

Abortion and predispersal seed predation in the American Proteaceae *Roupala montana* Aubl.

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ABSTRACT.—Two populations of *Roupala montana* Aubl. growing in a shrubland and in a forest were studied to assess the relative contribution of abortion and predispersal seed predation to the final seed set. Predispersal reproductive losses were similar to those observed in Australian and African Proteaceae. In both populations a final seed set of less than 2% was determined. Although *R. montana* produced conflorescences with numerous flowers (≥ 100), a high proportion of confructescences had few fruits (≤ 10) or were even barren due to flower-fruit abortion (97% in the shrubland and 96% in the forest), which represents the main constraint to seed production. Seed abortion and seed predation were of a lower magnitude than flower-fruit abortion. In the shrubland the only seed predator was a weevil, while in the forest at least two seed predators and hymenopterous parasitoids were found. Fruits with a single formed seed (the other one aborted) suffered less predation than fruits with two formed seeds.

KEYWORDS.—low seed set, predispersal seed losses, flower-fruit abortion, seed abortion, seed predators, parasitoids

INTRODUCTION

The family Proteaceae comprises about 1 500 species mainly concentrated in southwestern Australia and the Cape of South Africa, although there are some representatives in tropical regions of Central and South America (Johnson and Briggs 1975; Prance and Plana 1998). The proposed 83 American species are grouped in eight genera, all belonging to the subfamily Grevilleoideae, and five of the genera are endemic to this region (Prance and Plana 1998). Different reproductive features have been described in the various proteaceous species, with hermaphroditism as the predominant sexual system (Johnson and Briggs 1975). In plants with hermaphroditic flowers the progeny represents only a small fraction of their fecundity due to the loss of reproductive structures before dispersal, and the fruits to flower as well as the seeds to ovule ratios are frequently less than one (Stephenson 1981; Lee 1988; Ayre and Whelan 1989; Ehrlén 1991). Reproductive studies in Australian and African Proteaceae have pointed out low fruit and seed

production as a characteristic of the family, with mean seed set values below 10% of their fecundity (Lamont et al. 1985; Ayre and Whelan 1989; Hermanutz et al. 1998; Lamont and Groom 1998).

In plants the main factor of predispersal loss of reproductive structures is abortion, which limits considerably the amount of seeds produced (Stephenson 1981; Sutherland 1986). This loss may occur by massive abortion of ovules, expressed as flower and/or fruit abortion, or by selective abortion, expressed as ovule and/or seed abortion as individual units. Flower-fruit abortion has been regarded as the main constraint to seed production in a large number of plants because it has a higher selective value than ovule and seed abortion (Stephenson 1981; Sutherland 1986, 1987; Ramírez 1992), and it has been claimed as the primary reproductive loss in proteaceous species (Lamont et al. 1985; Ayre and Whelan 1989).

Proximal (ecological) and ultimate (adaptive) hypotheses have been proposed as explanations for the low fruits to flower ratios observed in hermaphroditic Protea-

ceae, because the loss of a great proportion of flowers does not lend a clear benefit to these plants in terms of overall fitness (Ayre and Whelan 1989). Sometimes, transient ecological conditions (i.e. insufficient pollen reaching the stigmas due to pollinator or genetically compatible pollen limitations, restriction of resources to transform all the fertilized flowers into fruits, or predation of flowers and/or ovules) might explain the high rates of abortion of flowers and fruits (Ayre and Whelan 1989). Nevertheless, the high rates of abortion could be adaptive if a benefit is obtained regardless of the loss of an important proportion of the flowers (i.e. production of excess flowers acts as a mean to attract more pollinators, increases the male success through the pollen donation role of hermaphroditic flowers, allows the selection of progeny with higher fitness among a greater number of pollinations and/or fertilizations, or allows the production of more fruits and seeds in a season with more available resources) (Ayre and Whelan 1989).

Another factor of reproductive loss before dispersal is seed predation. Although predispersal seed predation is not a reproductive factor per se, it may cause the destruction of a great proportion of the seeds produced and in some cases this constitutes the main limitation for the number of seeds to be dispersed (Janzen 1971; Vaughton 1990). The extent of predispersal seed predation depends both on plant features that protect them against predators and on external factors like vegetation structure, competition with other seed predators and/or the presence of their natural enemies (Janzen 1971; Jermy 1993; van der Meijden and Klinkhamer 2000). Weevils, moths and wasps have been reported as seed predators on Australian Proteaceae, causing losses from 5% up to 60% of the fruits and seeds produced (Scott 1982; Zammit and Hood 1986; Auld and Denham 2001).

The genus *Roupala* Aubl. is one of the five proteaceous genera endemic to America and it grows from Central America to Perú and Brazil, grouping ca. 55 species (Prance and Plana 1998; Steyermark 2004). In Ven-

ezuela it is represented by 12 species, with *Roupala montana* Aubl. as the most widespread in different community types. The aim of this study was to explore the predispersal reproductive losses due to abortion and seed predation in *R. montana* in order to increase the baseline information about its reproductive biology. The results can give general trends in the reproductive losses of this species and determine if these losses are comparable with those observed in Australian and South African Proteaceae. At the study sites we determined the losses due to each one of the abortion levels and by predispersal seed predation. Also, we assessed which of the predispersal seed losses may be regarded as the main limitation to seed production and the reproductive efficiency was estimated. Additionally, the seed predators were identified and the features of seed predation was described.

MATERIALS AND METHODS

Study sites

Samples of reproductive structures were collected from two natural communities in Venezuela. One corresponds to a mesothermic shrubland located at the northern-central portion of the Gran Sabana Plateau, in southern Venezuela (Parque Nacional Canaima, Estado Bolívar, 5° 45' N-61° 24' W, 1 380-1 400 m asl). Such mesothermic shrublands are characterized by the predominance of evergreen sclerophyll shrubs clustered in small and dense groups separated by bare areas. These shrublands develop over deep white sandy soils of alluvial origin, described as very poor due to their low nutrient content (Huber 1994). The other community corresponds to a cloud forest, where areas of original vegetation are intermingled with extensive disturbed areas, and *R. montana* remains among the original species of the forest (Aristeguieta and Matos 1959). This forest is located in northern Venezuela, at the Coastal Cordillera (Bosque de los Guayabitos, Estado Miranda, 10° 24' N-66° 52' W, 1 200-1 430 m asl).

Study species

Roupala montana Aubl. is a shrub or medium-sized tree that can reach a height of 15 m, but in these study sites individuals did not grow more than 5 m high. The flowers are arranged in pairs (true inflorescences), forming a higher order unit named conflorescence (Johnson and Briggs 1975). Conflorescences are axillary or apical racemes, 7 to 15 cm long, with numerous flowers. The flowers are hermaphroditic, white, creamy or greenish white, fragrant, 8 to 15 mm long, with two pendulous ovules in the ovary. The fruit is best described as a hard follicle, with two winged and compressed seeds. This species presents protandry (anthers dehiscence prior to stigma receptivity), herkogamy (spatial separation between anthers and stigma) and a self-incompatibility system, all of which render this species xenogamous (Oliveira and Gibbs 2000).

Number of reproductive structures

Twelve individuals in the shrubland and fifteen in the forest were used to collect reproductive structures. Conflorescences/confructescences were treated as the reproductive units. Ten to twenty units were sampled per plant depending on their availability. Conflorescences were preserved in 70% alcohol, individually separated in paper bags, and the number of flowers was determined on each one. Flowers in anthesis or well developed floral buds from the base, middle and apical zone of the conflorescence were dissected to establish the number of ovules per ovary. The number of fruits was recorded from mature confructescences that were kept individually in single paper bags. Barren confructescences were also counted. All mature fruits were opened and examined in the laboratory to assess the total number of seeds per fruit. This total number included normal (well-formed) and aborted (non well-formed) seeds. The latter showed a developed wing and an undeveloped embryo. The number of aborted seeds was counted in each fruit. Fruits were scored either with none or with one aborted seed.

No fruits containing two aborted seeds were observed. The number of preyed upon seeds per fruit (seeds with the embryo damaged or with an evident damage to the cotyledons due to insect larvae activity) was also determined directly. Fruits were scored into three categories: zero, one or two preyed upon seeds.

Reproductive losses: abortion and seed predation

Flower-fruit abortion was estimated as $1 - [\text{number of mature fruits per confructescence} / \text{number of flowers per conflorescence}]$. Flower and fruit abortion were considered together because both determine the final number of mature fruits in the confructescence. Ovule abortion was also estimated as $1 - [\text{total number of seeds in all the fruits} / \text{total number of ovules in these fruits}]$. Seed abortion was calculated relating the number of aborted seeds in all the examined fruits to the total number of seeds in these fruits. Seed predation was estimated relating the number of preyed upon seeds in all the examined fruits to the number of well formed seeds in these fruits (after subtracting aborted seeds). All the estimations were done using mean values and all the losses were expressed as percentages.

Final reproductive efficiency

Final reproductive efficiency may be regarded as the proportion of seeds that remains to be dispersed after predispersal losses occurred. This estimation also refers to the conflorescence as the reproductive unit. It was calculated as $[\text{final number of seeds per fruit} \times \text{number of fruits per confructescence}] / \text{number of ovules per conflorescence}$ (Ramírez 1992). The final number of seeds per fruit considers those seeds that remain after abortion and predation. This estimation also was done using mean values.

Predispersal seed predators

Fruits were collected after full maturation, when maximum damage was to be

expected. Fruit samples from both sites were placed in rearing chambers at room temperature in the laboratory. Rearing chambers consisted of plastic baskets covered with mesh bags for the aeration of the fruits. These chambers were periodically monitored to observe the emergence of adult insects. When an insect emerged from a fruit it was removed from the chamber and kept elsewhere for later identification.

Data Analysis

Owing to the sampling design, the fruits and the flowers were not counted in the same conflorescences, so comparison of flower-fruit abortion between sites was assessed performing an independence G-test (Sokal and Rohlf 1995) using mean values of flowers per conflorescence and fruits per confroctescence. The reproductive efficiency also was compared with a G-test using mean values of ovules, flowers, fruits and final seeds. To compare seed abortion and seed predation the test was performed using the total aborted, preyed upon and

formed seeds in all the examined fruits in each site. Finally, 2 × 2 contingency tables were used to ascertain whether or not there was any association between abortion and predation of the seeds in the fruits. Moreover, the contingency tables were also used to test if there was association of each level of these reproductive losses with the final number of seeds that remained to be dispersed per fruit. Cramér's contingency coefficient indicates the strength of the association between column and row variables. In all the tests a confidence level of $p \leq 0.05$ was accepted as significant. STATISTICA for Windows version 4.0 (1993) was used for data analysis.

RESULTS

Number of reproductive structures

The number of flowers per conflorescence and fruits per confroctescence at both sampling sites are shown in Fig. 1. In both sites the conflorescences had numerous flowers and the overall fruit set was low. There was a strong left skewing of the fre-

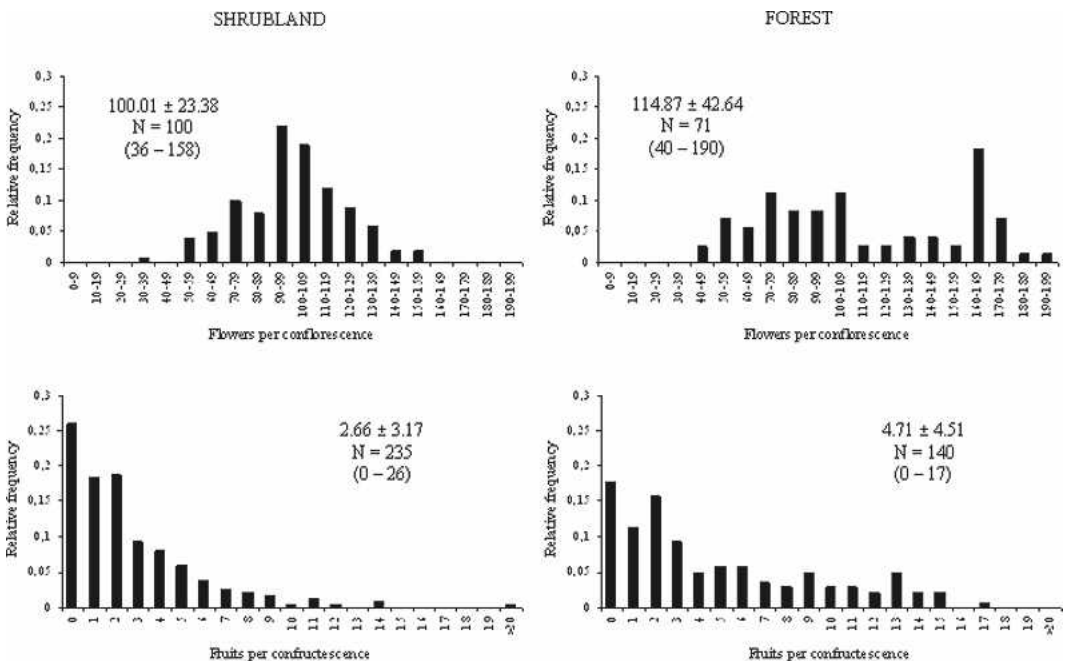


FIG. 1. Frequency distribution of flowers per conflorescence and fruits per confroctescence in *Roupala montana* in the shrubland and in the forest. Mean numbers ± standard deviations, sample sizes and ranges were indicated

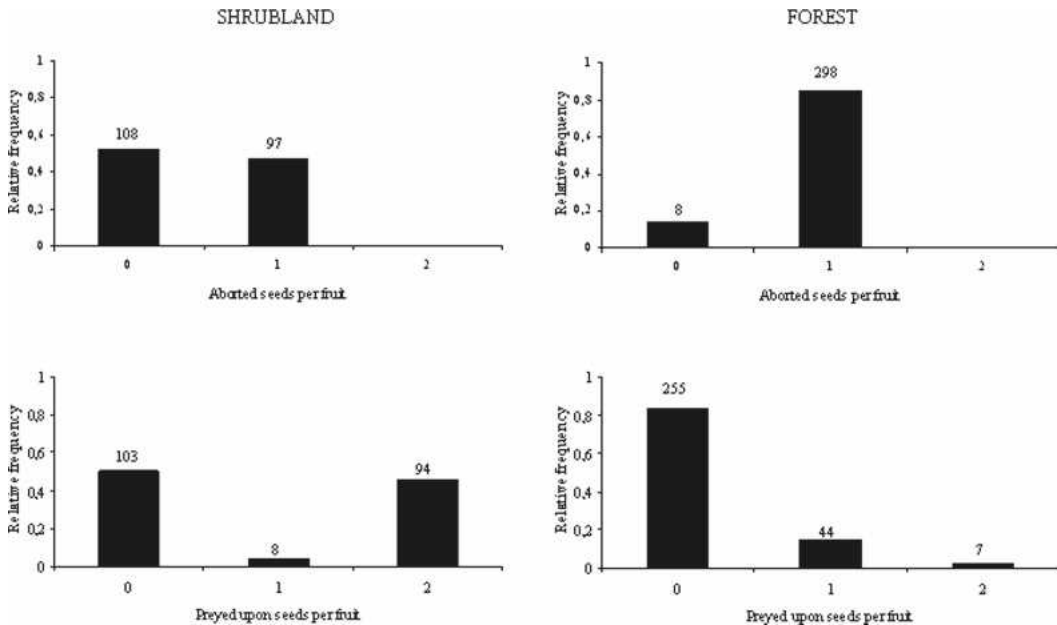


FIG. 2. Frequency distribution of aborted and preyed upon seeds per fruit in *Roupala montana* in the shrubland and in the forest. The number of fruits in each category was indicated over each column

quency distributions of fruits due to the presence of barren confructescences (61 of 235 in the shrubland and 25 of 140 in the forest) and the high proportion of confructescences with few fruits (167 of 174 confructescences with fruits in the shrubland and 94 of 115 in the forest had ≤ 10 fruits). The number of ovules was two in all the dissected flowers and the number of total seeds was also two in all the examined fruits at both sites.

Aborted and preyed upon seeds were found in the shrubland and in the forest (Fig. 2). At both sites there were fruits with no seeds aborted and with one seed aborted. The proportion of fruits with no seed abortion in the shrubland was similar to the proportion of fruits with one seed aborted, while in the forest the great majority of fruits showed one seed aborted. There also were fruits which showed no seed predation, or with one or two preyed upon seeds at both sites. In the shrubland the proportion of fruits with no seed predation was similar to the proportion of fruits with the two seeds damaged, while in the forest a large majority of fruits showed no seed predation.

Reproductive losses: abortion and seed predation

Overall, flower-fruit abortion was very high at both sites and the difference was not statistically significant (Table 1). Seed abortion and seed predation were of a lower magnitude than flower-fruit abortion. Seed abortion was significantly higher in the forest than in the shrubland while seed predation was significantly higher in the shrubland than in the forest.

In both sites the two seeds were preyed upon in a large proportion of the fruits with

TABLE 1. Predispersal reproductive losses and final reproductive efficiency of *Roupala montana* in the shrubland and in the forest.

	Shrubland	Forest	$G_{adj.}$
Flower and immature fruit abortion	97.33%	95.90%	0.31
Seed abortion	23.60%	48.73%	66.93*
Seed predation	62.75%	18.43%	194.43*
Final reproductive efficiency	0.76%	1.71%	0.85

G-values with asterisk are significant at $p \leq 0.001$ - $df = 1$ for all comparisons

TABLE 2. Association between seed abortion and predispersal seed predation in *Roupala montana* in the shrubland (top) and in the forest (bottom).

	Predispersal seed predation		
	0	1	2
$\chi^2 = 156.47$ d.f. = 2 - V = 87%			
Seed abortion	0	14	0
	1	89	8
			94
			0

	Predispersal seed predation		
	0	1	2
$\chi^2 = 266.88$ d.f. = 2 - V = 93%			
Seed abortion	0	1	0
	1	254	44
			7
			—

χ^2 -values were significant at $p \leq 0.0001$ for all the tests. V is the Cramér's contingency coefficient.

no seed abortion, while there was no seed predation in most of the fruits with one seed aborted (Table 2).

The association between seed abortion and the final number of seeds that remained to be dispersed per fruit at both sites is shown in Table 3. In a large proportion of the fruits when there was an aborted seed the other seed remained viable, but if there was no abortion a major proportion of the fruits did not have any seed left for dispersion (due to predation).

In the shrubland many of the fruits showed the two seeds damaged and consequently no seeds to be dispersed (Table 4). Nonetheless, a proportion of the fruits did not showed seed predation and one seed remained to be dispersed because the other was aborted, or the two seeds remained available to be dispersed. In the forest a

TABLE 3. Association between seed abortion and final seed per fruit in *Roupala montana* in the shrubland (top) and in the forest (bottom).

	Final seed set per fruit		
	0	1	2
$\chi^2 = 175.43$ d.f. = 2 - V = 93%			
Seed abortion	0	94	0
	1	8	89
			14
			—

	Final seed set per fruit		
	0	1	2
$\chi^2 = 68.80$ d.f. = 2 - V = 47%			
Seed abortion	0	7	0
	1	44	254
			1
			—

χ^2 -values were significant at $p \leq 0.0001$ for all the tests. V is the Cramér's contingency coefficient.

TABLE 4. Associations between predispersal seed predation and final seed per fruit in *Roupala montana* in the shrubland (top) and in the forest (bottom).

	Final seed set per fruit		
	0	1	2
$\chi^2 = 205$ d.f. = 4 - V = 71%			
Predispersal seed	0	0	89
predation	1	8	89
	2	94	—
			—

	Final seed set per fruit		
	0	1	2
$\chi^2 = 306$ d.f. = 4 - V = 71%			
Predispersal seed	0	0	254
predation	1	44	0
	2	7	—
			—

χ^2 -values were significant at $p \leq 0.0001$ for all the tests. V is the Cramér's contingency coefficient.

major proportion of the fruits did not showed seed predation but they kept a single seed for dispersion (again, the other seed was aborted), while a smaller proportion of the fruits had their only seed damaged, thus they contained no viable seeds to be dispersed.

Final reproductive efficiency

The final reproductive efficiency of *R. montana* both in the shrubland and in the forest was statistically comparable (Table 1). Only a fraction of all the initial ovules in the conflorescences at both sites remained as formed seeds ready to be dispersed. Flow chart in Figure 3 illustrates the reproductive path from flowers to seeds indicating the specific losses of ovules at each level.

Predispersal seed predators

Fruits from both sites were infested by the same weevil. This insect was identified as a new genus near *Eulechriops* (Coleoptera: Curculionidae, Zygopinae) (C. O'Brien, personal communication). This insect attacks the embryo portion of the seeds and forms a hard pupal chamber between them and the inner side of the fruit, affecting both seeds. The adults emerge through a circular exit hole on the outer side of the fruit before it opens.

Two other types of seed damage besides

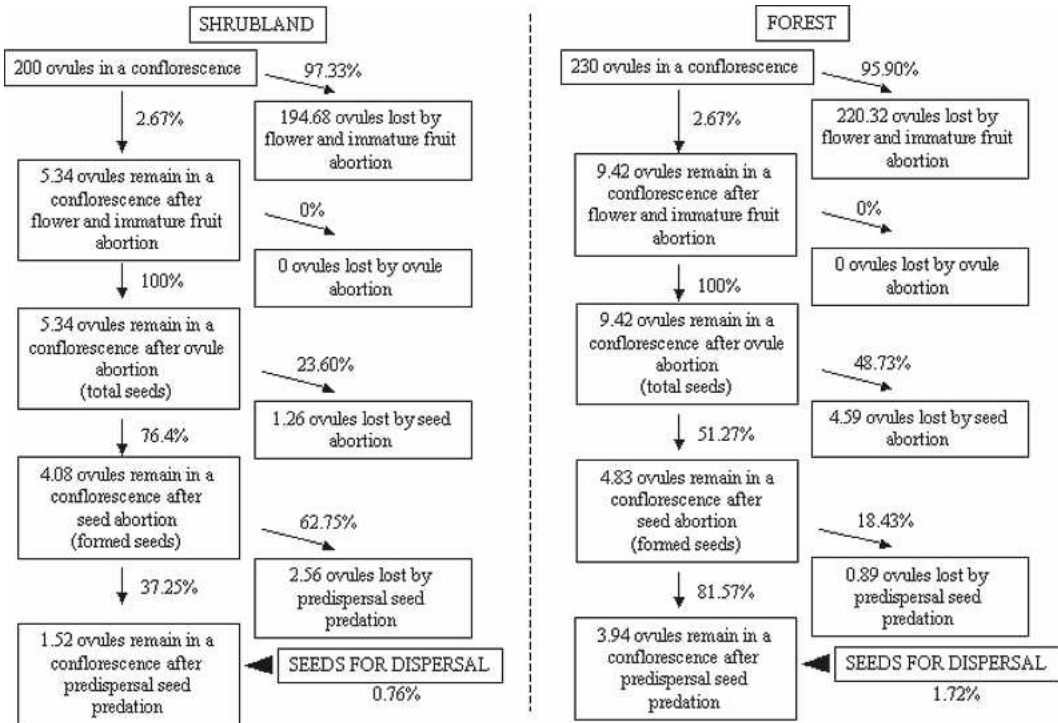


FIG. 3. Flow charts of ovule losses due to abortion and predispersal seed predation in the shrubland and in the forest. Numbers were calculated using conflorescence/confructescence as reproductive unit and related to the number of ovules that remain after each loss

that done by the weevil were observed in samples from the forest. In some fruits small punctures in the chalazal end of the embryo portion of the seed could be seen. While the cotyledons and seed coat remained almost entire the embryo axis was completely destroyed, and only one seed per fruit looked affected (sometimes the other was aborted). Exit holes smaller than the ones made by the weevil were noted near the base of those fruits. However, that kind of damage could not be associated with any adult insect. In other fruits, the embryo portion of the seeds was completely destroyed (including the seed coat) and the presence of only frass was noted inside the fruits because both seeds were affected. Circular exit holes, also smaller than those made by the weevil, were seen. When this type of damage was present some cocoons attached to the mesh bags were always noticed. These cocoons were transferred to rearing chambers and six months later adults of a *Microlepidoptera*

emerged from them. Also, three different morphotypes of Hymenoptera were reared in these same fruits. They were identified as Ichneumonidae, a family of parasitoid wasps (M. El Souki, personal communication). Two of them were recognized as males and females of the same species and the third one was separated as another species. Two other morphotypes of wasps, which were identified as Braconidae (M. El Souki, personal communication), were found in other fruits; some adults of these insects were observed inside the walls of these fruits.

From the total number of fruits showing seed predation in the forest, 2.63% exhibited damages associated to the weevil, 13.16% presented partial destruction of the seeds which could not be ascribed to any of the reared insects, and 84.21% were totally destroyed due to the presence of the microlepidopteran larvae. In all the fruits with seeds preyed upon, only one exit hole was observed, suggesting the de-

velopment of a single adult of any of the seed predators.

DISCUSSION

Reproductive losses and efficiency in seed production

Overall, the seed production of *R. montana* was very low as it represents less than 2% of its fecundity in the two study sites. In this context, seed production seems to be comparable with those observed in other species within the family Proteaceae, and specifically in the subfamily Grevilleoideae, in which fruit and seed production is very low regardless of breeding, mating and pollination system, and other reproductive features such as flower structure and fruit type (Lamont et al. 1985; Groom and Lamont 1996; Goldingay and Carthew 1998; Hermanutz et al. 1998; Kalinganire et al. 2001). Also, this species resembles the pattern of losses observed in almost all the Australian and South African Proteaceae because the same general pattern of predispersal losses of reproductive structures was observed: flower-fruit abortion was the main restriction to seed set, followed by seed losses as individual units due to abortion and predation, there was not ovule abortion, and there was a considerable proportion of barren or few-fruited confructescences. High flower-fruit abortion and the consequently low seed set are topical issues in this family and have been related with transient ecological conditions, but also with adaptive reasons that could explain why a benefit is gained regardless of an important proportion of flowers is lost (Ayre and Whelan 1989).

Seed abortion was lower than flower-fruit abortion but its contribution to the loss of fecundity at both studied sites was comparable to that observed in other Proteaceae (Scott 1982) although was higher than in other non-proteaceous species (Ramírez 1992). In proteaceous species with follicles and few seeds in the fruit, the production of single seeded fruits from ovaries with two ovules is a common observation (Scott 1982; Vaughton 1990). These fruits had two sets of seed wings and seed coats suggest-

ing not ovule but seed abortion, as was the case for *R. montana*. Factors that were pointed out to explain seed abortion in plants are mainly related with competition between developing embryos, progeny selection and resource limitations (Wiens et al. 1987; Uma Shaanker et al. 1988; Siemens & Johnson 1995). Besides, seed abortion has also been related with predispersal seed predation because it was proposed as a mechanism that may reduce the overall insect damage to seeds by decreasing the amount of available resources in a fruit (Mitchell 1977; Scott 1982; Coetzee and Giliomee 1987; Fuentes and Schupp 1998). In some Proteaceae it has been proposed that seed predation imposed a selective pressure over the number of seeds per follicle because the survival of only one seed per fruit would ensure that some species of insects do not have sufficient food for adult development (Scott 1982). Our results showed that the fruits with only one formed seed (and the other one aborted) suffered lower predation than the fruits with two formed seeds. In *R. montana*, predispersal seed predators contributed to the lowering of the fecundity and the observed pattern of seed loss due to this factor is fairly comparable with those observed in other Proteaceae (Zammit and Hood 1986; Vaughton 1990; Auld and Denham 2001).

Predispersal seed predators

Presence of weevils and moths as predators of the seeds in species of this family was noted previously in the Australian genera *Grevillea* and *Banksia* (also belonging to the subfamily Grevilleoideae as does *Roupala*), and in some cases parasitization of the larvae by wasps was described (Scott 1982; Zammit and Hood 1986; Auld and Denham 2001), although this is the first report of seed predators in an American Proteaceae. Of interest here is that proteaceous species, at least Grevilleoideae species, apparently may have evolved a relationship with these groups of insects as predispersal seed predators in many of the areas where these plants grow.

Another interesting finding was the presence of the same weevil both in the forest

(north) and in the shrubland (south), suggesting a widespread distribution of these insects in Venezuela. Moreover, the weevil seems to be a specialist seed predator on *R. montana* as it was not found on any other plant species from the shrubland, during a study which included all the shrubby species in this community (personal observation). Some previous studies in other proteaceous and non-proteaceous species reported close associations between weevils and plants, with the insects radiating out from the plants (Scott 1982; Auld 1991; Auld and Denham 2001). This proposed specificity of the weevils would signify that the ones founded in this study may predate seeds of *R. montana* wherever the plant and the weevil are both present.

All the damage observed in the fruits and seeds of *R. montana* collected in the shrubland can be invariably attributed to the weevil, since no other seed predator insects could be caught from the seeds. Conversely, in the forest the weevil could be considered as only a secondary seed predator because the damage it caused was minor related to that done by the other insects. The moth seems likely to be the major seed predator in this community as most of the damage appears to be attributable to it. There are some microlepidopteran groups which have been related to the Proteaceae as seed predators elsewhere and their specificity has also been pointed out (Powell 1980; Scott 1982; Zammit and Hood 1986). If the moths are as host-specific as the weevils, their absence from fruits from the shrubland could be due to their absence from this site. Further sampling of fruits from other sites and in other seasons should confirm or reject these suggestions and help us to understand the specificity relationships between these groups of insects and *R. montana*.

Some of the reared wasps were identified as parasitoids belonging to the family Ichneumonidae. These wasps were associated with parasitization of weevils in the seeds of some Australian Proteaceae, in which the eggs and the first-instar larvae of these predispersal seed predators were attacked (Scott 1982). Two facts support the hypothesis that the ones reared in *R. montana* are

also predated the weevil larvae. First, these parasitoids were never caught in fruits with signs of weevil damage. They grew in fruits in which there also grew the moth pupae, thus apparently the wasps were not parasitizing moth larval stages. In these fruits the damage noted in the seeds corresponded to that observed when moths grew alone. Second, the damage attributable to the weevil in the forest is the smallest of the damages observed there, and it was much less than the damage observed in the shrubland. These findings could indicate a complex trophic relationship between the weevils, the moths and the wasps, in which this last group parasitizes a very early phase of the curculionid larvae or even their eggs, hence permitting the ulterior presence of the moth larvae.

Together with the ichneumonids two Braconid wasps were caught. This group has been described as parasitoid of different orders of insects, and there even seems to be a strong relationship between them and diverse families of microlepidoptera (M. El Souki, personal communication). Braconid wasps have also been described as phytophagous, either as seed predators (Macêdo et al. 1998; Flores et al. 2005) or as gall formers in reproductive (Macêdo and Monteiro 1989) and vegetative tissues (Infante et al. 1995; Austin and Dangerfield 1998). In the present study no sign of parasitization of the moths by these wasps was detected, and one of the braconid species was reared from the fruit walls. This may indicate a galling habit, although the presence of a third kind of damage in the seeds, not attributable to the weevil nor to the moth, could also mean a phytophagous habit as seed predators. In some species of *Grevillea*, wasps were reported as the main agents responsible for seed losses due to predation, although in those cases Eurytomidae wasps were involved (Auld and Denham 2001). The scant knowledge about the biology of hymenopterans in neotropical regions preclude confirmation of the phytophagous habit of the reared Braconidae.

In conclusion, predispersal seed losses observed in *R. montana* are comparable to those observed in Australian and South Af-

rican Proteaceae, contributing to the general observation that high flower-fruit abortion and low seed set is characteristic to this family. Nevertheless, experimental manipulations and the study of more populations could confirm the relative importance of each loss in the serial adjustment of the reproductive output in this American species.

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