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# Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana

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**Summary.** A comparative study was conducted on the recruitment patterns of two non-pioneer tree species, one dispersed by arboreal mammals and birds (*Virola michelii*, Myristicaceae) and the other by rodents (*Moronobea coccinea*, Clusiaceae). These species differ in fruiting phenology, seed size, dispersal distance, germination time and seed nutrient exhaustion. In both species, establishment patterns were consistent with the escape hypothesis and the Janzen–Connell model. *Virola* seeds need not be buried to survive and germinate, and may produce a seedling carpet beneath the parent. *Moronobea* seedlings only establish from seeds buried by scatterhoarding rodents in the surrounding understory. One-year survival of *Virola* seedlings was 47.8% and was greater >10 m than <10 m from the largest parent tree. In contrast, survival of *Moronobea* seedlings was 56% 3 years after seed dispersal. Survival of juveniles was greater in gaps than in the understory for *Virola* but not for *Moronobea*. *Moronobea* survival was greater than *Virola* survival in both microhabitats. Both species establish in the understory, yet both grew faster in gaps. *Virola* appeared to be more gap-dependent than *Moronobea* which may persist several years in the understory until a gap occurs. *Virola* and *Moronobea* illustrate two intermediate recruitment patterns along an hypothetical continuum of non-pioneer species replacement (Bazzaz and Pickett 1980; Swaine and Whitmore 1988).

**Key words:** Non-pioneer species – *Moronobea coccinea* – Recruitment pattern - Tropical tree – *Virola michelii*

In neotropical forests, seed dispersal by birds and mammals is prevalent (Charles-Dominique et al. 1981; Foster 1982; Prevost 1983; Sabatier 1983, 1985; Janson 1983; Foster and Janson 1985). Fruit syndromes can influence seed dispersal; large- and small- seeded species, for example, are dispersed by large and small dispersers, respectively (Janson 1983; Foster and Janson 1985). Although such categorizations may coincide with the common dichotomy between pioneer and non-pioneer groups of recruitment patterns (sensu Swaine and Whitmore 1988), the continuous unimodal distribution of seed mass in the Amazonian rainforest of Peru (Foster and Janson 1985) may support the hypothesis of a continuum of recruitment patterns (Schulz 1960; Bazzaz and Pickett 1980; Hartshorn 1978, 1980; Whitmore 1978, 1984; Denslow 1980, 1987; Coley 1983, 1988; Augspurger 1984; Oberbauer and Donnelly 1986).

While Swaine and Whitmore's (1988) dichotomy based on germination strategies helped clarify the tangle of terms used to describe the ecological group of species, it obscures what appears to be extreme and important variation in regeneration strategies. Their further subdivision into four height class subgroups may lead to more confusion than understanding of forest regeneration. Indeed, there is no evidence that a given tree stature is characteristic of one recruitment pattern.

While evidence to date suggests the existence of a continuum of regeneration strategies, there is little known about the diversity of tree-to-tree replacement patterns of tropical tree species. Denslow (1987) suggested that the incidence of light in disturbances may determine the range of recruitment patterns along a continuum of regeneration niches (Grubb 1977; Brokaw 1987) from the understory to the large gap. However, the abilities of plants to establish and grow in the understory as well as in gaps also depend on seed dispersal effectiveness and on seed survival rates; seed dispersal and seed survival are both affected by seed size and by the presence of gaps (Schupp et al. 1989; see also Hartshorn 1978; Hubbell and Foster 1986).

Many neotropical non-pioneer species can establish in the understory, although they also colonize small gaps and the edges of larger gaps due to seed disperser behavior (Howe and Primack 1975; Howe and Estabrook 1977; Charles-Dominique et al. 1981; Wheelwright and Orians 1982; Roosmalen 1985; Forget 1988; Schupp et al. 1989). Greater seed size appears to be associated with a higher concentration of seeds around the parent, and a lower probability of dispersal into a gap. Thus, following Denslow's (1987) notion, the recruitment patterns of non-pioneer species may have evolved in response to a sequence of regeneration niches ranging from the small gap openings through a continuous range of light environments found in the understory (Lieberman et al. 1989), similar to a continuity of pioneer niches (see in the Brokaw 1987). By assuming a continuum of species replacement (Bazzaz and Pickett 1980), one may describe a sequence of recruitment patterns nonpioneer species group that can be considered evolutionary adaptations to a wide range of seed sizes (Foster 1986) and seed-dispersal patterns and distances (Howe and Smallwood 1982; Howe 1986; Price and Jenkins 1986).

In this paper I describe and compare the recruitment patterns of *Virola michelii* (hereafter referred as *Virola*) Myristicaceae, and *Moronobea coccinea* (hereafter referred as *Moronobea*) Clusiaceae, two non-pioneer tree species of French Guiana forests which differ, among other traits, in seed size and seed dispersal agents.

## Comparative natural history

*Virola* and *Moronobea* are both canopy trees common in pristine Guianan forests, although neither occurs in dense stands as does *Eperua falcata* (Forget 1988, 1989), a frequently associated species (see Schulz 1960). Trees can reach > 30 m in height and > 50 cm in diameter. In other respects the species are quite different (Table 1).

In general seeds of the species in the genus *Virola* are dispersed by birds (e.g., *Rhamphastos* spp., *Pteroglossus* spp., *Penelope* spp.), monkeys (e.g. *Ateles* spp. and *Alouatta* spp.) and kinkajous (*Potos flavus*) (Howe and VandeKerkhove 1980, 1981; Charles-Dominique et al. 1981; Howe 1983; Sabatier 1983; Roosmalen 1985; Julien-Laferriere 1989; D. Julien-Laferriere and P.-M. Forget pers. obs.).

Though *Moronobea* fruit features evoke a bat seed-dispersal syndrome, I never found evidence of bats feeding on this species (i.e. peeled fruits under parent tree or bat roosts). *Moronobea* seeds fall beneath the parent and are scatterhoarded (Morris 1962) by diurnal rodents such as acouchies *(Myoprocta exilis)* and agoutis *(Dasyprocta leporina)* (see Dubost 1988; Forget 1990), and by nocturnal rodents such as spiny rats (*Proechimys sp.*) (P.-M. Forget pers. obs.).

In both species, the embryos of newly-dispersed seeds are undifferentiated. After a maturation period of 1–2 months in *Virola* and several months (4–6) to more than 1 year in *Moronobea*, seeds germinate in the understory (Sabatier 1985; P.-M. Forget pers. obs.). In the latter species, seedling establishment seems to be highly dependent on seed burial by rodents; 100% of a set of whole fruits ($n = 25$) placed under the parent tree crown on the ground and protected from mammals rotted after pulp and seed infestation by *Pyralidae* while pulp-cleaned seeds ($n = 25$) dehydrated (P.-M. Forget unpubl. data). Terrestrial rodents are also seed predators of both species. There is no evidence that *Virola* seeds are infested by insect larvae as in *Virola surinamensis* in Panama (Howe et al. 1985), and despite high seed-predation by animals, especially rodents, seedlings were observed under parent trees (Forget 1988, present study).

**Table 1.** Comparison of some features of *Virola* and *Moronobea* recruitment patterns

| | *Virola* | *Moronobea* |
|---|---|---|
| Phenology | Annual | Supra-annual |
| Fruiting timing | January–February–March | April–May–June |
| Fruit type | Capsule | Drupe |
| Exposed color | Red (aril) | Green-yellowish (epicarp) |
| Fruit crop | hundreds to > 10000 | < 10000 |
| Fruit size (cm) | 2.5–3.0 × 2.0–2.5 | 3.0–4.0 |
| Seed size (cm) | 1.4 × 2.0 | 2.5–3.5 × 1.5–2.0 |
| Dispersal method | Endozoochory | Synzoochory |
| Dispersal agent | Arboreal mammals/ birds | Terrestrial rodents |
| Dispersal distance (m) | > (30) 50 | < 30 (50) |
| Germination timing | < 2 months | > 2 months |
| Seedling carpet | Possible | Never |
| Seedling height (cm) | 16.1 ± 3.7 (N = 30) | 34.6 ± 8.5 (N = 41) |

## Study site

This study was carried out at the Ecerex research field station (5° 30′ N, 53° 0′ W) (Le projet Ecerex 1983) at a mature moist forest plot where vegetation was not perturbed although the fauna has suffered from intensive hunting for the last 10 years. Large monkeys have nearly disappeared from the study area. Average annual rainfall is 3196 mm (10-years data CTFT). A 10-month wet season alternates with a short dry season (September-October). Usually, the wet season is interrupted by a period of lower rainfall in February, March or April. The tree population (> 20 cm in dbh) is dominated by species in the families Lecythidaceae (26% of the individuals), Caesalpiniaceae (22%) and Chrysobalanaceae (12%). Myristicaceae and Clusiaceae are represented by less than 1% and 3%, respectively, of the individuals (Lescure 1981). The community-wide fruiting season occurs during the wet season and peaks from January through June; seasonality varies depending on fruit morphology and seed dispersal methods (Sabatier 1985).

## Methods

Recruitment was analysed for both species in a 3500 m$^2$ (50 × 70 m) plot of mature forest. The plot was divided into 100 m$^2$ (10 × 10 m) subplots in the understory, and into 25 m$^2$ (5 × 5 m) subplots in one gap (90 m$^2$ sensu Brokaw 1982). Three *Virola* and two *Moronobea* trees > 20 cm in dbh occured in this plot. In this paper, "seedling" refers to the first stages of growth after seed germination. In this case, seedling age is known to within about 1–3 months. The term "juvenile" refers to older (> 6–12 month to several or even tens of years old) individuals for which time of emergence is unknown. Juvenile populations are described in three (< 50 cm, 50–100 cm and > 100 cm) height classes (spatial distribution) and in 10 cm-interval height classes (height distribution).

### *Dynamics of seedlings*

*Virola.* Three-month-old *Virola* seedlings (emergence in May-June) were first mapped and tagged in September 1985 on 2500 $m^2$ of the plot. The sample consisted of all seedlings > 10 m from the largest adult *Virola* and a random sample of 100 seedlings beneath the crown of this adult (< 10 m). Seedlings were censused for survival in September 1986 (> 1 year post-establishment and approximately > 1.5 year post-dispersal). In addition, *Virola* survival under the canopy (< 10 m) was compared with survival away from the canopy (> 10 m) of the largest tree.

*Moronobea.* Newly-emerged (< 1 month) *Moronobea* seedlings were marked in September 1986 on the whole plot. Most of these were assumed to arise from 1986 fruiting (no fruiting in 1985, P.-M. Forget pers. obs.), though because of the delayed germination some may have emerged from dormant seeds from previous fruit crops. They were censused for survival in May 1989 (> 2.5 years post-establishment and assumed > 3 years post-dispersal).

### *Dynamics of juveniles*

By May 1985, juveniles of both species were mapped, marked with numbered labels, described, and measured to the terminal bud. In order to study the dynamic responses of survival and growth to environmental factors, juvenile populations were separated into understory (> 5 m from gap edge) and gap (in gap or < 5 m from gap edge) populations. Growth and demographic data were compiled over 4 years up to May 1989.

## Results

### *Dynamics of seedlings*

*Virola.* In September 1985, 148 seedlings were observed in the understory or around the gap areas on 2500 $m^2$ > 10 m from the largest tree (DBH = 48 cm). Beneath that tree a carpet of more than 100 seedlings was growing. Several clumps of 20–30 seedlings each occured in the plot. The other two adult *Virola* had, respectively, 9 and 16 seedlings beneath the crown. After 1 year, survival was 47.8%. Survival was greater for seedlings > 10 m from the trunk of the largest adult (0.56 ; $n = 148$) than for those < 10 m from the trunk, and therefore beneath the crown (0.36 ; $n = 100$) ($\chi^2 = 9.63$, $P < 0.001$, $df = 1$). Causes of mortality are unknown. Live seedlings in September 1986 had an average leaf number of 3.3 ± 1.0, a mean increase of 1 leaf per year.

Depending on microsite and light availability, however, the increase ranged from 0 to 4 leaves. Seedling height increased with the number of leaves (Table 2).

*Moronobea.* In September 1986, 44 young seedlings were found in the plot, three of which were dried and dead. All seedlings found in the plot were from rodent-buried seeds. Survival was 56% 3 years after seed-dispersal. The slow exhaustion of seed reserves makes *Moronobea* vul-

**Table 2.** Number of leaves and height (cm) of *Virola* seedlings in September 1986 (> 15 months after establishment)

| No. | leaves | Height ± SD | range | *n* |
|---|---|---|---|---|
| | 2 | 14.6 ± 3.3 | 9–22 | 21 |
| | 3 | 17.8 ± 3.8 | 12–25 | 29 |
| | 4 | 21.5 ± 5.5 | 12–38 | 20 |
| ≥ | 5 | 26.9 ± 7.6 | 17–45 | 13 |

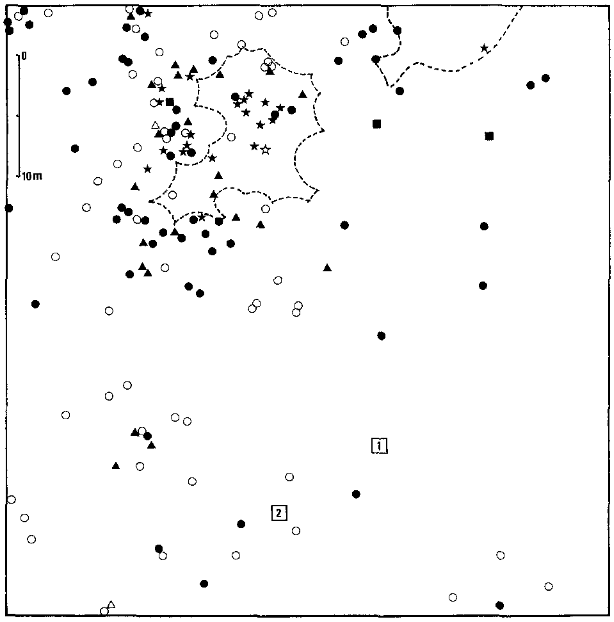

**Fig. 1.** The spatial distribution of *Virola* juveniles in a 2500-$m^2$ plot in May 1985. *Numbered squares*: parent trees (DBH > 30 cm); *black square*: 5 cm < DBH < 20 cm ; *point:* < 50 cm tall; *triangle:* 50–100 cm tall; *star:* > 100 cm tall; *open* and *full symbols* represent, respectively, juveniles that died during the study and those still alive in May 1989. *Dashed lines* are limits of gap openings

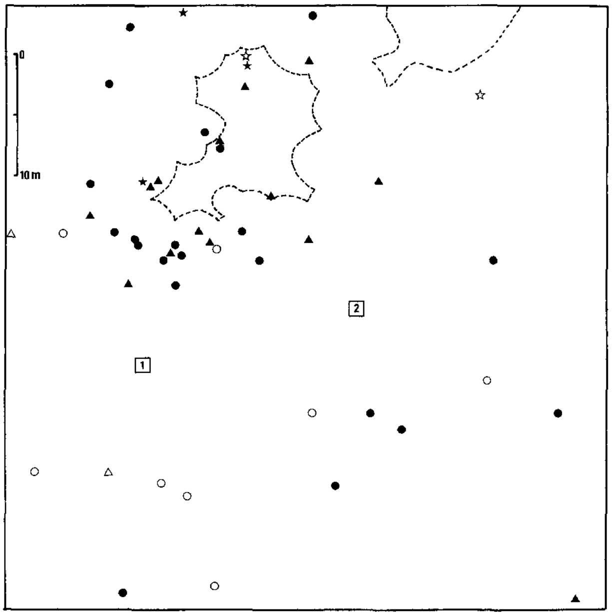

**Fig. 2.** The spatial distribution of *Moronobea* juveniles in a 2500-$m^2$ plot in May 1985. Symbols as in Fig. 1

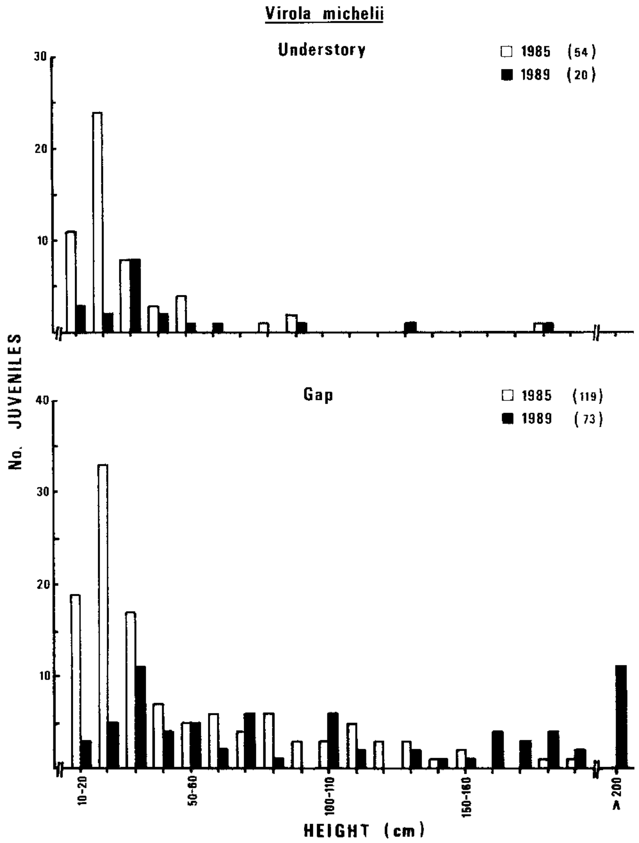

**Fig. 3.** Height distribution of *Virola* juveniles in May 1985 and May 1989 in understory and gap sites

nerable to continued seed predation as rodents uproot the seedlings to reach the seeds. If not eaten, however, the large seed reserves allow seedling growth to continue in the shade. Indeed, 20 of 23 live seedlings in May 1989 grew a mean of 11.3 ± 11.0 cm (range 1–51 cm). Though most seedlings grew in the understory, the largest increments, respectively 18 cm, 20 cm, and 51 cm, were observed in a gap. Death was apparently due mostly to drying and to rodent predation.

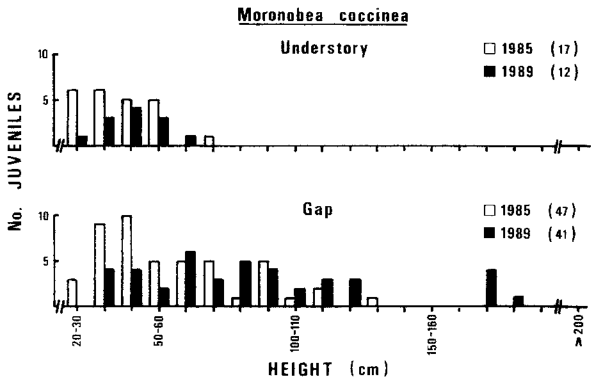

**Fig. 4.** Height distribution of *Moronobea* juveniles in May 1985 and May 1989 in understory and gap sites

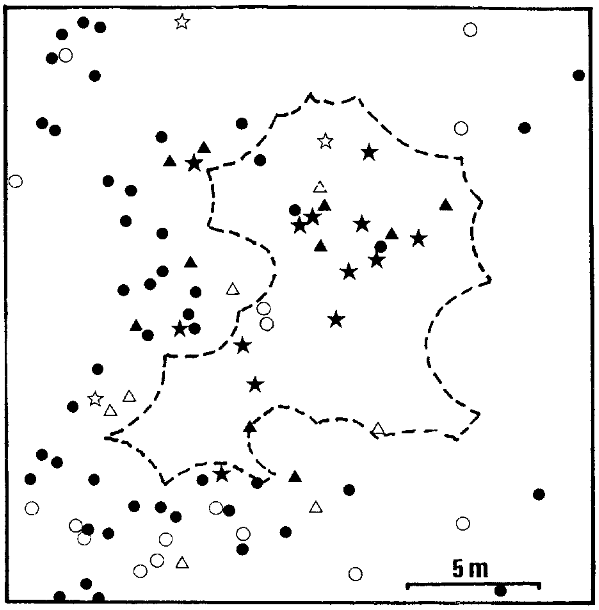

**Fig. 5.** An example of the spatial distribution of 4-year height growth increments in live *Virola* (*full symbols: point:* 0–49 cm; *triangle:* 50–99 cm; *star:* > 100 cm) and *Moronobea* (*open symbols: point:* 0–29 cm; *triangle:* 30–49 cm; *star:* > 50 cm) juveniles in and near a small gap (90 $m^2$) in May 1989. The *dashed line* shows the gap opening

**Table 3.** Mean 4-year height increments (cm) in understory and gap sites among *Virola* and *Moronobea* juveniles alive in May 1989, and which had grown since May 1985. For both species 4-year height growth was significantly greater in the gap than in the understory ($P < 0.001$)

| | *Virola* | | | *Moronobea* | | |
|---|---|---|---|---|---|---|
| | Mean ± SD | range | *n* | Mean ± SD | range | *n* |
| Understory | 13 ± 14 | 2–49[a] | 10 | 6.4 ± 4.2 | 1–15 | 10 |
| Gap | 54.8 ± 47.9 | 2–161 | 60 | 30.0 ± 19.4 | 4–99 | 39 |

[a] new gaps occured in the vicinity of juveniles

*Dynamics of juveniles.* As an example of spatial distribution and dynamics, juvenile maps are given of 2500 $m^2$ of the studied plot (Fig. 1, 2) and 4-year height increments are presented for live juveniles in May 1989 (Fig. 5). In both species, clumps of juveniles were observed near and in gaps (Fig. 1, 2) with a higher frequency of juveniles > 100 cm tall (Fig. 3, 4). For *Virola*, survival over the 4 years was greater in the gaps (0.61) than in the understory (0.37) ($\chi^2 = 8.83$, $P < 0.001$, $df = 1$). In contrast, survival of *Moronobea* did not differ between gap (0.87) and understory (0.70) juveniles (Fisher's Exact Test, ns). In *Moronobea* the proportion of individuals that grew during the study was not associated with habitat (0.95 in gaps, 0.83 in understory, Fisher's Exact Test, ns) whereas in *Virola* a greater proportion of juveniles in gaps (0.82) grew than of juveniles in the understory (0.50) (Fisher's Exact Test, $P = 0.005$). Four-year height growth increments were greater in the gaps than in the understory (Table 3) in both *Virola* ($t = 5.49$, $P < 0.001$, $df = 47$) and *Moronobea* ($t = 6.68$, $P < 0.001$, $df = 68$). This difference was obvious even though some *Virola* juveniles previously in the understory received increased lateral light after gaps opened nearby in 1987 and 1988. Comparing recruitment features of the two species, survival of *Moronobea* was greater than of *Virola* both in the understory ($\chi^2 = 5.60$, $P < 0.001$, $df = 1$) and in the gaps ($\chi^2 = 31.88$, $P < 0.001$, $df = 1$). Conversely, height growth increment was greater for *Virola* than for *Moronobea* ($t = 3.58$, $P < 0.001$, $df = 97$) (Table 3). As an example, Fig. 5 shows that in *Virola* the greatest 4-year height growth increments were mostly at the center and the edge of the small gap, while they were restricted to the edge of the gap and the understory in *Moronobea*.

## Discussion

At Ecerex station, *Virola* is likely to be dispersed mainly by kinkajous and toucans. Consequently, the pattern of seedfall may differ from that found in areas with a more natural coterie of dispersal agents. Still, seed dispersal of *Virola* at Ecerex yields a seedling distribution in the understory and at gap edges > 30 m from the nearest parent trees. Gap centers without standing trees are apparently avoided by dispersal agents (Schupp et al. 1989), and thus were empty of *Virola* seedlings. The juveniles in the gap center probably established as seedlings before the canopy opened.

There is a striking difference between the results of the present study and those of Howe et al. (1985) for *Virola surinamensis* (the species identification should probably be changed to *V. nobilis*, R. Foster pers. comm., P.-M. Forget pers. obs.) at Barro Colorado Island (BCI), Panama. The differences in seed and germinating seedling mortality lead to large differences in both the quantity and the spatial pattern of seedling recruitment of *V. surinamensis* on BCI and *V. michelii* in French Guiana. In the former, seedling production is low and surviving seedlings are generally isolated from conspecific seedlings and adults, while in the latter more seedlings germinate and can be found in clumps and concentrated beneath adult crowns.

The short-distance seed dispersal in *Moronobea* increases the chance that seeds will germinate and grow in the understory. As a consequence of the rodent seed-dispersal syndrome, few seedlings and juveniles were observed in the gap center. Results of the present study partially support Foster's (1986) hypotheses that large-seeded species produce very shade-tolerant seedlings capable of surviving in the shaded understory until gap occurence. Furthermore, delayed emergence of seedlings for more than a year after seed-dispersal may provide new recruitment cohorts during unreproductive periods and compensate for rodent predation.

The absence of *Moronobea* seedlings, the paucity of *Virola* juveniles under the parent, and the disproportionate mortality of *Virola* seedlings beneath conspecific adults suggest that, in both species, there is an advantage to dispersal in the understory away from the parent. Dispersal allows seeds (Janzen 1970) and seedlings (Connell 1971) to escape from a zone of high mortality due to insects, rodents and seedling pathogens. Their establishment pattern is thus consistent with the escape hypothesis (Howe and Smallwood 1982) and the Janzen-Connell model (Clark and Clark 1984).

Although both species germinate in the shade, long-term offspring survival and growth is likely to depend on the chance of a gap opening over shaded seedlings (Hartshorn 1978; Hubbell and Foster 1986). While growth was stimulated in the gaps for both species, differences in comparative dynamics suggest a contrast between the recruitment patterns of the arboreal mammal and bird-dispersed *Virola* and the rodent-dispersed *Moronobea*. As a result of differences in seed dispersal patterns and their growth and survival responses to gaps and understory sites, the patterns of recruitment differ for these species, and they differ from others in the same forest. Seedlings and juveniles of both species studied have a lower tolerance for the understory habitat ("understory-tolerance") than do the short-distance dispersed *Eperua falcata*, a species which is abundantly represented in the understory (Forget 1988, 1989). The supra-annual recruitment of *Moronobea* is associated with long-term seedling and juvenile survival while in *Virola*, annual fruitings compensate for high seedling mortality in the understory. The result for both species is a small persistent juvenile bank. A balance exists between both seed size and the probability of dispersal to particular microhabitats on one hand, and the ecophysiological ability to survive in the understory on the other hand (Whitmore 1978; Hartshorn 1978, 1980; Denslow 1980, 1987; Brokaw 1985; Foster 1986; Schupp et al. 1989); large-seeded species are unlikely to be dispersed into a gap, but their seedlings are able to persist for many years in the understory (Forget 1988).

Although *Virola* and *Moronobea* may be classified in the large climax species subgroup of Swaine and Whitmore (1988), the range of features of their recruitment patterns show that a simple dichotomy based on germination requirements and tree stature is insufficient to describe the enormous variety of dynamic processes that influence forest regeneration and species diversity. This study documents examples of apparently typical recruitment syndromes of endozoochorous and synzoochorous species which would be adapted to early (*Virola*) or late (*Moronobea*) colonization of small gaps. However, other species with similar seed dispersal syndromes may show contrasting recruitment patterns, i.e. *Faramea occidentalis* (Schupp 1990) and *Gustavia superba* (Sork 1987). Despite the diversity of strategies among these non-pioneer species, all four appear to fit on the hypothetical continuum of species replacement strategies (Bazzaz and Pickett 1980) between *Eperua falcata* (Forget 1989) at one extreme, and *Trema micrantha* (Brokaw 1987), at the other extreme.

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