

## Seed Rain *vs.* Seed Bank, and the Effect of Vegetation Cover on the Recruitment of Tree Seedlings in Tropical Successional Vegetation

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**Abstract:** We assessed the relative contribution of the seed rain and soil seed bank, and the effect of ground vegetation on the density and recruitment of tree seedlings in contrasting successional habitats (primary forest, secondary forest, and pasture) in southeastern Mexico. To assess the relative importance of the seed rain and seed bank on seedling recruitment, we set up two treatments: (1) destruction of the seed bank, and (2) exclusion of the seed rain. To assess the effect of vegetation cover, we removed all seedlings and herbaceous plants from plots established at each habitat; and compared seedling recruitment rates to those in undisturbed control plots. In both experiments, over a period of one year we counted the number of seedlings being recruited and grouped them into early successional (ES) and late successional (LS) tree species. Overall natural tree seedling density was significantly lower in the pasture than in secondary and primary forest. For LS trees, seed rain was more important than seed bank in primary forest and pasture, while in secondary forest the situation was reversed. For ES trees, the importance of the seed rain greatly increased in secondary forest, whereas in primary forest and pasture, both seedling sources had a similar contribution. For LS trees, ground vegetation favours recruitment in primary forest but has a negative effect in secondary forest. In contrast, for ES trees vegetation cover limits seedling recruitment in primary forest and pastures. We discuss whether seed predators, dispersers, proximity to forest remnants, abiotic conditions and species life history differentially affect recruitment in the different successional forest stages.

*Key words:* rainforest, regeneration, seedlings, seed bank, seed rain, Selva Lacandona, vegetation cover

### Introduction

Natural regeneration of tropical rainforest trees depends on different propagule sources, including newly dispersed seeds ('seed rain'), dormant soil seeds ('seed bank'), suppressed seedlings and saplings (collectively known as 'advanced regeneration'), resprouting of broken trees, and lateral growth of tree crowns (BAZZAZ

1984). The relative importance of these regeneration sources varies depending on the magnitude of forest disturbance and on the life history of the species (BAZZAZ 1991; BROKAW & BUSING 2000). For example, in small gaps, as those created by the falling of tree branches and limbs, crown growth and advanced regeneration are the major regeneration sources, while in large gaps, as those created by multiple tree falls, the seed rain/bank increases in importance (BAZZAZ 1984, 1991). Regarding tree life histories, short-lived, fast growing, strongly light demanding trees depend exclusively on seeds to regenerate; their germination and establishment being tightly linked to the occurrence of large forest openings. On the other hand, long-lived, slow growing, shade-tolerant trees produce seeds that rapidly germinate and translate the regenerative stage to seedlings and saplings that may remain in the shade under a 'dormant' condition until a canopy gap opens. These two life-history types have been thought to be the extremes of a continuum of regeneration strategies (MARTÍNEZ-RAMOS & SAMPER 1998). The former species are recognised as early successional (ES), obligately gap demanding, or pioneer species, while the later species are known as late successional (LS), primary, shade-tolerant, climax, non-pioneer, or persistent species (DENSLOW 1987; SWAINE & WHITMORE 1988; WHITMORE 1989).

Seed rain plays a primary role in the colonization of new areas, both in ES and LS tree species. Seeds landing in a given forest patch come from local and external patch sources (MARTÍNEZ-RAMOS & SOTO-CASTRO 1993). Local seeds are produced *in situ* by fruiting trees inside the patch. Fruiting trees found outside the patch produce immigrant seeds, which are dispersed by abiotic or biotic vectors. In the short term, immigrant seeds play a paramount role in creating heterogeneity on the species composition and structure of the seed bank and advanced regeneration communities. In the long term, such heterogeneity may promote the maintenance of forest species diversity (MARTÍNEZ-RAMOS & SOTO-CASTRO 1993; WEBB & PEART 1998).

When strong anthropogenic forest disturbance occurs, some processes associated with regeneration sources could inhibit the capacity of forest trees to regenerate. Contemporary deforestation of the rainforest in southern Mexico has led to replacement of native vegetation by patches of crop fields, pastures, second-growth forests of various ages, and forest remnants scattered in the landscape. Frequently, non-productive agricultural fields are abandoned after few years, leading to large areas of degraded land where rainforest is often hard to recover. Factors such as decreased nutrient availability, soil compaction, competition with pasture grasses, drought, low rates of seed colonization, and seed and seedling predation, make forest regeneration extremely difficult in these areas (AIDE & CAVELIER 1994; NEPSTEAD *et al.* 1996; HOLL 1999). Destruction of the seed and seedling banks after slash and burn agriculture and inability of several animal dispersers to cross open areas make plant colonization extremely difficult (BUSCHBACHER *et al.* 1988; UHL *et al.* 1988). Seeds that do arrive on abandoned pastures, and the seedlings emerging from surviving seeds are exposed to harsh environmental conditions that prevent germination and successful establishment (NEPSTEAD *et al.* 1990). In some cases, seeds germinate successfully but seedlings fail to establish due to competition with pasture grasses (GONZÁLEZ-MONTAGUT 1996; HOLL 1999). However, individuals of some species may succeed, giving place to the formation of secondary forests that in most cases compared to mature forest, have more simpler structure and a high proportion of early successional species compared to mature forest (BROWN & LUGO 1990).

Generally, the advanced regeneration community disappears or is strongly reduced in places where slash and burn practices have been applied. Local seed rain is

confined to those isolated remnant trees left for management purposes (GUEVARA & LABORDE 1993). Thus, depending on the kind of disturbance (*e.g.* clear-cutting with or without burning, shifting cultivation, cattle grazing), tree regeneration and species composition in degraded tropical areas depends on immigrant seeds, surviving seed banks, and re-sprouts of logged trees that survived after disturbance (KAUFFMAN 1991). The arrival of immigrant seeds depends on the amount and spatial arrangement of remaining forest fragments, on remnant isolated forest trees (GUEVARA & LABORDE 1993; MARTÍNEZ-GARZA & MONTAGUT 1999; OTERO-ARNAÍZ *et al.* 1999), and on the availability of animal vectors (bats and birds) that venture into open areas (MEDELLÍN & GAONA 1999).

In general, we expect that as secondary succession progresses in an abandoned field the relative regenerative role of different propagule sources may change. For example, if the managed field was subject to fire regimes, the seed bank will be important in the recruitment of tree seedlings until the secondary succession processes restore such propagule source. Also, such seed bank recovery may differ between species with different life history strategies, as recalcitrant seeds of LS species are more labile to high temperatures than seeds of ES species (BRINKMANN & VIEIRA 1971, C. VÁZQUEZ-YANES, pers. comm.).

In this study we explore the relative importance of seed bank and seed rain as sources of seedlings for ES and LS species across different successional stages, encompassing recent abandoned pastures, young secondary forest, and mature (human non-disturbed) forest. Most studies measured the potential contribution of seed rain and seed bank on forest regeneration by counting the number of seeds collected in seed traps or present in soil cores. In contrast, our study individually assesses the relative contribution of both sources on the basis of recruited seedlings. A second aim was to investigate the role of understorey vegetation cover as biotic facilitator or barrier on tree seedling recruitment in contrasting successional habitats. In particular, we approach the questions: (1) Do ES and LS species have different seedling density and recruitment rates in primary forest, secondary forest and pasture habitats? (2) Do ES and LS species have different abilities to disperse and establish into different successional habitats? (3) Do ES and LS species differ in their ability to cope with the interference of pre-existing ground vegetation in different successional habitats?

## Material and Methods

### Study site

The study was conducted at the 'Chajul' Biological Station, located within Montes Azules Biosphere Reserve (MABR), Chiapas, SE Mexico (16° 06' N, 90° 56' W, 120 m). MABR is situated within the so-called Selva Lacandona region that comprises part of Guatemala in Central America (MEDELLÍN 1994). Land use in the area dramatically reduced the original forest area (500,000 ha) by two-thirds in 40 years. The MABR contains the majority of the remaining forest of the region (3310 km<sup>2</sup>). The primary vegetation type is lowland tropical rainforest, with trees reaching up to 40 m in height in alluvial terraces along main rivers (SIEBE *et al.* 1995). Structurally, the most important tree species are (M. MARTÍNEZ-RAMOS, unpubl. data; nomenclature follows MARTÍNEZ *et al.* 1994): *Dialium guianense* (Aublet) Sandw. (Leguminosae), *Brosimum alicastrum* Swartz (Moraceae), *Spondias radlkoferi* J.D. Smith (Anacardiaceae), *Guarea glabra* Vahl (Meliaceae), and *Manilkara zapota* (L.) Van Royen (Sapotaceae). There are about 4,000 species of vascular plants (MEDELLÍN 1994), and a total of 258 tree species ( $\geq 10$  cm dbh), have been recorded within 8-ha of primary forest (M. MARTÍNEZ-RAMOS, unpubl. data).

Maximum and minimum annual temperatures are 31.8 °C (April-May) and 18 °C (January-February), respectively. The mean annual precipitation (11 years period) is around 3,000 mm, seasonally distributed along the year, with less than 60 mm per month from February through April, and more than 100 mm per month from May to October (MEAVE DEL CASTILLO 1990). Various forest patches of different sizes, cattle pasture, and secondary forests of various ages and successional stages compose the landscape of the Marqués de Comillas region, which is close to MARB in its southwestern portion. This area was opened to agricultural cultivation in the early 1970's; presently, about 60 % of the area is covered by fragmented primary forest, the remaining area by fields, pastures and secondary forest of less than about twenty years (MÉNDEZ-BAHENA 1999). Generally, agricultural management includes non-machinery techniques, low use of fertilizers, and moderate use of herbicides (MÉNDEZ-BAHENA 1999).

### Experimental design

For the purposes of this study, we define secondary forests as those originated as consequence of human impact on rainforest lands (BROWN & LUGO 1990). Three different successional habitats were selected: (1) one site in primary continuous forest; (2) one secondary forest, ca. 10-years old, about 8 ha in area, and with trees up to 25-m tall dominated by *Cecropia* sp.; and (3) one cattle pasture, abandoned for ca. 5 years, 10 ha in area, and with sparse woody vegetation up to 3 m tall. The secondary forest was bordering primary forest on one of its sides, while the pasture was 120 m away from the nearest forest remnant.

Five parallel 100-m transects (20 m apart), were placed within the three successional habitats. For each habitat, eight 0.5 m × 0.5 m permanent plots were randomly positioned along each transect, giving a total of 40 plots per habitat. We decided to use small plots (0.25 m<sup>2</sup>) to facilitate experimental manipulation. At the beginning of the study, for all habitats we counted the number of tree seedlings (5-50 cm tall) in each plot and identified them to species when possible. Subsequently, ten plots per habitat were randomly assigned to each of four treatments (see below), which were used for two different experiments.

One experiment was designed to assess the relative contribution of the seed rain and seed bank on the recruitment of seedlings within and among habitats. We applied two treatments that consisted in the elimination of one of each propagule source. To evaluate the contribution of the seed rain, we removed all the vegetation and fine litter from ten randomly selected plots and poured ca. 3 l of boiling water twice within a week on uncovered soil (Fig. 1). The first addition of boiling water kills ca. 80 % of tropical soil seeds (BRINKMANN & VIEIRA 1971; VÁZQUEZ-YANES 1974; C. VÁZQUEZ-YANES & A. OROZCO-SEGOVIA, pers. comm.). We added boiling water for a second time to kill those seed species that could have survived high temperatures and/or germinated, such as *Ochroma lagopus* Swartz (VÁZQUEZ-YANES 1974; C. VÁZQUEZ-YANES & A. OROZCO-SEGOVIA, pers. comm.).

To evaluate the contribution of the seed bank, we removed all vegetation and fine litter from each of ten randomly selected plots. Afterwards, each plot was completely covered with a 1 mm transparent mesh mounted in a 40 cm tall wire frame (Figs 2, 3). Seedling recruitment was recorded in all plots every four months over one year (September 1996-September 1997). For each inventory, every recruited seedling was labelled and identified to the lowest possible taxonomic group.

The use of the mesh could have affected light income and seed and seedling predation. However, in mature forest we found no significant differences on photosynthetically active radiation (PAR, LI-190SA Quantum Sensor) between plots with mesh and those without (log transformed PAR values *t*-test = 2.16, d.f. 18, *p* = 0.6). In meshed plots PAR (mean ± SD) was 50.1 ± 103.2 μmol s<sup>-1</sup> m<sup>-2</sup>, in uncovered plots 85.5 ± 192.8 μmol s<sup>-1</sup> m<sup>-2</sup> (range between 4.63-434.7 μmol s<sup>-1</sup> m<sup>-2</sup>, and between 6.42-815.8 μmol s<sup>-1</sup> m<sup>-2</sup>, respectively). In pasture, we observed that many herbaceous species, characteristic of open habitats, were recruited in very high numbers within meshed plots. If the mesh had effectively excluded seed and seedling predators, we could have expected higher overall seedling recruitment in meshed plots as compared to uncovered ones. However, we observed seedlings with herbivorous injuries and no higher overall tree seedling

recruitment in meshed plots. Differences among meshed and unmeshed plots might fall within the natural micro-environmental heterogeneity present in the forest understorey.

A second experiment was designed to investigate the effect of understorey vegetation cover on the recruitment of woody species in different successional habitats. At each habitat, twenty 0.25 m<sup>2</sup> plots were randomly selected. In ten plots we removed by hand all seedlings of woody species and all herbaceous plants including their roots and the fine litter; ten control plots were left undisturbed. The seedlings present in the control plots were labelled and identified to species. As in the first experiment, seedling recruitment was recorded in the plots every four months over the same year period. To reduce vegetation interference and edge effects, we removed the vegetation 50 cm around all experimental plots (the area where we recorded seedlings) and also applied treatments (removal of vegetation cover, addition of boiling water, exclusion of the seed rain, and control). This practice was especially useful in pasture as grasses strongly interfered with the plots.

To facilitate comparisons of tropical trees, and due to the low number of recruits found in our experiments, we grouped seedling species into two major regeneration groups: late successional (LS), and early successional (ES) tree species (based on IBARRA-MANRÍQUEZ *et al.* 1997; PENNINGTON & SARHUKÁN 1998; G. IBARRA-MANRÍQUEZ, pers. comm., J. BENÍTEZ-MALVIDO & M. MARTÍNEZ-RAMOS, pers. obs.). To the ES group, we assigned those species that establish under large canopy gaps and open areas, germination or seedling survival and growth being restricted to such places. It is known that these species disappear from a secondary successional chrono-sequence in less than 100 years (SARUKHÁN *et al.* 1985). Species that can germinate, survive, and grow under the shaded forest understorey were assigned to the LS group. These species are the most frequent components of mature forest and they can live for more than 100 years (MARTÍNEZ-RAMOS & ALVAREZ-BUYLLA 1998).

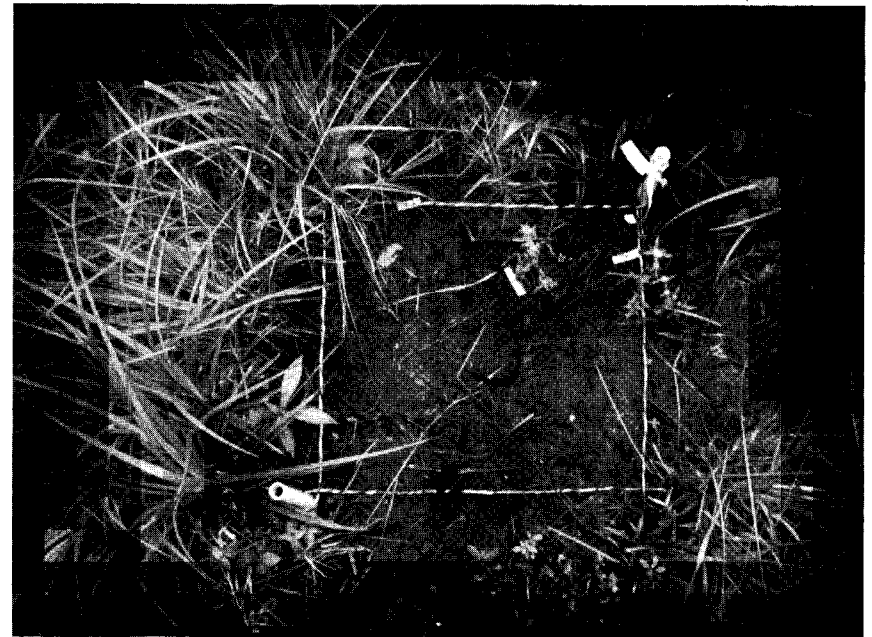


Fig. 1. Experimental 0.25 m<sup>2</sup> plot, one year after having been established within the pasture habitat. The photograph shows the aspect of the plots where we evaluated the importance of the seed rain on the recruitment of tree seedlings.



Fig. 2. Experimental 0.25 m<sup>2</sup> plot covered with a transparent mesh. The plot was located within primary forest and was used to exclude seed rain and to evaluate the contribution of the seed bank on the recruitment of tree seedlings.



Fig. 3. Seedlings recruited through the seed bank within a 0.25 m<sup>2</sup> plot, at a secondary forest in the Selva Lacandona, Mexico. All recruited seedlings were recorded for a year period.

### Statistical analysis

Because we had only one replicate per habitat type, to avoid pseudoreplication *sensu* HURLBERT (1984), we pooled all tree seedlings recorded in all plots at each site or treatment/site to perform the analyses. To assess the relative contribution of seed rain (SR) and seed bank (SB) to recruited seedlings, we obtained the SR/SB ratio, SR being the yearly amount of recruited seedlings in all plots where seed bank was excluded, and SB the yearly amount of recruited seedlings in all plots where the seed rain was excluded. This ratio was obtained for each habitat type, for each tree regeneration group, and pooling all seedlings. For each regeneration group, to test differences in SR/SB ratio among habitats we performed a habitat-type (three levels)  $\times$  seedlings source (two levels) contingency  $\chi^2$  test.

To assess statistical differences in seedling density among habitats (primary forest, secondary forest and pasture), and the effect of habitat type and vegetation removal on seedling recruitment rate, we used generalised linear models and analysis of deviance procedures (see CRAWLEY 1993; GREEN & PAYNE 1994). A Poisson error and a log-link function were used as indicated for cases of count dependent variables. In these models, the amount deviance explained by the independent variables approximates to  $\chi^2$  values (CRAWLEY 1993). To test the effect of habitat type on seedling density (3-1 degrees of freedom), we performed separate analyses of deviance for LS and ES species. To test the effect of vegetation removal (VR) and habitat type (HT) we used the amount of deviance explained by the VR  $\times$  HT interaction term. In this case degrees of freedom were calculated as the number of vegetation removal plots minus times number of habitat types minus one. This test was performed separating LS and ES trees as well as pooling all seedlings. All statistical tests were run using the GLIM statistical package (GREEN & PAYNE 1994).

### Results

#### Natural densities of tree seedlings

Before experimental manipulation, we recorded a total of 375 tree seedlings in the three habitats ( $n = 120$ , 0.25 m<sup>2</sup> plots), amounting to 73 species, 59 of which were classified as LS and 14 as ES trees (Appendix 1). The pasture site showed significantly lower tree seedling density than primary and secondary forest, whether analysing LS and ES tree species separately or lumping all species (Fig. 4). Seedling density (mean  $\pm$  SE), per m<sup>2</sup>, declined from secondary forest (17.0  $\pm$  2.4), to primary forest (14.2  $\pm$  1.6), to pasture (7.4  $\pm$  1.7). However, while density of LS trees declined from primary forest to secondary forest to pasture, density of ES seedlings was higher in secondary forest (Fig. 4). Thus, percentage of LS seedlings was highest in pasture (86.8 %) and primary forest (83.0 %), and lowest in secondary forest (62.2 %).

#### Patterns of seedling recruitment

One year after experimental manipulation, a total of 170 new recruited seedlings from tree species were recorded in all plots and habitats. These seedlings represented 46 species (29 LS species, 15 ES species, 3 undetermined), 20 of which were not recorded in the first census at the beginning of the study (Appendix 1). The annual mean ( $\pm$  SE) number of recruits per m<sup>2</sup> declined from pasture (7.1  $\pm$  2.0), to primary forest (5.4  $\pm$  1.7), to secondary forest (4.4  $\pm$  1.7). The density of LS tree seedlings was very similar for all habitats, ranging from 24 in primary forest to 27 in the pasture site. In contrast, fewer ES seedlings were recruited into the secondary forest (18 compared to 31 in the primary forest and 44 in the pasture site).

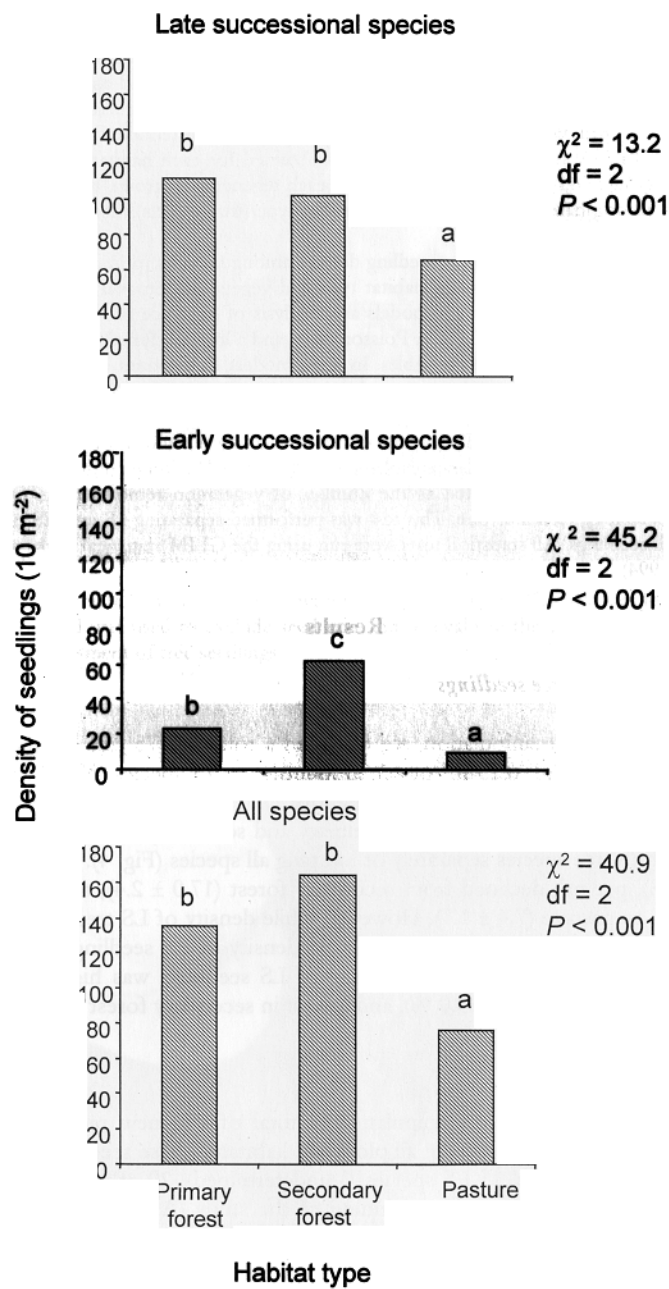


Fig. 4. Variation in standing density of tree seedlings among habitat types at the Lacandon region, southeast Mexico. Bars sharing the same letter are not significantly different ( $\chi^2$ ,  $p > 0.05$ ).

#### Seed rain vs. seed bank

The seed rain/seed bank ratio changed among habitats (Fig. 5). Relative contribution of these two sources of seedlings varied depending on habitat type and tree group. For LS trees, seed rain was significantly more important than seed bank as a source of seedlings in primary forest and pasture, while in secondary forest the situation reversed. For ES trees, the importance of the seed rain greatly increased in secondary forest; whereas in primary forest and pasture, seed rain and seed bank had numerically similar contribution in the number of recruited ES seedlings. Overall, considering LS and ES trees together, the tendency was that tree seedlings were recruited predominantly from the seed bank in secondary forest, while in primary forest and pasture seed rain and seed bank tended to equally contribute to seedling recruitment.

#### Effect of vegetation cover

In the presence of lower vegetation, recruitment rate of tree seedlings in pasture was significantly lower than in primary and secondary forests, whether analysing ES tree species separately or combining all species (Fig. 6). This pattern dramatically changed, depending on habitat type and tree group, when the lower vegetation was removed. Removal of vegetation cover in primary forest produced a significant decline in seedling recruitment rate for LS species; while the opposite occurred in secondary forest and the rate remained unchanged in pasture. For ES seedlings, vegetation removal significantly enhanced seedling recruitment in primary forest and in pasture. Considering all tree species, removal of vegetation only had a significant effect in pasture, where elimination of grasses and associated plants resulted in a significant increase of seedling recruitment. Clearly, lower vegetation had opposing effects on recruitment of LS and ES trees in the primary forest, a negative effect on recruitment of LS trees in secondary forest, and a negative effect on recruitment of ES trees in pasture.

#### Discussion

##### Standing density of seedlings

The lower density of seedlings in pastures as compared to primary and secondary forest could be the result of reduced seed dispersal. Studies in different tropical areas have shown that reduced seed dispersal, compared to reduced seed germination, harsh microclimate, and soil characteristics, is probably the most important factor limiting forest recovery in abandoned pastures (NEPSTEAD *et al.* 1990; HOLL 1999). Most tropical trees are dispersed by vertebrates (HOWE & SMALLWOOD 1982), many of which are unable to cross large forest clearings. In our study site, birds and especially bats are known to disperse seeds from many rainforest species into more open areas (MEDELLÍN & GAONA 1999). The presence of bushes and small trees ( $\leq 3$  m tall,  $\geq 1$  cm dbh), could have influenced the recruitment of forest species into the pasture as they act as perching sites for birds that disperse forest immigrant seeds in the form of faecal loads (GUEVARA & LABORDE 1993; VIEIRA *et al.* 1994), or simply by producing seeds that are locally deposited on the soil.



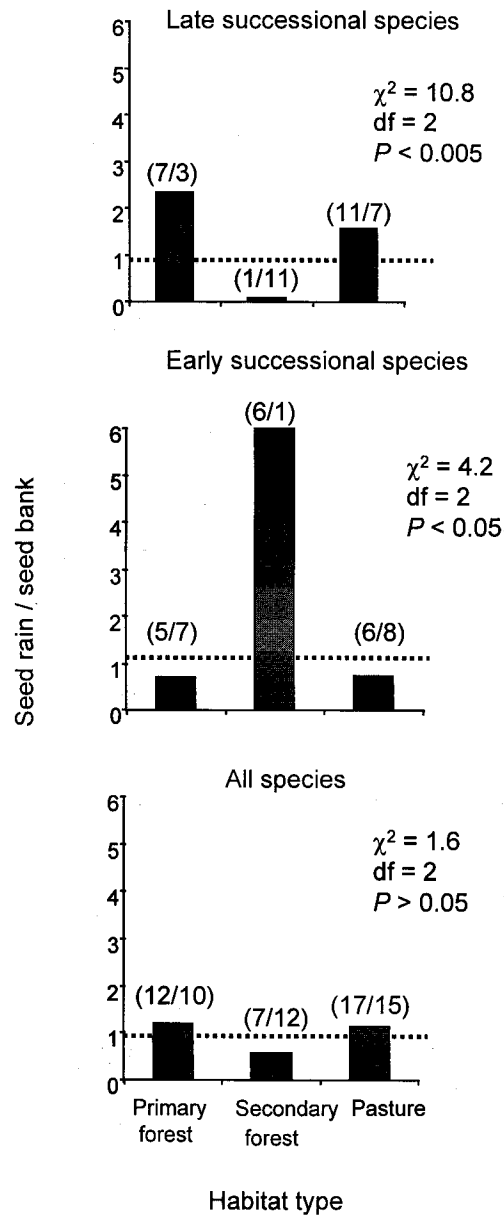


Fig. 5. Variation of the SR/SB ratio among habitats at the Lacandon region, southeast Mexico. For each habitat, in parenthesis the number of recruited seedlings originated from seed rain (numerator) and seed bank (denominator) is provided. Recruitment values are given in seedlings per  $2.5 \text{ m}^2 \text{ yr}^{-1}$ .  $\chi^2$  values indicate deviation from the expected random ratio (dotted lines).

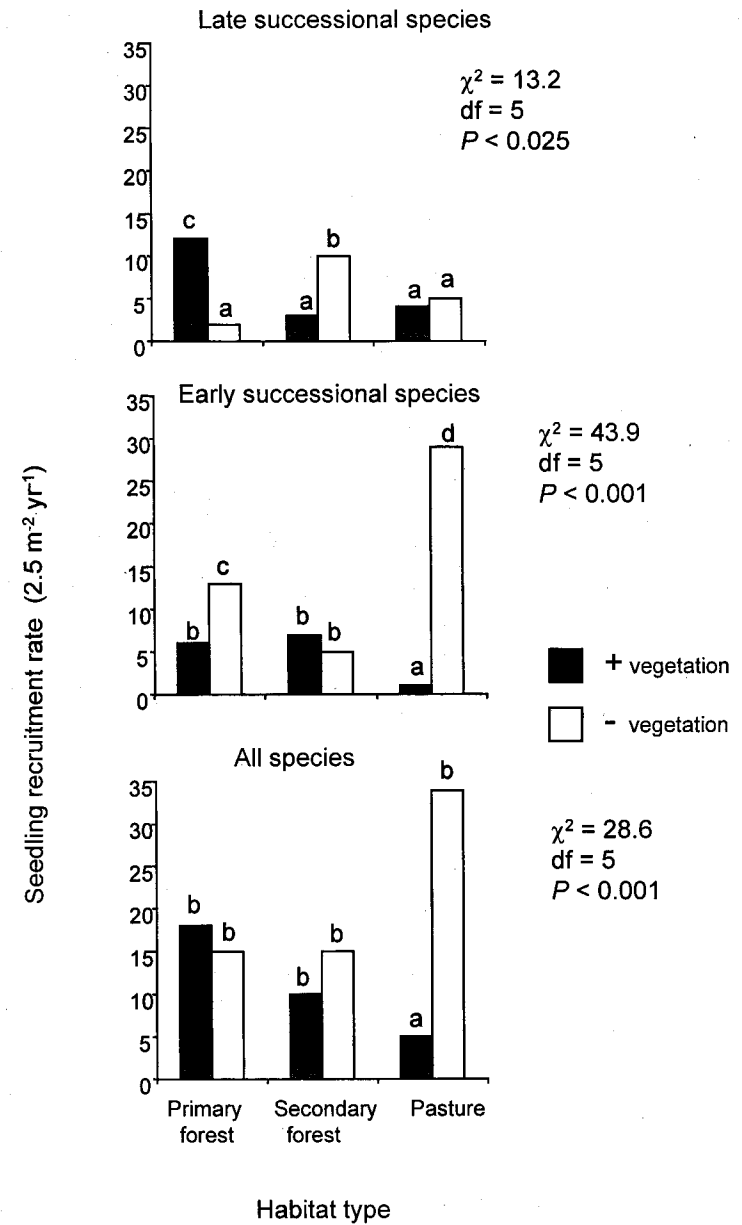


Fig. 6. Effect of habitat type (HT) and vegetation removal (VR) on tree seedling recruitment rate at the Lacandon region, southeast Mexico.  $\chi^2$  values indicate the HT x VR interaction effect. Bars sharing the same letter are not significantly different ( $\chi^2$ ,  $p > 0.05$ ).

It is likely that most of the seedlings present in pastures may have originated by animal dispersed seeds, though in the study area more than 85 % of seeds present in bat and bird faeces are from ES species, many of the LS species recorded are also dispersed by these groups of animals (MEDELLÍN & GAONA 1999). In contrast, in primary and secondary forests seedlings could have been recruited through the seed shadows of local trees or from immigrant seed species (see MARTÍNEZ-RAMOS & SOTO-CASTRO 1993).

The presence of more LS than ES seedling species in pastures, can also be related to physiological limitations. In Barro Colorado, Panama, and Paragominas, Brazil, it has been observed that LS species growing in tree fall gaps and abandoned pastures, respectively, are more drought-tolerant than ES seedlings, and hence able to establish and grow under this condition (ROBINCHAUX *et al.* 1984; NEPSTEAD *et al.* 1990). Thus, ES species may not be always abundant in large open areas. Reduced recruitment of ES species in pastures have been observed for *Cecropia obtusifolia* and *Heliconia appendiculata* at Los Tuxtlas, Mexico (GONZÁLEZ-MONTAGUT 1996). The high density of LS and ES seedlings in primary and secondary forest could have resulted from the presence of higher number of reproductive trees, seed dispersers, and/or the absence of extreme environmental conditions.

For recruitment of ES tree species, secondary forest seemed the most suitable habitat. Higher density of ES seedlings in secondary forest than in primary forest and pasture could be attributable to reduced competition and solar radiation when compared to pasture, and to greater canopy openness and higher seed production by ES mature individuals (DALLING & DENSLow 1998), when compared to primary forest.

#### Seed rain vs. seed bank

The results of this study show that the relative importance of seed rain and seed bank as a regeneration propagule source is similar among sites that represent contrasting forest successional stages. However, this similarity resulted from a counterbalance of the opposite patterns found for ES and LS groups, indicating that seed rain and seed bank play different regenerative roles for species differing in life history, depending on the habitat type.

In the pasture, seed rain tended to be more important than seed bank for recruitment of LS tree seedlings, and the inverse trend was observed for ES species. These results are in accordance with the fact that recalcitrant seeds from LS trees are more sensible to high temperature compared to orthodox seeds of several ES trees. In both tree groups, most recorded seedling species are animal dispersed (Appendix 1), which indicates that animal vectors are fundamental for the recovery of pasture areas (HOLL 1999). In primary forest, seed rain was the major source of seedlings for LS species. It has been documented that seed rain is fundamental for primary forest regeneration and for the maintenance of diversity in the understorey (MARTÍNEZ-RAMOS & SOTO-CASTRO 1993; WEBB & PEART 1999).

In contrast, recruitment of LS species through seed rain in secondary forest was much lower, and most LS seedlings were recruited from the seed bank, while the opposite pattern was observed for ES trees. In Panama, soil seed bank densities in secondary forests are very variable, being unrelated to time of abandonment but highly dependent on abundance of seed-bank-forming species in the standing vegetation (DALLING & DENSLow 1998). These findings suggest: (1) some LS species can survive in the soil seed bank at least for one year; (2) seeds of some ES tree

species do germinate in the forest understorey, as has been found elsewhere (*e.g.* ALVAREZ-BUYLLA & MARTÍNEZ-RAMOS 1990, 1992; DALLING *et al.* 1998); and (3) soil seeds may not have the greatest contribution to seedling emergence in tropical ES trees (DALLING *et al.* 1998).

#### Vegetation cover

This study shows that, depending on the habitat type and species successional status, vegetation cover may have positive, negative or neutral role on the recruitment of tropical tree seedlings. The presence of vegetation cover reduced recruitment of ES seedlings in primary forest and pasture and had no effect in the secondary forest. In contrast, vegetation removal had a negative effect on recruitment of LS species in the primary forest, a positive effect in secondary forest, and no effect in pasture.

Apparently, grass vegetation and forest litter cover are factors that have similar effects on seedling emergence and predation. For both cases, their effects are species-specific or at least depend on the ecological group of the species involved. At the emergence stage, it is likely that large-seeded LS species are able to grow through a thick litter layer or a dense grass sward, whereas at least for some small-seeded ES species, absence of litter/grass cover is vital for germination and establishment (VÁZQUEZ-YANES *et al.* 1990; MOLOFSKY & AUGSPURGER 1992; GONZÁLEZ-MONTAGUT 1996; HOLL 1999).

Both litter and grass cover modify the conditions of the microsites, *e.g.* humidity, nutrient and light availability, in which seeds germinate and seedlings establish (VÁZQUEZ-YANES *et al.* 1990; FACELLI & PICKET 1991; GONZÁLEZ-MONTAGUT 1996). Several studies in tropical pastures showed higher germination of tree seeds in areas where grass cover is present, probably because grass strongly modifies the microclimatic conditions near the soil surface (AIDE & CAVELIER 1994; GONZÁLEZ-MONTAGUT 1996; HOLL 1999). Grass cover in pastures may facilitate seed germination by reducing (high) soil temperatures and seed desiccation, but clearly limits seedling emergence and growth through below and above-ground competition (NEPSTEAD *et al.* 1991; GONZÁLEZ-MONTAGUT 1996; HOLL 1999).

The amount of litter on the forest floor affects the abundance and diversity of macro-arthropods (VASCONCELOS 1990), with important seed and seedling predation (MARTÍNEZ-RAMOS & SAMPER; 1998; BENÍTEZ-MALVIDO & KOSSMANN-FERRAZ 1999). In our study, the higher recruitment of LS species in primary forest, can be consequence of lower seed/seedling predation within plots covered by litter and vegetation. Reduced predation of seedlings in the presence of litter has been observed for the tropical tree *Micropholis venulosa* in Manaus, Brazil (BENÍTEZ-MALVIDO & KOSSMANN-FERRAZ 1999); whereas at 'Los Tuxtlas', Mexico, the shade tolerant palm *Astrocharyum mexicanum* has shown lower predation of its large seeds in the presence of litter (RODRÍGUEZ-VELÁZQUEZ & MARTÍNEZ-RAMOS, unpubl. data), probably because seeds/seedlings were less apparent to herbivores. In primary forest, the presence of vegetation cover may as well diminish the risk of seed/seedling predation. At 'Los Tuxtlas', the removal of understorey vegetation (plants < 1 m height) led to a significant reduction in seedling recruitment rate of LS species in experimental plots open to mammal predators but not in plots fenced to exclude these animals (MARTÍNEZ-RAMOS 1991). In secondary forest, higher recruitment of LS seedlings within plots free of vegetation and litter could be consequence of lower abundance of seed/seedling predators.

## Conclusions

Because each habitat type was not replicated, our results can not be extrapolated to the Selva Lacandona region. However, the results demonstrate that in our study sites tree seedling density and recruitment rate depend on habitat type, the regenerative strategy of the species involved, and on vegetation cover. Our study also showed that the relative importance of the seed rain and seed bank on the recruitment of tree seedlings differs among habitat types, and species ecological groups. The differences in seedling abundance and recruitment we found might be consequence of a complex interplay of biotic and abiotic factors that affect seedling establishment and survival within different tropical rainforest successional stages.

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**Appendix 1.** List of tree seedling species found in the present study for three successional habitats at the 'Chajul' Biological Station, Southeast Mexico (nomenclature follows MARTÍNEZ *et al.* 1994). Habitat: F = present in primary forest; Sf = present in secondary forest; and P = present in pasture. Ecological group: LS = late successional species; and ES = early successional species. Dispersal syndrome: Z = zoochory, A = anemochory, Au = autochory, and U = undetermined (ecological group and dispersal syndrome based on IBARRA-MANRÍQUEZ *et al.* 1997; PENNINGTON & SARHUKÁN 1998; G. IBARRA-MANRÍQUEZ, pers. comm., J. BENÍTEZ-MALVIDO, pers. obs.). Record: 1 = species found at the beginning of the study, 2 = species recruited into the experimental plots, respectively.

Species	Habitat	Ecological group	Dispersal syndrome	Record
<b>ACTINIDIACEAE</b>				
<i>Saurauia</i> sp. 1	F	LS	Z	2
<i>Saurauia</i> sp. 2	F	LS	Z	2
<b>ANACARDIACEAE</b>				
<i>Spondias radkolferi</i> J. D. Smith	F	ES	Z	2
<b>ANNONACEAE</b>				
<i>Cymbopetalum mayanum</i> Lundell	F, Sf	LS	Z	1
<i>C. penduliflorum</i> (Dunal) Baill.	F, Sf	LS	Z	1, 2
Annonaceae sp. 1	F, Sf	LS	U	1
Annonaceae sp. 2	P	LS	U	1
<b>APOCYNACEAE</b>				
<i>Sternmaderia donell-smithii</i> (Rose) Woodson	F, P	ES	Z	1
<i>Tabernaemontana alba</i> Mill.	Sf, P	ES	Z	1, 2
<i>Thevetia abouai</i> (L.) A. DC.	P	ES	A	1, 2
Apocynaceae sp. 1	F	U	U	1
<b>BIGNONACEAE</b>				
Bignoniaceae sp. 1	F	LS	U	2
<b>BURSERACEAE</b>				
<i>Bursera simaruba</i> (L.) Sarg.	F	LS	Z	2
Burseraceae sp. 1	F	LS	Z	2
<b>CAPPARIDACEAE</b>				
<i>Capparis</i> sp.1	F	LS	U	1
Capparidaceae sp. 1	F	LS	U	1
<b>CARICACEAE</b>				
<i>Jacaratia dolichaula</i> J. D. Smith	F	ES	Z	1
<b>CHRYSOBALANACEAE</b>				
<i>Hirtella americana</i> L.	F	LS	Z	1
<i>H. racemosa</i> Lamarck	P	LS	Z	1
<b>EUPHORBIACEAE</b>				
<i>Alchornea latifolia</i> Swartz	Sf, P	LS	Z	1, 2
<i>Croton schiedeannus</i> Schlecht.	F, Sf	ES	Au	1, 2
<i>Croton</i> sp. 1	Sf	ES	Au	2
<b>FLACOURTIACEAE</b>				
<i>Casearia</i> sp. 1	Sf	LS	Z	2
Flacourtiaceae sp. 1	Sf	LS	Z	1
Flacourtiaceae sp. 2	Sf, P	LS	Z	1

## Appendix 1. (continued)

GUTTIFERAE					
<i>Vismia camparagney</i> Sprague & Riley	Sf, P	ES	Z	2	
LAURACEAE					
<i>Nectandra reticulata</i> Ruiz & Pavón	F, Sf	LS	Z	1,	
<i>N. salicifolia</i> (H. B. K.) Nees	F, Sf	LS	Z	1, 2	
<i>N. sanguinea</i> Rottb.	F	LS	Z	1	
<i>Nectandra</i> sp. 1	F, Sf	LS	Z	2	
Lauraceae sp. 1	F	LS	Z	1, 2	
LEGUMINOSAE					
<i>Acacia cornigera</i> (L.) Willd.	F, Sf	ES	Z	1, 2	
<i>A. glomerosa</i> Benth.	Sf, P	ES	Z	1, 2	
<i>A. mayana</i> Lundell	F, Sf	ES	Z	1, 2	
<i>A. usumacintensis</i> Lundell	F, Sf	Z	Z	1, 2	
<i>Acacia</i> sp. 1	F, Sf, P	ES	Z	1, 2	
<i>Dalbergia glabra</i> (Miler) Standley	P	LS	A	2	
<i>Dialium guianense</i> (Aublet) Sandw.	F	LS	Z	1, 2	
<i>Inga pavoniana</i> Don	F	LS	Z	1	
<i>I. sapindindioides</i>	F	LS	Z	1	
<i>I. vera</i> Willd.	F	LS	Z	1	
<i>Inga</i> sp. 1	F	LS	Z	1	
<i>Lonchocarpus guatemalensis</i> Benth.	F	LS	Z	1	
<i>Schizolobium parahybium</i> (Vell.) Blake	F, P	ES	A	1, 2	
<i>Vatairea lundellii</i> (Standley) Killip ex Record	F, Sf, P	LS	A	1	
<i>Zapoteca portoricensis</i> (Jaq.) H.	P	ES	Au	2	
Leguminosae sp. 1	Sf	U	U	1, 2	
Leguminosae sp. 2	P	U	U	2	
MALPIGHIACEAE					
Malpighiaceae sp. 1	Sf	LS	Z	1	
MELASTOMATACEAE					
<i>Mouriri myrtilloides</i> (Swartz) Poiret	P	LS	Z	1	
ssp. <i>parviflora</i> (Benth.) Morley					
MELIACEAE					
<i>Guarea glabra</i> Vahl	F, Sf	LS	Z	1	
<i>Guarea</i> sp. 1	F	LS	Z	1	
<i>Trichilia erythrocarpa</i> Lundell	Sf	LS	Z	1	
<i>Trichilia</i> sp. 1	F	LS	Z	1	
MONIMIACEAE					
<i>Mollinedia viridiflora</i> Tulasne	F	LS	Z	1	
MORACEAE					
<i>Brosimum alicastrum</i> Swartz	F, Sf	LS	Z	1	
<i>B. costaricanum</i> Liebmann	F, Sf	LS	Z	1	
<i>Castilla elastica</i> Cervantes	F	LS	Z	1	
<i>Cecropia peltata</i> L.	F, P	ES	Z	1	
<i>Ficus obtusifolia</i> (Liebm.) Miq.	F	ES	Z	1	
<i>Trophis racemosa</i> (L.) Urban	F, Sf, P	LS	Z	1, 2	
Moraceae sp. 1	F	LS	Z	2	
MYRISTICACEAE					
<i>Virola koschnyi</i> Warb.	F, Sf	LS	Z	1, 2	
<i>V. guatemalensis</i> (Hemsl.) Warb.	F	LS	Z	1, 2	

## Appendix 1. (continued)

MYRSINACEAE					
<i>Icacorea compressa</i>	F, Sf	LS	Z	1, 2	
<i>Parathesis membranacea</i> Lundell	F	LS	Z	1	
<i>Parathesis</i> sp. 1	P	LS	Z	2	
MYRTACEAE					
<i>Eugenia mexicana</i> Steud.	F, P	LS	Z	1	
<i>Eugenia</i> sp. 1	P	LS	Z	1, 2	
<i>Psidium guajaba</i> L.	P	ES	Z	2	
OCHNACEAE					
<i>Ouratea lucens</i> (H. B. K.) Engler	F, Sf	LS	Z	1, 2	
RUBIACEAE					
<i>Faramaea occidentalis</i> (L.) A. Rich.	F, Sf, P	LS	Z	1	
<i>Posoqueria latifolia</i> (Rudge) R. & Pi.	F, P	LS	Z	1	
<i>Psychotria chiapensis</i> Standley	F	LS	Z	1	
<i>Psychotria</i> sp.	P	LS	Z	1	
Rubiaceae sp. 1	Sf	LS	Z	1	
Rubiaceae sp. 2	P	LS	Z	1	
Rubiaceae sp. 3	F	LS	Z	1	
SAPINDACEAE					
<i>Cupania dentata</i> DC.	P	LS	Z	1	
<i>Cupania glabra</i> Swartz	P	LS	Z	2	
<i>Cupania</i> sp. 1	P	LS	Z	2	
<i>Matayba</i> sp. 1	P	LS	Z	1, 2	
SAPOTACEAE					
<i>Chrysophyllum mexicanum</i> Brandegee	P	LS	Z	1	
Sapotaceae sp. 1	F, Sf	LS	Z	1	
TILIACEAE					
<i>Trichospermum meicanum</i> (A. DC.) Baill.	Sf, P	ES	A	1	
ULMACEAE					
<i>Ampelocera bottlei</i> Standley	F	LS	Z	1	
VERBENACEAE					
<i>Aegiphila monstrosa</i> Moldenke	F	LS	Z	1	
VIOLACEAE					
<i>Orthion subsessile</i> (Standley) Standley & Steyerl.	P	LS	Au	1, 2	
<i>O. malpighifolium</i> (Standley) Standley & Steyerl.	Sf	LS	Au	1	
<i>Rinorea hummelii</i> Sprague	F, Sf	LS	Au	1, 2	
VOCHYSIACEAE					
<i>Vochysia guatemalensis</i> J.D. Smith	F, P	LS	A	1, 2	
UNDETERMINED					
Tree sp. 1	Sf	U	U	2	
Tree sp. 2	Sf	U	U	2	
Tree sp. 3	Sf	U	U	2	