fruits were separated in the laboratory and, after dissection, non-predated seeds (we designated all non-predated seeds viable seeds) from non-infested fruits were put into transparent Gerbox containers (11 cm x 11 cm x 4 cm) lined with soaked (distilled water) wet filter papers. The percentage of germination was evaluated under five constant (15ºC, 20ºC, 25ºC, 30ºC, and 35ºC) and an alternating temperature (20-30ºC), and also under seven light conditions (0h, 2h, 4h, 8h, 12h, 18h, and 24h). The alternating temperature had the light period corresponding to the highest temperature. Each treatment was repeated 8 times with 25 seeds for each replicate (one Gerbox). Gerbox containers were wrapped in transparent plastic bags to prevent water losses. Sulphuric acid was applied to all seeds for 10 minutes to increase the speed of seed germination (Fowler and Carpanezzi, 1998). For the temperature and light tests, seeds were kept under 8 hours of white light [fluorescent 15 W lamps (78 μmol s^{-1} m^{-2})] and 25ºC, respectively (Brasil, 1992). It is important to mention that the abnormal seedlings were not considered as a successful germination. Therefore, the abnormal seedlings were excluded from the calculation of the percentage of germination. Plants that presented shoots without roots, and vice-versa, were classified as abnormal seedlings.

To evaluate if water contents (%) of seeds were homogeneous, immediately before each germination test, seeds were put into iron cans (50 seeds per can) and weighed with a semi-analytical scale (wet weight). After weighing, seeds were dried (105 ± 3ºC for 24 hours) and reweighed

(Brasil, 1992). Therefore, water contents were calculated by subtracting the wet from the dry weights. Each can corresponded to a replicate, and twelve and fourteen replicates (equivalent to two replicates per temperature and light regime) were adopted before temperature and light experiments, respectively.

Two ANOVA (Zar, 1999) were run to compare the mean percentage of germination between the different temperatures and light regimes, respectively, and paired comparisons of means were run by the Least Significant Difference (*LSD*) test (Zar, 1999) when appropriate. The Student's *t*-test (Zar, 1999) was run to compare the mean percentage of water contents between seeds used for light and temperature experiments. For statistical analyses, germination and water contents data were transformed (arcsine √prop).

Effects of seed predation

Likewise, we first separated the infested from the non-infested fruits, but after dissection, predated and non-predated seeds were removed from the fruits. Viable seeds from infested and non-infested fruits were then separated and put into transparent Gerbox containers lined with wet filter papers. The percentage of germination and the percentage of dead seeds from infested and non-infested fruits were compared by the Student's *t*-test (data in arcsine √prop). This experiment was carried out at the alternating temperature 20-30ºC under 18 hours of light, since we considered these conditions as optimum for seed germination (see Results). Each treatment was repeated 15 times with 25 seeds for each replicate, and Gerbox containers were wrapped with transparent plastic bags to prevent water losses. Sulphuric acid was applied for 10 minutes on all seeds to increase the speed of seed germination. Immediately before the germination tests, water contents of seeds were determined as described above, and 20 replicates were considered for each treatment (viable seeds from infested and non-infested fruits). The Student's *t*-test was run (data in arcsine √prop) to compare

the mean percentage of water contents of seeds. To evaluate if seeds damaged by *A. schrankiae* were able to germinate, the predated seeds were also put into Gerbox containers (8 replicates with 25 seeds each) at the optimum temperature and light conditions estimated. Sulphuric acid was not applied on seeds in this case.

After all germination tests, we returned to the study site and 200 new fruits were collected at random from each selected plant; therefore, each plant represented a replicate (4,000 fruits distributed in 20 replicates) for statistical analyses. Again, we separated non-predated seeds from the infested and non-infested fruits; however, in this case, the number of unviable seeds was also recorded. We considered as unviable those aborted seeds that presented irregular development during fruit maturation. Usually, unviable seeds of *M. bimucronata* present dark color and have much less weight than viable seeds, being unable to germinate. For the infested fruits, the mean number of seeds attacked per fruit was also estimated. All viable seeds from each plant were counted and put into small paper bags separating those from infested and non-infested fruits. After that, seeds were dried (105 ± 3°C for 24 hours) and then weighed with a semi-analytical scale. Therefore, dry weights of viable seeds were estimated for each plant. Due to the unequal number of viable seeds, the dry weight was divided by the number of weighed seeds (weight estimated for one seed) and these values were used for statistical analyses. To estimate the proportion of unviable seeds, the number of unviable seeds recorded for each plant was divided by the total number of non-predated seeds per plant, and these calculations were computed only for seeds

from infested fruits. The Student's *t*-test was run to compare the mean dry weights of viable seeds between infested and non-infested fruits. Finally, we estimated the proportion of predated seeds per plant (n° of predated seeds/total n° of seeds), and a correlation analysis (Zar, 1999) between the proportion (arcsine √prop) of predated seeds and the proportion (arcsine √prop) of unviable seeds among plants was computed.

For all experiments, seven-day-old germinated seeds were used for recording the percentage of germination, and we considered as germination the emergence of 2 mm of radicle.

RESULTS

Comparison of mean percentages of seed germination between the different temperatures did not show significant differences (Table 1). However, for the light levels investigated, significant differences in seed germination were observed (Table 1). Seeds under 18 hours of light presented the highest percentage of germination, and germination was reduced to zero in full darkness (Fig. 1). Germination was also significantly reduced for seeds under 24 hours of light (Fig. 1). In the absence of light, we found 98% of abnormal seedlings and 2% of dead seeds, justifying zero percent of germination in this condition. Under 24 hours of light, the percentage of abnormal seedlings was also relatively high (27.5%). Although significant differences between light regimes were observed, seeds responded well from 2 to 18 hours of light, since the percentages of germination were similar (Fig. 1). Seeds were very homogenous for

TABLE I

Results from two ANOVA comparing the mean percentages of germination among the different temperatures and light regimes

Source of variation	Degrees of freedom	Mean Square	F	P-values
% Germination (temperatures)	5	0.0495	1.4097	0.2405
% Germination (light levels)	6	1.6140	80.2421	< 0.001

light and temperature experiments as their mean water contents did not differ statistically (t = -0.9803; df = 24; P = 0.3367; N = 14 and N = 12, for light and temperature treatments, respectively).

Even though seed germinability did not differ between the temperatures tested, the alternating temperature 20-30°C was considered as optimum for germination because it presented the highest mean percentage of germination (Fig. 2). Therefore, the alternating temperature 20-30°C under 18 hours of light was considered as optimum for seed germination, explaining the evaluation of the effects of seed predation under these conditions. The mean water contents of seeds from infested and non-infested fruits did not differ statistically (t = -0.9606; df = 2; P = 0.4381; N = 2, for each treatment). However, the mean percentage of germination of viable seeds from non-infested fruits (87.73% ± 11.36%) [Mean (± Standard Deviation)] was significantly higher than the mean percentage of germination of viable seeds from infested fruits (59.73% ± 13.39%) (t = -6.006; df =

28; P < 0.001; N = 15 for each treatment). Predation by *A. schrankiae* also caused an increase in the proportion of dead seeds, as the mean percentage of dead seeds was significantly higher in infested (26.4% ± 10.56%) than in non-infested fruits (5.6% ± 6.56%) (t = -6.640; df = 28; P < 0.0001; N = 15 for each treatment). Predated seeds were strongly affected because we observed that all predated seeds did not germinate. For all collected fruits (infested + non-infested) a mean of 6.39 [± 1.23 (SD)] seeds per fruit was found, and the infested fruits presented a mean of 3.88 [± 1.55 (SD)] predated seeds per fruit.

Although the mean dry weights of viable seeds from infested and non-infested fruits did not differ statistically [t = 0.879; df = 34; P = 0.3857 (N = 20 and N = 16 for infested and non-infested fruits, respectively, as four plants did not present non-infested fruits)], predation by *A. schrankiae* may affect the production of unviable seeds because a significant positive correlation between the proportion of unviable seeds and the proportion of predated seeds was observed among trees (Fig. 3).
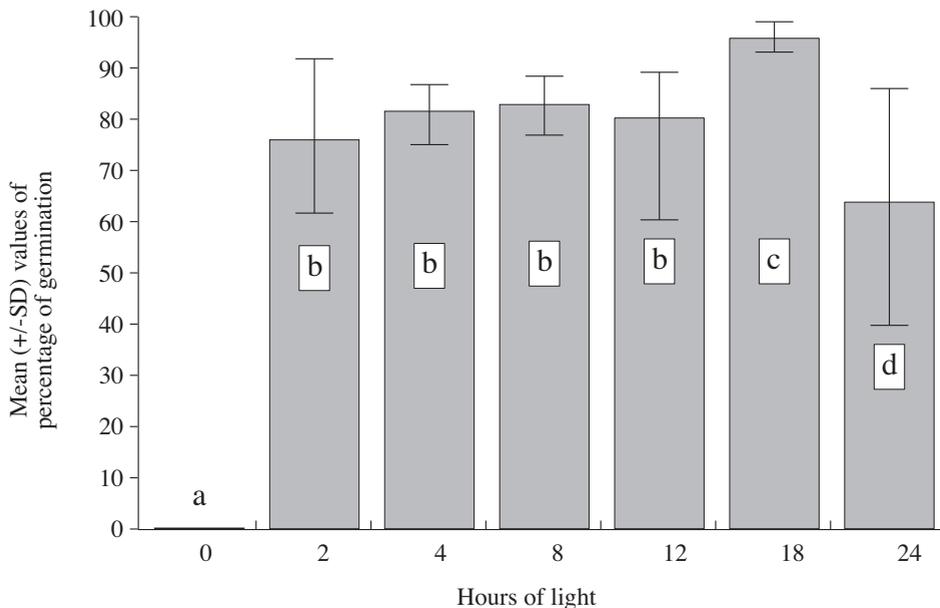
Figure 1: Mean (± Standard Deviation) values of percentage of germination of seeds under different light regimes. Means followed by different letters differed statistically by the Least Significant Difference (*LSD*) test (P < 0.05). Abnormal seedlings were not considered in the calculations.
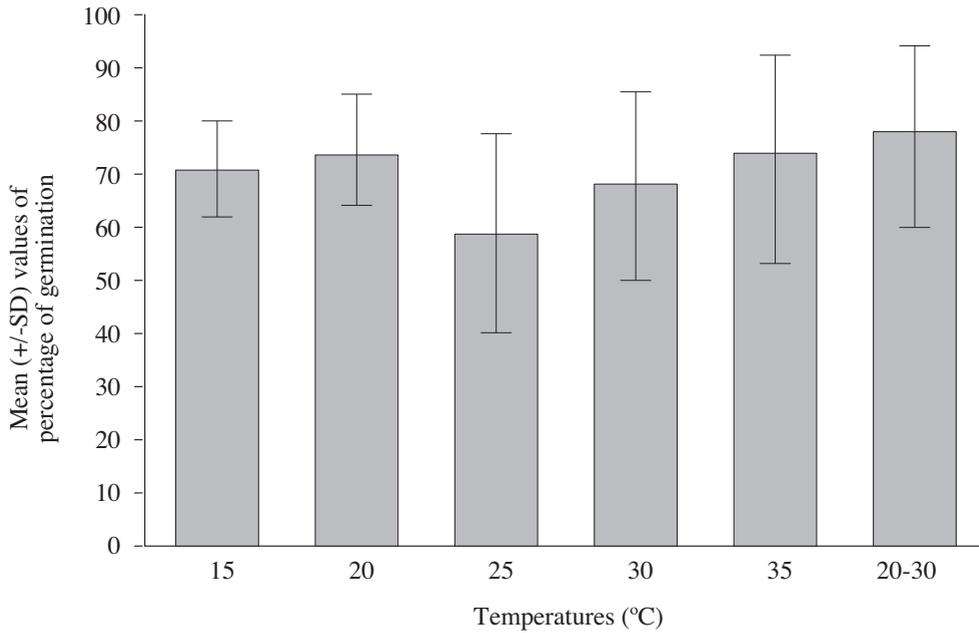
Figure 2: Mean (± Standard Deviation) values of percentage of germination of seeds under different temperatures. Means did not differ statistically by ANOVA test ($P > 0.05$). Abnormal seedlings were not considered in the calculations.
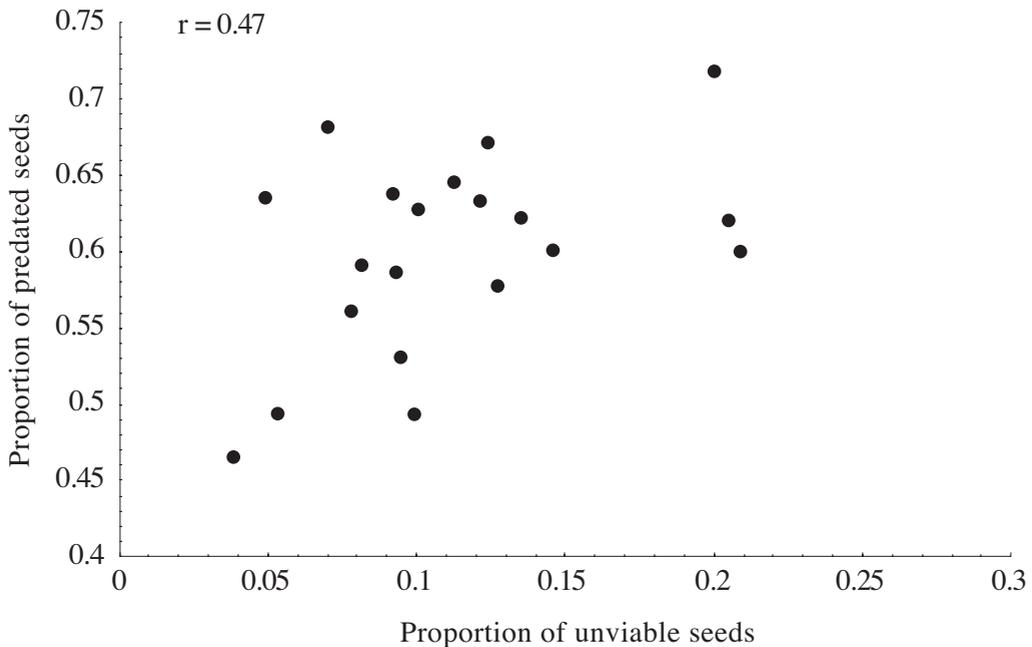
Figure 3: Positive correlation between the proportion of unviable seeds and the proportion of predated seeds among trees [$P = 0.0369$; $N = 20$ (results from transformed data)]. Each point represents untransformed data from a specific plant.

DISCUSSION

Although we considered the alternating temperature 20-30ºC as the best condition for seed germination, the impact of different temperature regimes on seed germination was similar for all tested temperatures (Fig. 2). Existing studies concerning *M. bimucronata* seed germination usually show low temperature amplitudes and the temperatures of 25 and 30ºC were frequently used (Ferreira, 1976; Ferreira and Callegari-Jacques, 1980; Ferreira et al., 1981; Ferreira et al., 1992; Ribas et al., 1996; Fowler and Carpanezzi, 1998). However, although not significant, we observed that the lowest mean percentages of germination were reached at 25ºC and 30ºC (Fig. 2). Curiously, the alternating temperature 20-30ºC was not used as a control treatment for seed germination in such studies.

In spite of the fact that temperature did not have a strong effect on seed germination, significant differences in germination among different light regimes (Fig. 1) indicate that seeds of *M. bimucronata* can be light sensitive. With respect to the effect of light on seed germination of *M. bimucronata*, more conclusive studies are needed. Ferreira (1976) reported that either the presence or absence of light did not interfere on germination of *M. bimucronata* seeds. However, we showed that germination was significantly increased under 18 hours of light, and seeds did not germinate in complete absence of light (Fig. 1). Yet, germination was significantly reduced for seeds at 24 hours of light (Fig. 1). Our findings also differ from Ferreira et al.'s (1981) study, which shows that the absence of light did not inhibit germination. However, recall that the abnormal seedlings were not considered as a successful germination in our experiments.

The germination response of a given species is assumed by studying individuals from some area that are mixed together, providing information on the average response of a population (Cruz et al., 2003). Assuming that other populations respond similarly, extrapolations are made.

However, germination responses of seeds from different sources are quite variable. Such variations may occur either between populations, different individuals in populations or different parts of the same plant (Thompson, 1975; Westoby, 1981; Silvertown, 1984; Martin et al., 1995; Schütz and Rave, 2003; Cruz et al., 2003). Therefore, not all seeds may equally germinate when exposed to certain stimuli, which may be advantageous for seedling establishment of some species that usually experience high variability in environmental conditions (Venable, 1985; Cruz et al., 2003). Results from the Ferreira's (1976) and Ferreira et al.'s (1981) studies differed in part from our findings. As seeds used in those experiments were collected from plant populations naturally occurring in the state of Rio Grande do Sul (Brazil) and we collected seeds from a plant population located in the city of Botucatu, state of São Paulo, it is possible that such differences in germination occurred due to different environmental conditions (temperature, light intensity, water supply, etc…) that *M. bimucronata* populations have been experienced for several generations.

Herbivores have been considered important agents in enhancing germination of hard seeds (Halevy, 1974; Karban and Lowenberg, 1992). For example, Takakura (2002) suggested that the specialist bruchid beetle *Bruchidius dorsalis* (Fahraeus) played a crucial role in the seed germination of its host plant, *Gleditsia japonica* (Miquel), because in some circumstances germination was facilitated after predation. In this study, however, it was shown that *M. bimucronata* seeds could not germinate when damaged by *A. schrankiae*. For seeds with large amounts of cotyledonary reserve [some tropical trees (> 5g)] germination may occur even if the cotyledon is partially damaged (Dalling et al., 1997; Dalling and Harms, 1999). In contrast, *M. bimucronata* seeds may be smaller than seeds from those trees (<0.01g, MN Rossi, unpublished data) and developing larva can also damage the embryo when seeds are not completely mature. Therefore, *M. bimucronata* seeds

apparently cannot tolerate damages by *A. schrankiae* larvae not even before the complete larval development, this relationship being entirely antagonistic. A similar comment was presented by Takakura (2002) to explain the lack of germination of *G. japonica* seeds after being damaged by developed larvae of *B. dorsalis*.

The higher percentage of germination of seeds from non-infested fruits than from infested fruits clearly suggests that predation affects germination of viable seeds. In addition, the proportion of dead seeds was significantly increased in the infested fruits. This, combined with the significant positive correlation between the proportion of unviable seeds and proportion of predated seeds (Fig. 3), corroborates our hypothesis that *M. bimucronata* seeds can be affected by predation in several ways, at least in this studied site. The mechanisms by which predation interferes negatively on germination of viable seeds of *M. bimucronata* are not clear. Probably, they are associated with differences in the capacity of seeds from infested and non-infested fruits in allocating resources during fruit maturation. As, in the average, fruits were heavily infested in the studied site (3.88 seeds per fruit), it is possible that a considerable ingestion of essential nutrients by *A. schrankiae* larvae caused a reduction in the photoassimilate flux in fruits, which would reduce the assimilation of nutrients by the remaining seeds, thus reducing their viability. However, as water contents and dry weights of seeds did not differ between infested and non-infested fruits, biochemical studies aimed to compare the nutritional status of viable seeds from infested and non-infested fruits are encouraged in order to understand the mechanisms involved.

Our findings also have important practical implications. For example, effects of pre-dispersal seed predation on germination of viable seeds should be investigated in cultivated crops because damages caused by seed predators may be more severe than expected. Therefore, field experiments comparing germination of 'healthy' seeds from infested and non-

infested fruits are needed in crops that experience high levels of seed beetle predation during fruit maturation. Another important implication of our results resides in biological control strategies of weeds. As in some cases bruchid beetles can be useful as biocontrol agents (Kassulke et al., 1990; Wilson and Flanagan, 1991), the evaluation of their efficacy should be extended by evaluating the effects of predation on viability of non-predated seeds when predation occurs in the pre-dispersal phase.

In short, this study firstly suggests that seeds of *M. bimucronata* may respond differently to germination depending of the origin of the populations. Secondly, we demonstrated that seeds of *M. bimucronata* are strongly affected by predation because predated seeds did not germinate and non-predated seeds had their viability reduced when located in infested fruits. Therefore, we believe that this system provides an excellent opportunity to investigate many important basic and applied questions.

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