Relative Importance of Seed-Bank and Post-Disturbance Seed Dispersal on Early Gap Regeneration in a Colombian Amazon Forest

Luis S. Castillo1 and Pablo R. Stevenson
Universidad de Los Andes, Laboratorio de Ecología de Bosques Tropicales y Primatología, Centro de Investigaciones Ecológicas La Macarena, Carrera 1a No. 18A-12, Bogotá, Colombia

ABSTRACT

Early forest gap regeneration may be generated by postdisturbance seed rain and by seed, seedling, or bud banks (i.e., resprouting). The relative importance of each process may depend on several factors (e.g., fruit/seed production, abundance and behavior of seed dispersers, gap characteristics, etc.). We experimentally compared the importance of seed-bank and seed-rain affecting early recruitment of seedlings in an Amazonian forest (Zafire Biological Station, Colombia), using soil transplants from forests to gaps and seed rain enclosures. We found that, during the 8-mo study, the seed-bank contributed with a larger number of individuals and species than seed-rain. The low seedling recruitment rates may be associated with reduced populations of animal seed-dispersers due to hunting and/or low levels of forest fruit production.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: pioneer plants; secondary succession; seed dormancy; seed rain; Zafire Biological Station.

Natural gaps may play important roles in forest regeneration, floristic composition, and diversity in tropical forests. Canopy gaps contribute to environmental heterogeneity and, consequently, provide more niches to be exploited by organisms (Grubb 1977, Connell 1978, Denslow 1987, Wright 2002). The intermediate disturbance hypothesis describes how frequency, magnitude and time since disturbance may affect plant diversity, and predicts that the highest number of coexisting species should be found at intermediate magnitudes of these processes (Connell 1978). Gap regeneration is a complex process since dynamics are affected by a variety of factors associated with gap size and age, the surrounding plant and animal communities, weather, and human intervention, among others (Schupp et al. 1989).

Gap regeneration arises from four different sources: (1) the seed bank which refers to the seeds dormant or transient in the soil (Swaine & Hall 1983, Lawton & Putz 1988, Dalling & Hubbell 2002, Martins & Engel 2007); (2) the seedling bank, including recently germinated plants that were present in the site before gap formation (Teketay 1997, Frey et al. 2007); (3) the bud bank, representing damaged plants able to sprout after gap formation (Bond & Midgley 2001, Klimešová & Klimes 2007); and (4) the post-disturbance seed rain that corresponds to the seeds arriving to the gap after disturbance (Schupp et al. 1989, Gorchov et al. 1993, Estrada-Villegas et al. 2007). Few studies have made experimental approaches to quantify regeneration dynamics in gaps (Dalling & Hubbell 2002), and to our knowledge only Lawton and Putz (1988) have compared the importance of seed bank and postdisturbance seed rain in this process in a Costa Rican cloud forest. The aim of this study was to experimentally evaluate the relative importance of seed banks and seed rain in early seedling recruitment in natural Amazonian forest gaps, using a novel approach, with some elements from Lawton and Putz (1988).

METHODS

STUDY SITE.—Field work was conducted in a continuous, unlogged terra firme Amazonian forest in Zafire Biological Station (4°00’00” S, 69°53’57” W, 130 m a.s.l) between September 2007 and April 2008. The station is 27 km north of Leticia city (Colombia). Temperature is on average 26°C, with low variation over the year, and mean monthly precipitation is 280 mm, without consistent dry seasons (minimum monthly precipitation ca 160 mm), though the months with less rainfall tend to occur between June and August (IDEAM Institute 2001). We conducted the experiments in ten recently formed natural gaps (range: 2–24 mo old) distributed in 25 ha of forest, each one with an area of 101–309 m² (174.4 ± 67.2 SE) and average canopy openness of 21.7 percent (8.2–39.5%).

SOIL SAMPLES AND TREATMENTS.—We used four different treatments in each gap: seed-bank (SB), seed-bank plus seed-rain (SB + SR), seed-rain (SR), and a control (C). The SB treatment consisted of the transport of soil from primary forest to the gap and the obstruction of seed-rain with nylon nets (0.5 × 0.5 mm pores). Soil samples were collected from 0–10 cm deep, a depth at which many seeds are deposited by secondary seed dispersers (Andresen & Levey 2004) and are able to form the seed bank. The litter present in the soils was not excluded from the samples. In this treatment, all recruits came only from the seeds that were present in the primary forest soil bank. The SB + SR treatment differed from the SB treatment because it did not have the exclusion net. In this treatment, recruitment included seedlings emerging from the seed bank and the seed rain. The SR treatment consisted of sterilized primary forest soil, which then was carried to the gaps. The sterilization...
consisted in placing the soil sample during 2 h in a closed pot that was inside another pot with boiling water (Bell & Williams 1998). In the SR treatment, all seeds were killed so that recruits came only from the seed rain. The C treatment differed from the SR treatment because it had a net that prevented the arrival of seeds, thus we also excluded recruitment from the seed rain. The estimated volume of soil for each treatment was about 45 L (100 × 50 cm wide, 8–10 cm deep). All soil samples were taken from primary forest at least 30 m away from the corresponding gap and were situated randomly inside holes with the same dimensions and at least 2 m away from gap edge. The nets were box-shaped and situated upside down at 5 cm above the ground to allow the movement of small seed and seedling predators. This nylon net had larger dimensions than the area with translocated soil samples (110 × 60 cm wide, 60 cm high), to reduce seed rain contamination through the space between the net and the ground. For the SB, SR, and SB+SR treatments we performed two repetitions in each gap and the average was used in subsequent analyses as replicates. Our methodology resembles the protocol used by Lawton and Putz (1988), since both studies included translocation of primary forest sample soils to gaps, exclusions to isolate the effect of the seed rain, and soil sterilization. This study differs in two main aspects: (1) they spread the mature forest samples (1000 cm²) in a larger area (3600 cm²) inside gaps; and (2) in their study, the soil was sterilized with carcinogenic methyl-bromide application. As a result, chemical residuals might be affecting soil microorganism colonization and germination of seeds that come from postdisturbance dispersion.

**MEASURED VARIABLES AND STATISTICS.**—Recruited vascular and nonvascular seedlings > 1 cm were identified to morphospecies and marked to assess their fate over the next 8 mo. For each treatment in each gap we recorded the number of individuals, the cumulative number of individuals, species richness and calculated Simpson’s reciprocal index of diversity \(\text{index} = 1/\sum i^2\), where \(\pi\) represents the proportion of individuals of morphospecies \(i\) in the population (Krebs 1999)). Measurements were taken weekly for the first 2 mo, fortnightly for the next 2 mo, and a final reading 4 mo later. To evaluate the statistical differences among treatments over time, and since the assumption of sphericity of the variances (i.e., that differences of variances between any time period are the same) could not be met (Mauchly’s test for all variables; \(W = 0, P < 0.001\)), we used two alternatives to a repeated measures (RM) test: (1) we adjusted the RM \(F\)-ratio using a Greenhouse–Geisser (G–G) analysis; and (2) we summarized the responses for each treatment/time as a single value; the slope obtained in a regression analysis using log-transformed data (Quinn & Keough 2002, Gotelli & Ellison 2004). The calculated treatment slopes were measured in each gap as replicates and their means and variances were compared with a Kruskal–Wallis (K–W) test and, subsequently, with a Tukey multiple comparisons test. The significance level used was 0.05.

**RESULTS**

New seedlings first emerged during the second week after the treatments were set up in all gaps. During the following 6 weeks, the seedling emergence rate was relatively high and similar in the SB and the SB+SR treatments, but it gradually declined there after. In contrast, seedling emergence was very low in the SR and C treatments throughout the study (Fig. 1). Significant differences were observed between two groups of treatments (SB = SB+SR > SR = C) for all parameters (G–G RM test; number of individuals: \(F_{\text{treat}} = 19.4, F_{\text{treat×week}} = 11.0\); cumulative number of individuals: \(F_{\text{treat}} = 20.1, F_{\text{treat×week}} = 15.0\); number of morphospecies: \(F_{\text{treat}} = 19.6, F_{\text{treat×week}} = 10.7\); and Simpson’s reciprocal index of diversity: \(F_{\text{treat}} = 14.1, F_{\text{treat×week}} = 5.68, P < 0.001\); and K–W test of slopes: \(\chi^2 = 29.0; \chi^2 = 29.9; \chi^2 = 28.7; \chi^2 = 22.6\), respectively, \(P < 0.001\); Table S1). The most abundant taxa recruiting were mainly pioneer species: *Cecropia* spp. (Urticaceae), some members of Melastomataceae, *Apeiba* sp. (Malvaceae), and members of Dilleniaceae, Solanaceae, Annonaceae and Poaceae. The representation of shade tolerant species (e.g., *Iryanthera* sp.) was small in all treatments (6.6% of individuals in week 32).

**DISCUSSION**

In our study, the seed-bank played an important role in early gap regeneration compared with that from the seed rain. This pattern has been found in other studies (e.g., upland evergreen forest in Ghana: Swaine & Hall 1983; cloud forest in Costa Rica: Lawton & Putz 1988; moist tropical forest in Panamá: Dalling & Hubbell 2002; and seasonal semideciduous tropical forest in Brazil: Martins & Engel 2007), where the recruiting seedling community tightly reflected the seed bank composition. In our two seed bank treatments (SB and SB+SR), seed germination of pioneer species began in the first 2 weeks as a consequence of favorable conditions to which the seeds were exposed (Bazzaz & Pickett 1980, Garwood 1983, Kozlowski 2002). At the end of the experiment, these two seed bank treatments had more than six times the number of individuals and accumulated number of individuals, and three times the morphospecies richness and diversity, than those in the seed rain treatment and control. Seed rain after gap formation played a minor role in the early natural regeneration process in our site during the study period.

The data showed a nonsignificant trend for higher seedling emergence in the SB treatment compared with the SB+SR treatment (Figs. 1A and B). Possibly, independent of the species, the nylon net could reduce seedling predation, reduce seed removal (by predators and rainfall), and increase seedling survival (i.e., reducing the variability in humidity, temperature, and radiation). The sterilization method used in the SR and C treatments could reduce microorganism populations in the soil potentially affecting seedling emergence, growth, and survival. Nevertheless, since there were no physical or chemical barriers, we assumed that microorganisms could colonize in these soils again. We also assumed that the soil sterilization method did not considerably change the soil physical and chemical characteristics. The control treatment showed a reduced number of germinated seedlings, similar to the SR treatments. All those seedlings are of pioneer plants. We assume that the great proportion of those seedlings came from horizontal dispersion (e.g., earthworms: Willems & Huijsmans 1994; ants: MacMahon
At the end of the study seedling mortality was close to 30 percent in all treatments. It is possible that during the gap regeneration process, at some point, the recruitment rates from seed rain will become higher than those from the seed bank, due to a continuous seed input from the seed rain. Then, in the long run, the relative importance of these sources of recruitment will depend on the size of gaps and seed dispersal processes (Hubbell et al. 1999).

The differences between seed rain and seed bank recruitment in early regeneration have many explanations that are not exclusive. (1) The seed bank has more time to build up than the seed rain (Swaine 2001), and a great proportion of these seeds (i.e., pioneer species), can be dormant for a long period of time. (2) In contrast to the seed bank, seed rain could depend more closely on plants fruiting during the study period and on biotic and abiotic dispersal agents. Thus, dispersal limitation may affect the recruitment of plants from the seed rain (Hurtt & Pacala 1995, Hubbell et al. 1999, Nathan & Muller-Landau 2000), and not so strongly from the seed bank. (3) Young gaps may not be attractive to biotic dispersers like birds and bats, since in gaps these organisms may face high predation risks and low levels of resources (Schupp et al. 1989). Nevertheless, bats continue to be the most important agents of dispersion in open areas because they use these sites and they can defecate in flight (Gorchov et al. 1993, Medellín & Gaona 1999). Finally, (4) the Amazonian forest, like the one at Zafire Station, grows on old, nutrient-poor soils associated with sedimentation of black-water rivers (Irion 1978). Soil conditions limit forest productivity and, as a consequence, the community of seed dispersers shows low densities (Palacios & Peres 2005). The relationship between forest productivity and the abundance of dispersers has been documented in primates (Stevenson 2001, 2007b), birds (Loiselle & Blake 1991) and bats (Medellín et al. 2000).

The low representation of recruits from shade-tolerant plants may also be linked to the role and abundance of large seed dispersers (Peres & van Roosmalen 2002). We witnessed some degree of local hunting (L. S. Castillo pers. obs.), which is known to affect the densities of some important seed dispersers like primates and large birds (Peres & Palacios 2007). In addition, large seeds are transient in the seed bank because they do not have long dormancy periods.

---

**FIGURE 1.** Effects of experimental treatments (seed-bank plus seed rain [SB+SR], seed bank [SB], seed rain [SR] and control [C]) through time on four parameters of early gap regeneration dynamics: (A) mean number of individuals; (B) mean cumulative number of individuals; (C) mean number of morphospecies; and (D) mean reciprocal Simpson’s index. Sampling was performed in 10 different gaps. Each gap contained one 0.5 m² sample of each treatment in the Zafire Biological Station, Colombian Amazon. The ‘a’ group differs statistically from the ‘b’ group of treatments (Kruskal–Wallis test of Slopes and Greenhouse-Geisser RM analysis, P < 0.001). Error bars correspond to 95% CI.
(Swaine 2001, Martins & Engel 2007) and, as a result, their number in the soil seed community is reduced (Dalling & Hubbell 2002). Another potential factor affecting the low representation of large seeds is the higher predation risk that these face in gaps compared with mature forest (Schupp et al. 1989). This may result since they are easier to find, more nutritious than small seeds, and may be prone to predation in an impoverished seed environment (Stevenson 2007a). We predict that in sites where forest productivity is higher and animal dispersers are abundant, regeneration rates will be faster since the seed bank and seed rain will be enriched, and shade tolerant seeds will be less limited by dispersal. Nevertheless, it is necessary to undertake other studies in different sites to evaluate our predictions.

ACKNOWLEDGMENTS

We are grateful to M. C. Peñuela and the indigenous communities to allow the study in Zafire Biological Station. We thank the members of LEAMES (Laboratorio de Ecología de Bosques Tropicales y Primatología), C. Escallón and D. Cadena for their comments. We also thank the referees for their useful comments on an earlier version of this manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Slopes from the relationship between log time and four variables of early seedling regeneration.

Please note: Wiley-Blackwell Publishing are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED


