Control of *Avicennia germinans* recruitment and survival by *Junonia evarete* larvae in a disturbed mangrove forest in Colombia

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ABSTRACT. In the Ciénaga Grande de Santa Marta, a brackish lagoon system on the Caribbean coast of Colombia, about 60% of the mangrove forests died from hypersalinization. The die-back was first encountered in 1964 and mass mortality started in the late 1960s. Although efforts are being made to reestablish the destroyed areas, regeneration is slow, which may be partly due to *Junonia evarete* caterpillars defoliating *Avicennia germinans* seedlings. The interaction between insects and seedlings was studied. Both *J. evarete* butterflies and caterpillars were abundant during the main rainy season, the time of highest fruit production in *A. germinans*. During the dry season the herbivore disappeared. The caterpillars fed exclusively on *A. germinans* propagules, seedlings, and pneumatophores. They preferred young seedlings to older plants and did not feed on trees. At some sites, 100% of the *A. germinans* seedlings died due to the caterpillar attack. Seedlings at open, disturbed sites were attacked more than seedlings protected by small roofs and trenches or those under a closed canopy. Only seedlings protected by insect nets or seedlings germinating at the beginning of the dry season had good chances of survival. The results suggest that in the highly disturbed areas of the Ciénaga Grande regeneration of *A. germinans* is strongly inhibited by the feeding behaviour of *J. evarete* caterpillars.

KEY WORDS: *Avicennia germinans*, Colombia, herbivory, *Junonia evarete*, mangrove, plant–animal interaction, regeneration, seedlings

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INTRODUCTION

Successional processes in mangrove forests were thought to be driven primarily by physical factors associated with tidal inundation. However, the role played by fauna in shaping the forest structure and function has been revealed recently (Robertson 1991). One of the most important plant–animal interactions influencing mangrove ecosystems is herbivory. In this context, crustaceans (Beever *et al.* 1979, Camilleri 1989, Osborne & Smith 1990, Smith 1987b), insects (Anderson & Lee 1995, Clarke 1992, Ellison & Farnsworth 1993, Elster 1997, Onuf *et al.* 1977, Robertson *et al.* 1990, Whitten & Damanik 1986), and molluscs (Clarke & Myerscough 1993, Smith *et al.* 1989) are the major herbivores. The resulting damage on propagules and seedlings has a strong impact on regeneration and species distribution within mangrove forests (Osborne & Smith 1990, Robertson 1991, Robertson *et al.* 1990; Smith 1987a,b; Smith *et al.* 1989).

Some authors report pubescence (Schoener 1988) or chemical compounds (Lacerda *et al.* 1986, McKee 1995a) of the host plants to be determining factors for herbivory. However, sometimes disturbance of the ecosystem can cause a large increase in herbivore populations, which in turn leads to higher attack rates and a secondary disturbance of the whole ecosystem.

An interesting example of the influence of disturbance on plant–animal interactions is found in the Ciénaga Grande de Santa Marta on the Caribbean coast of Colombia. In highly disturbed parts of this brackish lagoon system, seedlings of *Avicennia germinans* (L.) Stearn are heavily attacked and consumed by caterpillars of the butterfly *Junonia evarete* Cramer (Syn.: *J. lavinia* Cr., *J. flirtea* F., *J. larinia* F., *J. esra* F., *J. cortez* Hbst., Seitz 1924), Lepidoptera: Nymphalidae. At some sites, all *A. germinans* seedlings are totally destroyed by the caterpillars.

J. evarete has been documented in Florida, the Bahamas, the greater Antilles, some of the lesser Antilles, along the coast of Mexico to Honduras, in southeast Brazil (D. J. Harvey *pers. comm.*), and also in warm zones of Colombia (L. M. Constantino *pers. comm.*, Salazar Escobar 1996). In Jamaica, *J. evarete* occurs in large, permanent, and sympatric populations with *J. genoveva* Cramer in and around mangroves and coastal scrubs. The larvae are reported to feed mainly on seedlings and cotyledons of *A. germinans* and were found to be most abundant in December (Turner & Parnell 1985). In other countries, caterpillars are reported to feed on different Verbenaceae (DeVries 1987). However, no report of such a massive attack as in the Ciénaga Grande or a mass mortality of the food plants could be found. Therefore, it may be possible that the extremely high infestation rates are caused by the disturbance of the ecosystem.

In the Ciénaga Grande, major disturbance began when human-induced changes in the hydrology of the lagoon system led to a severe increase in soil salinities. As a result, 30 000 ha of the original 51 150 ha of mangrove forest died (González 1991). Within the last 10 y, international projects have been

established to reopen obstructed waterways to thereby introduce more freshwater and reestablish the original hydrological system (Elster 1998). It is expected that the devastated areas will recover and mangroves will regenerate.

Investigating the regeneration process, we found the heavy attack of *J. evarete* caterpillars to be one of the most important factors influencing seedling growth and survival of *A. germinans*. Therefore, we studied the occurring herbivore patterns and densities and estimated the amount of damage done to seedlings by caterpillars. We addressed the following questions: (1) Does *J. evarete* larvae concentrate on a particular host plant species or developmental stage within this species? (2) Does *J. evarete* show any seasonality and what might be the underlying reasons? (3) Do mangroves at disturbed sites receive more herbivore attack than mangroves at intact sites? (4) Are there any options to prevent herbivore attack without biological or chemical agents? (5) Is *J. evarete* an important regulator of forest community structure in the study area?

STUDY SITES

The present study was carried out at four intact sites situated throughout the Ciénaga Grande and at two highly disturbed sites in the north part of the lagoon system. In this arid region, most rainfall occurs during the main rainy season between August and November. The mean precipitation is c. 700 mm y^{-1} and the mean temperature is 28 °C (IGAC 1973). The lagoon hydrological system is mainly influenced by the changes between the rainy and dry seasons and by the freshwater supply of several rivers. Between the seasons, the lagoon water level usually changes about 50 cm (Elster 1997) and prolonged inundations occur during the main rainy season.

Vital mangrove forests in this area are usually characterized by a fringe of *Rhizophora mangle* L. or, in some places, by *Laguncularia racemosa* (L.) Gaertn. f. bordering lagoons and channels. *A. germinans* stands, with few individuals of the other two species, dominate the interior. The estimated total vegetation cover varies between 30 and 45%.

Although the intact study sites were scattered throughout the Ciénaga Grande (Río Sevilla, La Rinconada, Caño Grande, La Aguja; 10°40′ to 10°59′N and 74°15′ to 74°38′W), all of them showed the normal vegetation pattern with the exception of La Aguja in the south of the lagoon system. In this area *R. mangle* is not encountered. However, at all sites the trees form a closed canopy and their maximum height is c. 15 m. Fruit production and seedling establishment is abundant. The soils are always moist, but flooded only during the main rainy season. Río Sevilla, the least elevated site, experiences the longest inundation period. All sites were located just behind the *Rhizophora/Laguncularia* belt near the shores of the lagoon system.

Formerly, the disturbed study sites had been covered by mangrove vegetation, too, but the forests died due to high soil salinities, which in some places still reach values of more than 250‰. The distance between existing forests

and the study sites is only a few kilometres and the main difference in the soil properties of disturbed and undisturbed sites is the salinity. At both undisturbed sites, however, obstructed waterways have been reopened to introduce more freshwater and to foster mangrove regrowth. Depending on the regeneration status, the vegetation covers between 0% and a maximum of 15% of the soils.

The first disturbed site, Barra Vieja, consists of some small islands in a shallow lagoon. The mangrove forest died *c*. 30 y ago, when a newly-built road separated the area from the main lagoon system. The original hydrological conditions were reestablished in 1989 by reopening the connection between the Ciénaga Grande and the hypersaline lagoon. Consequently, a slow natural regeneration process began. During the study period, few *R. mangle*, *L. racemosa* and *A. germinans* trees reached a height of *c*. 2 m and covered approximately one third of the sandy isles. Another third was covered by the halophytes *Batis'* *maritima* L. and *Sesuvium portulacastrum* L., the rest of the area was bare. Many *A. germinans* propagules reached the area, but only a few seedlings survived.

The second disturbed site was located at the Km 17 of the Caño Clarín, a channel which connects the Magdalena river with the Ciénaga Grande. Most trees died 20 y ago when sediment from the Magdalena river obstructed the channel. The Caño Clarín was reopened in January 1996, but during the first 6 mo the incoming freshwater showed little influence on the vegetation. Only in some areas, where freshwater washed the soil, were new seedlings able to establish themselves. Vast parts of the muddy and partly flooded area are covered by dead mangrove trunks. Only the channel is bordered by *A. germinans* and *L. racemosa* trees that reach a height of up to 4 m. Few plants of *B. maritima* and *S.' portulacastrum* prosper.

METHODS

Food plant species and seasonality

During the 1995 rainy season, *J. evarete* caterpillars were fed with seedlings and leaves of *A. germinans*, *L. racemosa*, *R. mangle*, *B. maritima* or *S.' portulacastrum* to find out on which of the plant species growing in the study area they feed in the absence of other food. Other alternative host plants do not grow in the study area. Caterpillars were raised in small cages covered with nylon gauze. The acceptance of the different plant species was estimated daily by the occurrence of feeding marks in the plant tissue. Alternative host plants were changed in each cage twice a week for about a month.

In the field, the feeding behaviour and seasonality of *J. evarete* caterpillars were studied from November 1994 to October 1996. At Barra Vieja, 35 seedlings each of *A. germinans*, *L. racemosa* and *R. mangle* were surveyed monthly. As a comparison, 10 seedlings of the three species were observed at each of the four intact study sites (total: 40 seedlings per species). The percentage of dead

plants and those attacked or partly eaten by *J. evarete* caterpillars were recorded.

Feeding behaviour on transplanted seedlings

A. germinans seedlings and saplings were grown in a greenhouse from propagules and transplanted on 1 December 1995 to the disturbed study sites. The seedlings were *c*. 2 mo old, 10–20 cm tall, and had one to three pairs of leaves expanded, the saplings were 1-y old, 25 to 40 cm tall, and had already several small twigs. All plants had been grown in direct sunlight in 40-cm high pots at a salinity of 30‰. None of them had been attacked by herbivores before. The transplantation took place at the end of the rainy season, when salinities of soil and ground water were low (15–29‰) and the moisture of the sandy soil was relatively high (*c*. 30% of the fresh weight). The young plants were set at random in bare ground, but newly established mangrove vegetation and halophytes were growing nearby. Field samplings were carried out 2 and 6 wk after transplantation. Percentages were recorded of plants with caterpillars, destroyed plants (nearly all or all leaves and part of the bark and stem eaten, frequently only a part of the stem was left) and dead plants.

To determine whether caterpillars prefer a particular developmental stage of *A. germinans*, we compared 40 seedlings with 40 saplings (four groups of 10 transplanted seedlings/saplings each) at Barra Vieja and checked bushes and adult trees for evidence of attack.

Variations in the herbivore attack between sites of different disturbance levels were investigated by comparing 70 seedlings planted at Barra Vieja, 70 seedlings planted at Km 17 and the 40 seedlings observed in intact forests (all seedlings planted in groups of 10, for intact forest seedlings, see experiment 2).

We further wanted to know, whether there are any options to prevent herbivore attack without using biological or chemical agents. Groups of 35 seedlings each were transplanted to Barra Vieja and either artificially protected or left unprotected. Surrounding water possibly keeps larvae from colonizing their host plants. Therefore, in early December, we planted two groups of seedlings in a trench of 10 cm depth and 5 m length which had a connection with the lagoon nearby and which was filled with the brackish lagoon water. As local fishermen destroyed one group, only one group was included in the data evaluation. Two additional groups were shaded with 30-cm high roofs made of wood laths to protect against egg-laying female butterflies and the remaining two groups were planted in direct sunlight without any artificial protection.

Feeding behaviour on propagules and naturally established seedlings

The impact of *J. evarete* larvae on *A. germinans* propagules and seedling establishment was determined by comparing unsheltered propagules with those covered with insect nets. The propagules were collected at an intact site (La Rinconada) and sown on 1 December 1995, at Barra Vieja and Km 17. At Barra

Vieja, three groups of 100 propagules each were sheltered and three groups were left unsheltered. At Km 17, groups consisted of only 60 propagules and only two sheltered and two unsheltered groups were set, due to limited propagule supply. As local fishermen destroyed two unsheltered groups at Barra Vieja and one unsheltered group at Km 17, these were not included in the data evaluation. Two weeks after sowing, the remaining viable propagules, seedlings with minor or no signs of attack, destroyed seedlings, as well as dead propagules and seedlings were counted. Then, the insect net was removed, because some of the seedlings already touched the upper part of the net. Four weeks later, the counting was repeated.

Seasonality and feeding behaviour of imagos

The adult butterflies were observed in the field to determine possibly occurring seasonalities and their feeding behaviour.

RESULTS

Food plant species and seasonality

In the laboratory, *J. evarete* caterpillars fed only on *A. germinans* seedlings. No traces of their activity were detected on leaves of *R. mangle*, *L. racemosa*, *S. portulacastrum* or *B. maritima* in absence of *A. germinans*. Some caterpillars were observed sucking the hemolymph of other caterpillars which were about to pupate, by boring holes in the still very soft pupal cases. All pupae died independently of the numbers of holes bitten and the amount of hemolymph removed.

The feeding behaviour in the field was very similar. Caterpillars were found on *A. germinans*, whereas they never occurred on *R. mangle* and *L. racemosa*. The larvae were most abundant on young seedlings where they fed mainly on leaves, very young stems or the bark of young stems, and propagules or cotyledons. In older plants, the green tips of the pneumatophores were eaten.

Caterpillars were most abundant during the main rainy season (August to December), when propagule production and seedling establishment was greatest in the Ciénaga Grande. The percentage of *A. germinans* seedlings with caterpillars rose abruptly during this time. One to several larvae were found in almost all *A. germinans* seedlings of the disturbed sites (Figure 1a). They consumed nearly all of the green plant tissue and often only a part of the stem was left. Although the young plants sometimes grew new leaves, the mortality rate was very high, especially when the new leaves were again fed upon. *J. evarete* seemed to be one of the main causes of death in *A. germinans* seedlings in the disturbed areas. In the drier months (January to July), very few or no specimens of *J. evarete* were found and the caterpillars usually left their host plant to feed on other seedlings before consuming all the green plant tissue. During this time, none of the young plants were destroyed by herbivores.

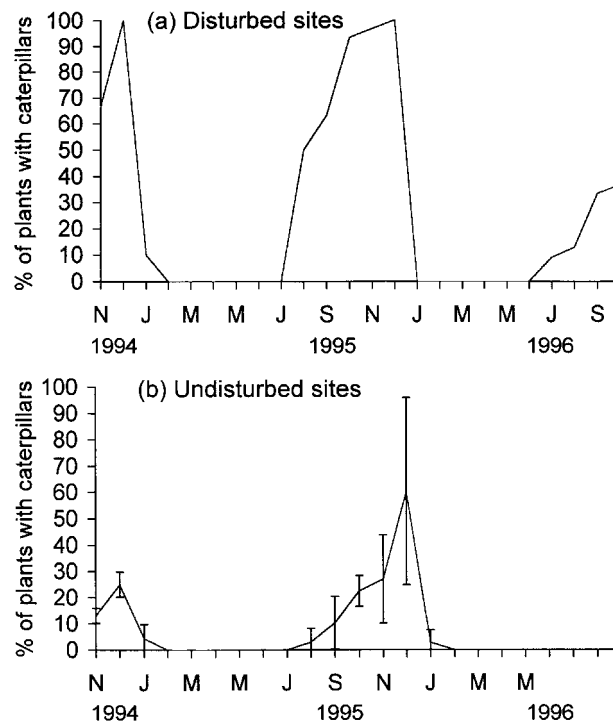At intact sites, the herbivore seasonality was similar, but fewer seedlings

Figure 1. *Avicennia germinans* seedlings at (a) disturbed (Barra Vieja) and (b) intact sites (mean ± SD between sites) attacked by *J. evarete* caterpillars. Figure 1(b) includes only data until May 1996.

were encountered with *J. evarete* larvae feeding on them (Figure 1b). Generally, highest attack rates were found in December. However, in December 1994 average attack was only 25%, while in 1995, it was much higher (60%) and attack rates varied extremely between the intact sites.

Feeding behaviour on transplanted seedlings

The comparison between the two developmental stages of *A. germinans* showed that caterpillars were much more abundant in 2-mo-old seedlings than in 1-y-old saplings and tended to consume more of the younger tissue. In December, the differences in numbers of attacked and destroyed plants between the two age classes were both highly significant (Figure 2a). The larvae left the study sites in January, leaving 74% of the seedlings and 40% of the saplings destroyed or dead. In this month, the percentage of destroyed saplings was higher than the percentage of destroyed seedlings, because of a much lower mortality in the saplings (Figure 2b). Many saplings survived the attack, whereas most seedlings had died already. In both months, seedling mortality was significantly higher than sapling mortality (Figure 2). In young shrubs, caterpillars were found only on branches close to the water and they were not encountered in trees. Older plants were never severely damaged by *J. evarete*.
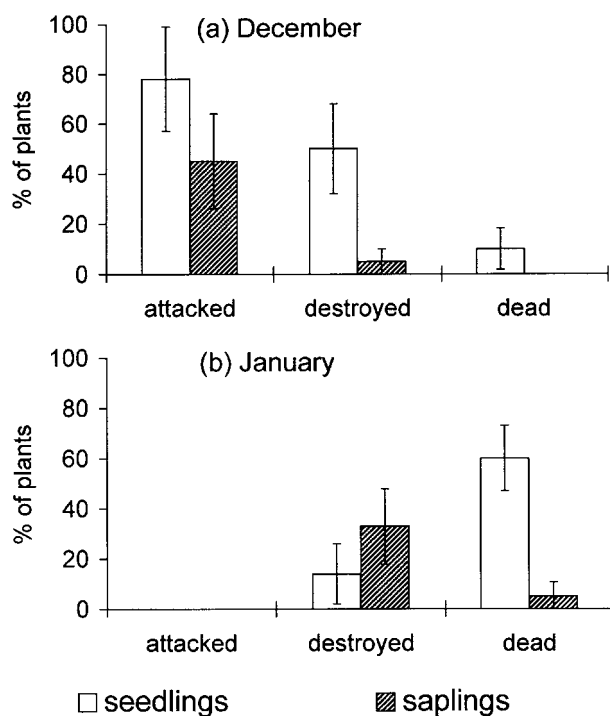
Figure 2. *Avicennia germinans* seedlings (2-mo-old) and saplings (1-y-old) attacked, destroyed or killed by *Junonia evarete* caterpillars in (a) December and (b) January. Percentages (mean ± SD between groups) were calculated for number of living seedlings during the previous visit. Differences between the two age groups were tested with χ^2-test (Fisher's exact test); December: caterpillar attack: P = 0.005, plants destroyed: P < 0.001, dead plants: P = 0.052; January: plants destroyed: P = 0.040, dead plants: P < 0.001.

The percentage of plants damaged at different study sites was highly variable. In forests with closed canopies, the percentages of attacked seedlings usually ranged from 18 to 50% in December. The only exception was Río Sevilla, the wettest site, with 100% of the seedlings attacked in December 1995. All newly established seedlings at this site were destroyed and subsequently died. For naturally established seedlings at the disturbed sites, on the other hand, we frequently encountered groups of seedlings with 100% attack and mortality rates.

The seedlings used in our experiments at the disturbed sites (Figure 3) had a comparatively low attack rate, because they were planted only 2 wk before the field sampling date and *J. evarete* did not colonize the plants that rapidly. Caterpillars were significantly more abundant and consumed more seedlings at Km 17, the more exposed and disturbed site, than at Barra Vieja (Figure 3). In December, the seedling mortalities at both sites did not differ much and were relatively low (16 to 22%).

The experiment to protect seedlings against herbivore attack showed that the number of *J. evarete* larvae and destroyed plants rose initially much faster at unprotected than at shaded sites. In mid-December 88% of the unprotected plants had caterpillars, whereas this was true for only 56% of the seedlings
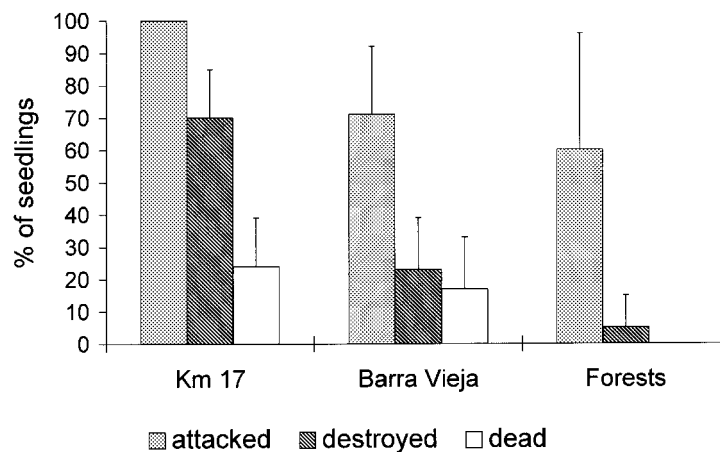
Figure 3. Comparison between the *Junonia evarete* attack in December 1995 at Barra Vieja, Km 17, and sites with intact forests (mean ± SD between groups). At Barra Vieja and Km 17 these are transplanted seedlings; at the forest sites they are naturally established seedlings. Differences in the caterpillar attack and the percentage of destroyed seedlings between the sites were highly significant (χ^2-test, Fisher's exact test $P < 0.0001$). Differences between the percentage of dead seedlings were not significant.

shaded with a 30-cm high roof. The plants which were surrounded by water were the least attacked (34%). In mid-December, all three sites differed significantly in caterpillar abundance and number of severely attacked plants (destroyed and dead seedlings taken together, Figure 4). During the following weeks, the larvae reached all seedlings and destroyed similar amounts of plants in the different treatments. Therefore, in January, destroyed seedlings in the three groups no longer differed significantly. As in all seedling groups planted at the beginning of December, highest mortality rates were encountered in January, after the heavy attack during the previous month (33 to 67%). Due to initially higher attack, total mortality between the three groups was still significantly different at the end of the experiment (Figure 4). Altogether, 81% of the seedlings in the unprotected group died, followed by the seedlings surrounded by water with 57%, and those shaded with a roof (44%). No caterpillars were found in late January.

Feeding behaviour on propagules and naturally established seedlings

In December, most propagules sheltered by insect nets germinated or stayed seemingly viable. None of the propagules or seedlings were attacked by insects, whereas most unsheltered propagules were eaten by the caterpillars and did not germinate or the seedlings were destroyed. At Barra Vieja, 94% of the unsheltered propagules were totally destroyed by *J. evarete* within 2 wk. Only 6% germinated, but the seedlings were eaten during the following 2 wk and died. Sheltered seedlings in good shape differed significantly from unsheltered seedlings before the removal of the insect net (Figure 5). After removal, most seedlings were destroyed and died. Seedlings in good shape survived only at
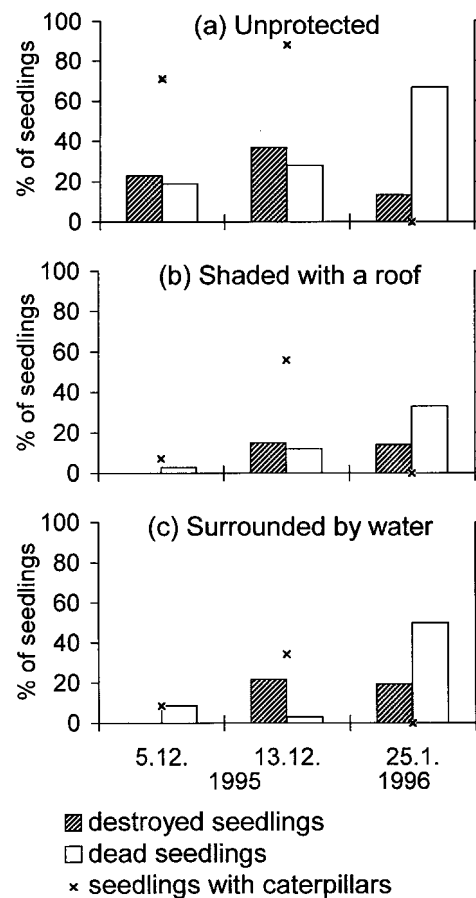
Figure 4. *Avicennia germinans* seedlings attacked, destroyed or killed by *J. evarete* caterpillars: (a) seedlings unprotected, (b) shaded with a roof of 30 cm height, and (c) surrounded by water. Percentages were calculated for numbers of living seedlings during the previous visit. Differences between the sites were highly significant in December and not significant in January (χ^2-test, on 5 and 13 December, 1995, seedlings with caterpillars: P < 0.0001, destroyed and dead seedlings together: P < 0.0001). At the three sites, differences between the total number of dead seedlings until January were highly significant (χ^2-test, P < 0.0001).

Barra Vieja. The difference between formerly sheltered and unsheltered seedlings was small in January. At Km 17, all seedlings—with the exception of two unsheltered plants—had died.

Some seedlings and high percentages of ungerminated propagules disappeared between December and January (in total up to 40%, Figure 5). A secondary dispersal of the propagules is not likely, since the sites were not inundated during the discussed time. The most probable explanation is total consumption of propagules and seedlings by herbivores.

Seasonality and feeding behaviour of imagos
Adult butterflies were most abundant during the main rainy season (August to December) as were their larvae. The imagos were observed visiting flowers
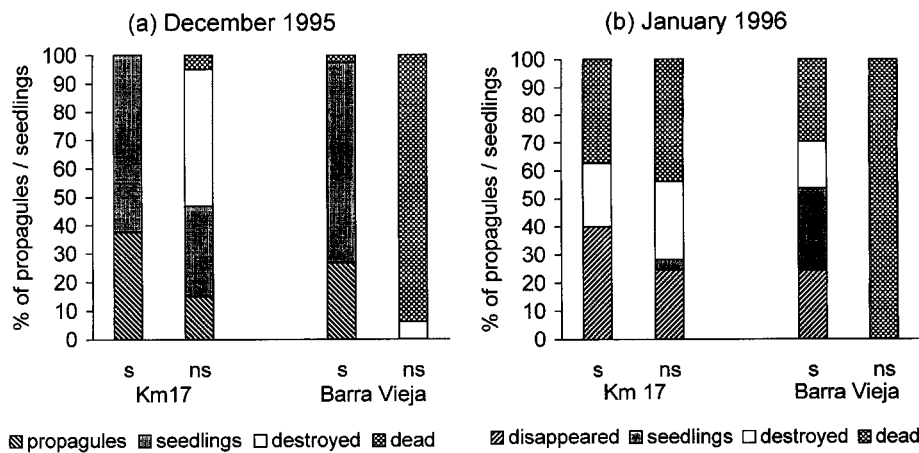
Figure 5. Set propagules and germinating *Avicennia germinans* seedlings attacked by *Junonia evarete* caterpillars. s: propagules and seedlings sheltered by an insect net for the first 2 wk in December, then the net was removed; ns: not sheltered; propagules: seemingly viable propagules that did not germinate; seedlings: minor or no signs of attack; destroyed: seedlings heavily attacked (most of the leaves up to nearly the whole seedling eaten); dead: propagules or seedlings died; disappeared: propagules or seedlings not found (probably totally eaten). Percentages were calculated for the total number of propagules set. Differences in numbers of seedlings with minor/no attack signs vs. destroyed/dead seedlings between the sheltered and unsheltered groups of both sites were highly significant in December (χ^2-test, Fisher's exact test, P < 0.0001). In January, the difference at Barra Vieja was highly significant as well (P < 0.0001), at KM 17 it was not significant.

of *A. germinans* and *L. racemosa*. These two mangroves as well as *R. mangle, B. maritima* and *S. portulacastrum* are the only flowering species in the study area and, therefore, the only available food source for the butterfly. However, nectaring on other plant species is possible outside the mangrove area.

DISCUSSION

In the Ciénaga Grande, *J. evarete* occurs most abundantly during the rainy season between August and December, butterflies and caterpillars disappear during the dry season. Similar patterns are observed in Costa Rica, where this species is reported in coastal areas during the rainy seasons (J. A. Jiménez, *pers. comm.*), while imagos migrate during the dry season to mountains and volcanoes. It is, therefore, possible, that the butterflies of the Ciénaga Grande migrate up the valleys of the Río Magdalena and the Río Cauca to warm zones of the eastern slopes of the Cordillera Occidental and the Cordillera Central, where specimens have been found by Salazar Escobar (1996) and L. M. Constantino (*pers. comm.*).

Reasons for the migration or a diapause within the study area may be climatic factors, such as strong trade winds (Raasveldt & Tomic 1958) and the decreasing humidity during the dry season. A strong dependency of *J. evarete* on humidity is indicated by the fact that caterpillars are never encountered more than a few cm away from water. Additionally, they occurred much more abundantly in the unusually long and wet rainy season in 1995 than during the

drier 1994. Although the abundance of caterpillars and butterflies coincides with the main propagule production and seedling establishment of *A. germinans*, a lack of food does not seem to be the main reason for the fauna occurrence pattern, since flowers and seedlings are available year round.

In our study area as in other countries (e.g. Turner & Parnell 1985), *J. evarete* caterpillars feed exclusively on *A. germinans*, while other authors report various Verbenaceae as their diet (E. Constantino, *pers. comm.*). Avicenniaceae and Verbenaceae, which are not always separated into two different families, share secondary compounds (Reddy *et al.* 1993) that may have influence on host plant choice. Caterpillars may be less specialized than they seem in our study area, because other appropriate food plant species are not available.

The butterflies feed on nectar of *A. germinans* and *L. racemosa*, as does *Junonia* sp. in Costa Rica (J. A. Jiménez, *pers. comm.*). Thus, *J. evarete* may pollinate their generalistic flowers and it is not only a detrimental but also a mutualistic species for *A. germinans*. However, the plants do not depend on *J. evarete* for pollination, because other visitors, mainly Diptera, but also Hymenoptera occur (Elster 1997).

J. evarete caterpillars consume large amounts of propagules and they prefer young seedlings to saplings. This may be due to the high nutritive value of the cotyledons, while in ageing leaves the nutrient content declines and the toughness increases (Choong 1996). Heavily attacked saplings have higher survival probabilities than attacked seedlings, which may be related to tougher bark and basal shoot tissue that protect reserve compounds and meristematic tissue, while the soft shoot tissue of young seedlings is frequently consumed totally. A better developed root system supports the survival of saplings additionally.

Up to 100% of the young *A. germinans* seedlings are attacked by the caterpillars and frequently more than 50% of the seedlings die within 1 mo. Therefore, in the more affected areas, up to 100% of the seedlings die by the end of the rainy season. There is no doubt that this high mortality is due to insect herbivory, because other factors that can lead to seedling mass mortalities did not reach critical values during our experiments: the studied plants grew in low salinities, had not been flooded more than a few cm, and had not dried out. Additionally, high salinities or other harmful soil conditions would have killed not only the *A. germinans* seedlings, but also the *A. germinans* saplings and nearby growing seedlings of *L. racemosa* and *R. mangle*. Propagule or seedling damage through crabs, as reported for many other mangrove areas (Clarke & Myerscough 1993, Jones 1984; McKee 1995a, b; Smith 1987a, b; Smith *et al.* 1989) is insignificant at our study sites (Elster 1997).

At open sites, shaded seedlings have lower attack rates than those without protection. Since all transplanted seedlings had the same origin and, thus, similar leaf qualities, varying herbivore attack is not due to differences in leaf palatability as might be suggested for seedlings grown in different light levels or soil properties. Instead, it is more likely that adult butterflies avoid laying eggs on seedlings growing under a roof. Thus, colonization relies on the slow movement of the

caterpillars and the seedlings are protected for a short while. Initially, seedlings surrounded by water had a low recruitment rate, as well. The reason is not known yet, since butterflies reach the plants easily and caterpillars were frequently observed floating in the water and reestablishing on novel host plants. The protective effect of shading and surrounding water, however, decreases with time and does not prevent herbivore attack for a whole rainy season.

Better habitat conditions for *J. evarete* imagos may be the reason for higher attack rates at open than at forested sites. Many authors (e.g. DeVries 1987, Seitz 1924) report that the butterflies prefer open ground with bare soil, and these conditions are found abundantly at the open disturbed sites of the Ciénaga Grande. Information on severe attacks of *J. evarete* at other locations is not known, and generally accounts of insect outbreaks in mangrove stands are very rare (Anderson & Lee 1995, Ellison & Farnsworth 1996, Saenger & Siddiqi 1993, Whitten & Damanik 1986).

In the study area, a mangrove mass mortality (Elster 1998, Serrano Díaz *et al.* 1995) created a suitable habitat for *J. evarete*. However, the butterflies' preference for open disturbed sites is detrimental to the regeneration process. While mangrove reestablishment became possible due to remedial hydraulic measures, many disturbed sites are only reached by *A. germinans* propagules and very few or no propagules of the other two species arrive (Schubert 1998). In addition to its propagule availability, *A. germinans* is appropriate to colonize the disturbed areas, because it is highly tolerant of salinities (Elster & Schnetter 1998, Mizrachi *et al.* 1980, Pannier *et al.* 1979). *L. racemosa* and *R. mangle*, on the other hand, experience severe problems in the still very saline soils. However, *A. germinans* might nearly be excluded due to the heavy herbivore attack. Therefore, in some areas, *J. evarete* may slow down the whole regeneration process, because the time of main fruit production and seedling establishment of *A. germinans* corresponds with the highest abundances of *J. evarete* caterpillars during the rainy season.

Without using chemical or biological insecticides that can influence disturbed ecosystems in unknown ways, there are only two efficient ways to improve survival in reforestation trials. One is to cover the propagules and seedlings with insect nets during their first rainy season. It is essential to leave the net in place until most larvae have disappeared (beginning of January). The other possibility is to set *A. germinans* at the beginning of the dry season.

As caterpillar attack is less severe in vegetated areas, it is probable that more *A. germinans* seedlings will survive once the regeneration process with *L. racemosa* and *R. mangle* has started. Additionally, regeneration may be alleviated by a natural development of an Ichneumonidae population, which can control the *J. evarete* population.

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