Pioneer tree species dispersion in treefall gaps in a tropical wet lowland forest

R. M. BRAYCE, B. J. GARCIA, M. E. LEPENE, A. E. SANTORO

Abstract. Treefall gap colonization plays an important role in tropical rain forest dynamics. Pioneer tree species dispersion among gaps is often assumed uniform as a result of even, prolific seed dispersion within the seed bank. We hypothesized that pioneer tree species may instead be dispersal limited, resulting in a clumped distribution among gaps. We found that *Cecropia obtusifolia* juveniles were clumped among treefall gaps, indicating dispersal limitation, while *Hampea appendiculata* were more evenly disersed. Forty-six percent of *C. obtusifolia* juveniles were found on logs; also, juveniles became more uniformly distributed with increasing height. Passive seed dispersal as well as colonization after a gap forms appear to be important for *C. obtusifolia* establishment. However, *H. appendiculata* seems to rely primarily on long-range animal dispersal . Thus, different pioneer species may utilize different gap-colonization strategies.

Key Words: clumped distribution, dispersal, forest gap dynamics, pioneer species, swing

INTRODUCTION

The high occurrence of treefall gaps in the tropical wet lowland forest of La Selva, Costa Rica, plays an important role in forest system dynamics (Denslow and Hartshorn 1994). Gaps provide a high-light environment for the establishment and rapid growth of pioneer species. It is assumed that pioneer tree species have long-range, random seed dispersal, and therefore, are distributed widely across many gaps (Lieberman and Lieberman 1994). Alternatively, it has been suggested that the seeds of pioneer species are typically dispersed short distances, which would lead to a high variance in seedling presence among gaps (Dalling, et al. 1998).

In this study, we examined the spatial distribution of two pioneer tree species, *Hampea appendiculata* and *Cecropia obtusifolia*, among tree fall gaps. Specifically, we asked: (1) Are *C. obtusifolia* and *H. appendiculata* locally abundant in a few gaps and not others (i.e. clumped across gaps)? (2) What factors determine the spatial distribution of pioneer species within a gap (e.g. substrate type, near-neighbor competition)? We predicted (1) that both *C. obtusifolia* and *H. appendiculata* would exhibit a clumped distribution among gaps (i.e., some gaps with many seedlings and others with few or none), and (2) that seed dispersal to a gap after it forms would play a large role in patterns of gap colonization.

METHODS

We censused the populations of *Cecropia obtusifolia* and *Hampea appendiculata* < 2 m tall in eight tree fall gaps located along three trails (Camino Experimental Sur, Camino Experimental Norte, and Camino Circular Cercano) near the Estacion Biologica La Selva, Costa Rica on 16, 17, and 18 February 1999. Gaps were defined as canopy openings extending to within 3 m of the forest floor with an area > 40 m^2. For our study, we excluded both newly formed gaps, those in which fallen logs showed no signs of decay and emergent vegetation was < 1 m tall, as well as older gaps, where vegetation was > 4 m tall. We measured the length of the gap along the longest axis of the canopy opening, from the boles of the overreaching canopy trees at either edge. Gap width was measured at the widest point perpendicular to the length. We calculated total gap area as the product of these two values.

To assess the spatial distribution of the juveniles within a gap, we measured the height and distance to the nearest conspecific neighbor for each *C. obtusifolia* and *H. appendiculata* individual. The substrate on which each individual was located was recorded as either ground or log. We then searched a 20 m radius around each gap for conspecific adults of each species. Dalling et al. (1998) reported that 98% of *Cecropia* seed rain was within this distance.

We assessed dispersion of each pioneer species among gaps by comparing observed juvenile densities (per 100 m^2) against a random expected frequency distribution (Poisson distribution) and calculating a coefficient of dispersion (CD = SD^2/mean) as described in Sokal and Rohlf (1981). Coefficients > 1 indicate clumped dispersion (i.e., more closely spaced than would be expected assuming a random distribution), while values < 1 indicate hyperdispersion (i.e. farther apart than would be expected if distributed randomly).

RESULTS

Gaps ranged in area from 135 to 1150 m^2 with a mean gap area of 495 ± 157.3 (SE) m^2 (n = 8). We located 108 *Cecropia obtusifolia* and 26 *Hampea appendiculata* individuals within the eight gaps. *C. obtusifolia* distribution among gaps was clumped (Fig. 1; CD = 7.02) while *H. appendiculata* juveniles were more evenly distributed (CD = 1.80). We found only two gaps with an adult *C. obtusifolia* (one at each gap) within the 20 m radius around gap edges; these two gaps also showed the highest density of *C. obtusifolia* juveniles, as they contained 44 % of total *C. obtusifolia* juveniles found in the eight gaps (Kruskal-Wallis: X^2 = 4.05, df = 1, P = 0.04; mean ± SE (ind./m^2): 0.12 ± 0.02, n=2), while those gaps without a proximal adult conspecific showed much lower juvenile densities (0.01 ± 0.01, n=6). No *H. appendiculata* adults were found within 20 m of any of the gaps sampled. We found one gap without *C. obtusifolia* juveniles and one without *H. appendiculata* juveniles.

Forty-six percent of *C. obtusifolia* juveniles (n = 49) were located on fallen logs. All of the *H. appendiculata* juveniles within the gaps were located on the ground; none were on logs. Also, juvenile *C. obtusifolia* were increasingly further apart from one another as juvenile size (height) increased (Fig. 2; Linear Regression: r^2 = 0.16, df = 1, P = 0.0001). However, we found no relationship between juvenile height and distance to nearest conspecific neighbor for *H. appendiculata* (Linear Regression: r^2 = 0.001, df = 1 , P = 0.86).

Mean height of *C. obtusifolia* juveniles was lower than *H. appendiculata* (Fig. 3; Kruskal-Wallis, X^2=56.9, df=1, P<0.0001). *C. obtusifolia* juvenile distribution within gaps was more clumped than *H. appendiculata* juveniles (Fig. 3; Kruskal-Wallis, X^2 = 21.1, df = 1, P = 0.0001).

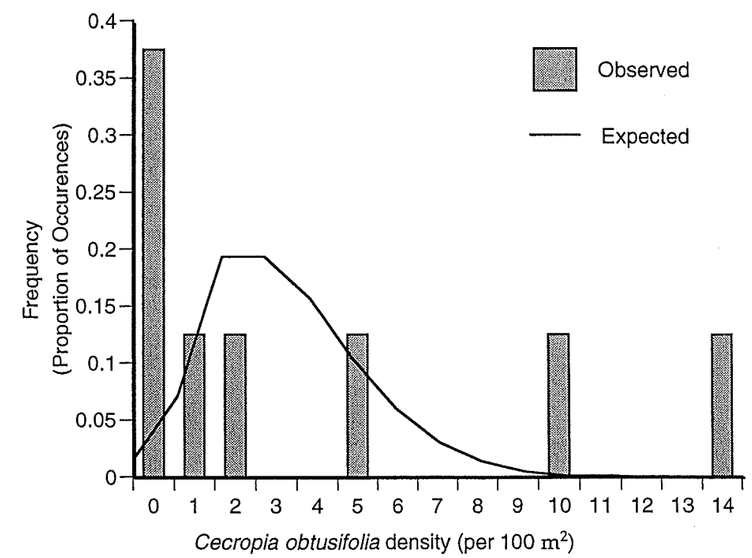

Fig. 1. Observed densities of *Cecropia obstusifolia* juveniles among eight treefall gaps at La Selva, Costa Rica. Dispersion among gaps is more clumped than would be expected assuming a random distribution. Dark bars indicate gaps with conspecific adults within 20 m of the gap edge.

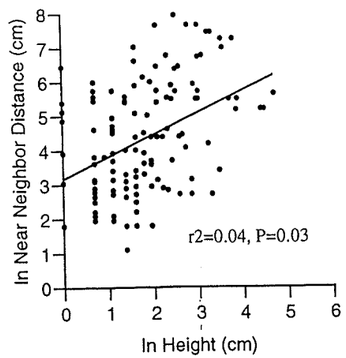

Fig. 2. Relationship between height and near neighbor distance for *C. obtusifolia* in treefall gaps at La Selva, Costa Rica. (n=108 juveniles in eight gaps).

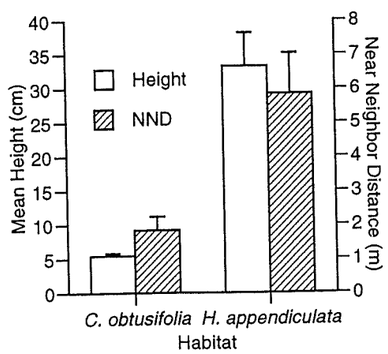

Fig. 3. Mean height and distance to conspecific neighbor (± SE) for seedlings of two pioneer species in eight treefall gaps at La Selva, Costa Rica.

DISCUSSION

If pioneer species have no limitations to their dispersal, distribution of these species among gaps would be expected to be random. However, juvenile *Cecropia obtusifolia* were found primarily in gaps near conspecific mature trees, which suggests that wide-range dispersal is limited. This is consistent with the fact that most seeds in the species are dispersed by wind Dalling, et al. 1998). Still, the presence of juveniles in gaps >20 m from conspecific mature trees suggests that long-distance (e.g. vertebrate) dispersal also influences their distribution.

Within gaps, the spatial distribution of juveniles was influenced by substrate type. Although fallen logs appeared to represent only a small proportion of total substrate in gaps, 46% of juvenile *C. obtusifolia* were found on logs. This result supports the findings of Dallison and Lepene (1999) that decaying logs support a disproportionate amount of seedlings of certain species. Also, as these fallen nurse logs appeared to be trees that fell during gap formation, the high density of *C. obtusifolia* juveniles on these logs indicates the prevalence of colonization by *C. obtusifolia* after gap formation, rather than advanced regeneration or germination from a long-term forest seed bank.

Distribution of juvenile *C. obtusifolia* also appeared to be influenced by juvenile size, with a positive association between height and distance to nearest conspecific juvenile (Fig. 2). As juvenile height increases, increased intraspecific competition (e.g. shading) may lead to higher mortality and a subsequent thinning of juvenile populations.

Several of these colonization patterns did not appear to hold for *Hampea appendiculata*. First, no juvenile *H. appendiculata* were found on nurse logs, suggesting that either post-gap formation seed dispersal or the presence of log substrates is less important for *H. appendiculata*. Juvenile *H. appendiculata* also had a greater mean height than *C. obtusifolia* across all gaps, indicating that *H. appendiculata* may either colonize gaps earlier or have higher growth rates. Finally, juvenile *H. appendiculata* had greater distances to conspecific juveniles, possibly indicating greater intraspecific competition or more evenly distributed seed dispersal within a gap than *C. obtusifolia* (Fig. 3). The presence of *H. appendiculata* juveniles in gaps despite the lack of conspecific adults within 20 m of any of the eight gaps implies that gap colonization by this species involves long-distance vertebrate dispersal.

Passive seed dispersal near parent trees appears to be the primary mechanism for the colonization of gaps by *C. obtusifolia* at La Selva, although long-distance vertebrate dispersal also appears to be important. Spatial distribution of *C. obtusifolia* also

appears to be influenced by the presence of nurse logs as well as juvenile height. However, this pattern of dispersal does not hold across all pioneer species, as another common pioneer species, *H. appediculata*, appears to use different gap-colonization strategies.

LITERATURE CITED

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79: 564-578.

Dallison, C. R. E. and M. E. Lepene. In press. Juvenile establishment on fallen logs versus forest floor in a high elevation tropical oak forest. Dartmouth Studies in Tropical Ecology.

Denslow, J. S. and G. S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. Pp. 120-127 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, Eds. La Selva. Chicago: The University of Chicago Press.

Lieberman, M. and D. Lieberman. 1994. Patterns of density and dispersion of forest trees. Pp.106-119 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, Eds. La Selva. Chicago: The University of Chicago Press.

Sokal, R.R. and F. J. Rohlf. 1981. Biometry. Second edition. San Francisco: W.H. Freeman and Company. Pp. 84-88.