

PHYSICAL DAMAGE TO ARTIFICIAL SEEDLINGS IN RELATION TO DISTANCE FROM TROPICAL FOREST EDGES

Ana C. Sánchez-Thorin^{1,2}, William F. Laurance¹, Catalina Perdomo¹ & Robert M. Ewers^{1,3*}

¹Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

²Current address: BP Exploration Company (Colombia) Ltda. Carrera 9A No. 99-02 Piso 9. Bogotá, Colombia

³Current address: Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK, and Department of Zoology, Cambridge University, Downing Street, Cambridge CB2 3EJ, UK

Abstract. Litterfall can be a major cause of seedling mortality and damage in tropical forests, and is often elevated near forest edges. We predicted that, in Soberanía National Park in central Panama, the proportion of experimental seedlings damaged by litterfall would be higher at forest edges than in the forest interior. Over a 16-week period during the rainy season, 41% of 1260 experimental seedlings were damaged, but just 4% were clearly damaged by litterfall. We found no consistent trend in litterfall damage with respect to distance from edge, although there were higher proportions of total seedling damage in the forest interior which were caused by factors other than litterfall.

Resumen. La hojarasca puede ser una de las causas más importantes en el daño y la mortalidad de plántulas en los bosques tropicales, y es frecuentemente más abundante en los bordes. Predijimos que en el Parque Nacional Soberanía en el centro de Panamá, la proporción de plántulas experimentales derribadas por hojarasca es más alta cerca del borde del bosque que en el interior. En un periodo de 16 semanas durante la estación lluviosa, 41% de las plántulas fueron derribadas pero solo 4% a causa de la hojarasca. No encontramos un patrón consistente en el daño causado por la hojarasca con respecto a la distancia desde el borde, aunque se encontraron proporciones totales más altas de daño de plántulas en el interior del bosque, ocasionadas por otros factores. Accepted 22 May 2006.

Key words: edge effects, experimental seedling damage, litterfall damage, seedling mortality.

INTRODUCTION

Forest fragmentation causes a proliferation of artificial edges that abut modified habitats such as pastures, croplands, regrowth forest and roads. Many abiotic factors, including insolation, wind penetration, air and soil temperatures, vapor pressure deficit, photosynthetic active radiation and evapotranspiration increase near edges, whereas other factors such as humidity, soil and litter moisture, and leaf-water content, decline (Lovejoy *et al.* 1986, Kapos *et al.* 1997, Williams-Linera *et al.* 1998, Didham & Lawton 1999). Such changes alter ecological dynamics of vegetation near the forest edge, with increased mortality of trees (Laurance *et al.* 1997, 1998a, 2000) and seedlings (Scariot 2000; but see Hewitt & Kellman 2004, Bach *et al.* 2005), alterations in population density and basal area of some tree species (Williams-Linera

1990, Laurance *et al.* 1998b, Tabarelli *et al.* 1999), and elevated litterfall (Sizer *et al.* 2000, Vasconcelos & Luizao 2004).

Environmental changes that alter seedling density could potentially have long-term consequences for forest composition (Benitez-Malvido 1998, Laurance *et al.* 1998b). Previous studies suggest that one important cause of seedling mortality in tropical forests is litterfall (Clark & Clark 1989, Mack 1998, Scariot 2000, Gillman *et al.* 2004), although vertebrate consumption (De Steven & Putz 1984, Howe *et al.* 1985) and disease (Augspurger 1984) are also important factors. Litterfall is known to increase near forest edges because of elevated wind turbulence and greater leaf abscission from drought stress (Laurance 2004). Scariot (2000) showed that physical damage to artificial seedlings from litterfall ranged from 28 to 35% per year in Amazonian forest fragments, compared with just 20–24% in continuous forest. Similarly, Clark & Clark (1987, 1989) found in two separate studies

* e-mail: robert.ewers@ioz.ac.uk

in a primary forest in Costa Rica that seedling mortality due to litterfall ranged from 14 to 19% per annum. Other studies of seedling damage from litterfall in tropical forests have also shown that between 10 and 40% of seedlings are impacted by this process (Aide 1987, Drake & Pratt 2001). Because rates of litterfall are typically elevated near edges (Lovejoy *et al.* 1986, Carvalho & Vasconcelos 1999, Sizer *et al.* 2000), we hypothesized that rates of litterfall damage to seedlings would also be higher at forest edges than in the forest interior.

METHODS

This study was conducted in Soberanía National Park, which is a tropical lowland forest of about 22 000 ha located along the western side of the Panama Canal (9°N, 79°W). It has a tropical humid climate with average annual precipitation of 2612 mm (SD = 446 mm), a relative humidity in the forest understory of 70–95%, temperatures that range between 23° and 32°C, and strong seasonality in rainfall (Windsor 1990). The rainy season extends from April to November and the dry season from December to March. This study was conducted in the rainy season, between June and September 2004. The study area was characterized by a mixture of primary and secondary forest (60–100 years old) with mature edges (81 years old).

Seven transects 120 m long were established perpendicular to forest edges created 81 years ago, two at forests bordering pastures, and five at forests which have road and secondary growth interfaces. At each of nine distances in from the forest edge (0, 10, 20, 30, 40, 50, 60, 80 and 120 m) we placed twenty artificial seedlings that were arranged parallel to the forest edge and separated by 1-m intervals. To allow rigorous comparisons of seedling mortality and damage proportions among independent studies (Murcia 1995), we followed the method of Clark & Clark (1989) and Scariot (2000) by constructing artificial, inert seedlings from two 20-cm-long green plastic straws that were attached together with staples to form a cross. A strong 13-cm wire was inserted 3 cm into the vertical straw and attached to the bottom of the cross with a thin flexible piece of wire, making a 10-cm root (Clark & Clark 1989). The top of the vertical straw was stapled at the top to prevent water penetrating inside the artificial seedling. Green straws were employed to avoid actively attracting animals (Scariot 2000).

The status of seedlings was checked at two-week intervals for the duration of the study (16 weeks). Seedlings were coded as (a) damaged or (b) undamaged, with damaged seedlings described in two ways: (1) flat or bent: those with a vertical straw that was either bent or broken such that one or both 'arms' were touching the ground, or (2) uprooted: the entire seedling 'root' pulled out of the ground. Damaged seedlings were further classified as having been damaged either by litterfall (where the seedlings were found bent or flattened beneath fallen leaves, branches or logs), or by unidentified causes (all other damaged seedlings). The latter were assumed to be largely the result of animal activity, although clear evidence of chewing, footprints, or other animal signs were often not apparent. All damaged seedlings were removed from the field and not replaced.

Cumulative seedling damage was assessed at the end of the 16-week period. Patterns in seedling damage along and between edge transects were analysed with general linear models (GLM). Because seedlings were recorded as damaged or not damaged, we specified a logit link function for data with a binomial error structure and tested for significance against the Chi-square distribution (ter Braak & Looman 1995). We tested for differences in seedling damage between distances to edge, transects, and their interaction. Transects were included as a predictor variable to assess the generality of any edge gradient detected – a significant transect effect would indicate that there is considerable site-specific variation between transects that is not explained by edge effects alone. Similarly, a transect-edge distance interaction would indicate that the edge effect differed between transects. Distance to edge and transects were both analyzed as factors, reflecting the ANOVA design of this experiment. Three tests were conducted, one for seedlings damaged by litterfall, one for seedlings damaged by unidentified causes, and one for all damaged seedlings together.

RESULTS

Over the 16-week period of this study, 41% of seedlings were damaged. Logistic GLM models showed significant differences in seedling damage among edge distances, transects, and their interaction for both total damage and animal-damaged seedlings (Table 1; Fig. 1). Litterfall damage was significantly affected by distance to edge, but did not differ among transects, nor was there a significant interaction effect

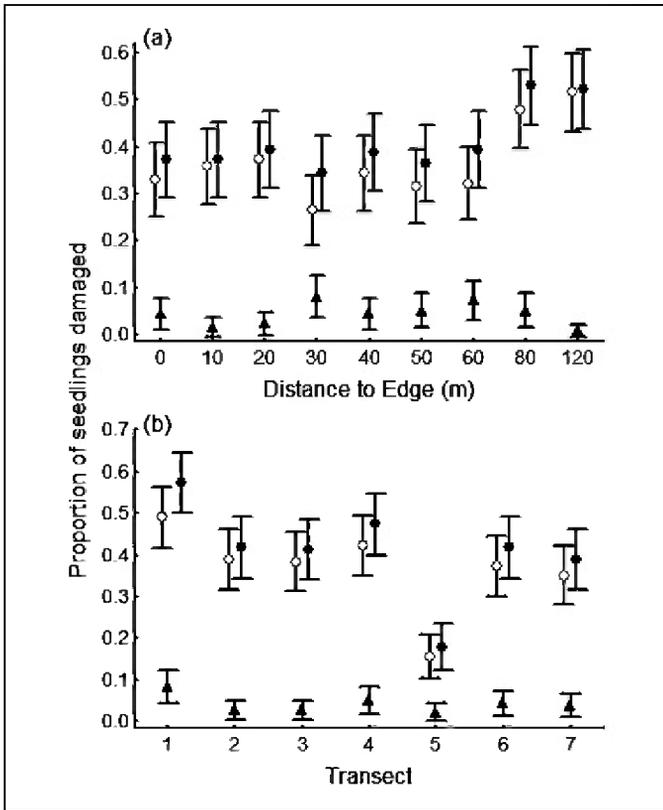


FIG. 1. Proportion of seedlings damaged with respect to (a) distance to edge, and (b) transect. Note the non-linear scale in (a). Transects 1 and 2 abutted pasture and all others abutted a road. Values are mean \pm 95 % CI. Triangles indicate damage from litterfall, open circles show damage from unidentified causes, and closed circles show total seedling damage.

TABLE 1. Results of binomial general logistic models comparing seedling damage between transects, edge distances and their interaction. Results from three tests are presented: (a) total seedling damage, (b) seedling damage from litterfall only, and (c) seedling damage from unidentified causes only. * significant at $P < 0.05$, ** significant at $P < 0.01$.

Factor	df	Deviance	Residual df	Residual Deviance
(a) Total seedling damage				
NULL			1259	1703.77
Transect	6	67.14	1253	1636.63**
Edge Distance	8	22.51	1245	1614.12**
Interaction	48	111.12	1197	1503.00**
(b) Litterfall damage				
NULL			1259	439.61
Transect	6	10.49	1253	429.12
Edge Distance	8	18.56	1245	410.56*
Interaction	48	61.35	1197	349.21
(c) Damage from unidentified causes				
NULL			1259	1654.94
Transect	6	53.80	1253	1601.14**
Edge Distance	8	32.16	1245	1568.98**
Interaction	48	120.05	1197	1448.94**

(Table 1; Fig. 1b). Total seedling damage was notably higher at 80 and 120 m from the edge than at all other distances, and this pattern was driven by an increase in damage from unidentified causes (Fig. 1a). In contrast, there was no consistent trend in litterfall damage with respect to edge; in fact, litterfall damage was lowest at 120 m into the forest.

DISCUSSION

Overall seedling damage rates in this study were comparable to those in La Selva, Costa Rica (Clark & Clark 1989), in which 75–90% of the seedlings were damaged over a one-year period. The survival model of Clark & Clark (1989) predicted that 38% of seedlings would be damaged over four months (the duration of our study), which is very close to the value of 41% we observed. However, just 4% of the seedlings in our study were damaged by litterfall, whereas in La Selva (Clark & Clark 1989) and Manaus, Brazil (Scariot 2000), 14–19% and 28–35% respectively of seedlings suffered damage from litterfall. The reduced rate of litterfall damage in our study probably reflects structural differences between the regenerating forest edges investigated here and the interior primary forests that were studied in La Selva and Manaus. This is consistent with other literature on litterfall-induced seedling mortality, which suggests that differences in forest architecture can cause widely varying rates of litterfall damage (Clark & Clark 1989, Gillman *et al.* 2004). It is also possible that rates of litterfall in our study area are lower in the wet season than in drier months (see below), although wet-season windstorms can certainly generate substantial litterfall.

Proportional seedling mortality did not systematically vary with respect to edge. Although litterfall damage was significantly affected by distance to edge, there was no consistent trend either toward or away from the forest interior. Thus, we must reject our initial hypothesis and conclude that, in this study area, rates of litterfall damage to seedlings are not higher at forest edges during the rainy season. Rather, they appear to be idiosyncratic, with local site effects being the predominant driver of seedling damage from litterfall.

We identify three possible reasons for the lack of an edge-related pattern in litterfall damage to seedlings in this study. First, litterfall damage is distributed patchily throughout forests in response to the patchy distribution of the species that are responsible for the litterfall (Gillman *et al.* 2002) and to small-scale var-

iations in topography (Mack 1998). Our results indicate that microsite conditions probably varied independently of distance to edge, overriding any edge effect that might have been present. Second, absolute increases in litterfall at forest edges may be a temporary phenomenon only (Sizer *et al.* 2000), and old edges such as the ones investigated in this study may no longer be prone to edge-induced increases in rates of litterfall. However we did not make direct measurements of litterfall to correlate with distance to edge, so cannot say for sure if this is the case. Third, the study was conducted during the rainy season, when litterfall rates from phenologically determined seasonal patterns of leaf fall (Machado *et al.* 1997, Funch *et al.* 2002) and drought stress (Laurance 2004) are probably at their lowest. Thus edge-induced increases in leaf litterfall (Sizer *et al.* 2000), and hence litter-driven seedling mortality, if present, might be expected to be more apparent during the dry season.

An important factor that negatively affected the artificial seedlings in this study was damage from unidentified causes, which resulted in a pattern of significantly higher total seedling damage in the forest interior (at 80 and 120 m) than at the forest edge. Presumably much of this damage was caused by animals that were trampling, kicking, biting, or digging up the seedlings (Clark & Clark 1989), possibly as a 'novelty response.' Some rainforest mammals are known to actively avoid forest edges (Goosem 1997), and an increase in their abundance near the forest interior could explain the observed pattern. However, the novelty response suggests that animal damage to artificial seedlings is not correlated with damage to natural seedlings (Gillman *et al.* 2002). Therefore we cannot infer that the pattern of increased artificial seedling damage in the forest interior has any implications for the spatial patterns of mortality of real seedlings.

Our study agrees with previous experimental studies in tropical forests that show that seedlings suffer high rates of mortality. Overall rates of seedling damage were similar to those in the interior of nearby Costa Rican rainforest (Clark & Clark 1989), although we attributed substantially less of the damage specifically to litterfall. While we failed to discern any apparent trend in litterfall damage with respect to edge, we have shown that total damage proportions are elevated in the forest interior. Therefore variables other than leaf litterfall should also be considered when investigating edge-related patterns of seedling mortality in tropical forests.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute for financial support, Soberanía National Park and Summit Gardens for logistical assistance, Sebastien Renault for discussion, and an anonymous reviewer for constructive comments.

REFERENCES

- Aide, T.M. 1987. Limbfalls: a major cause of sapling mortality for tropical forest plants. *Biotropica* 19: 284–285.
- Augsburger, C.K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65: 1705–1712.
- Bach, C.E., Kelly, D., & B.A. Hazlett. 2005. Forest edges benefit adults, but not seedlings, of the mistletoe *Alepis javida* (Loranthaceae). *J. Ecol.* 93: 79–86.
- Benítez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Cons. Biol.* 12: 380–389.
- Carvalho, K.S., & H.L. Vasconcelos. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biol. Cons.* 91: 151–157.
- Clark, D.B., & D.A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica* 19: 236–244.
- Clark, D.B., & D.A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225–230.
- De Steven, D., & F.C. Putz. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43: 207–216.
- Didham, R.K., & J.H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17–30.
- Drake, D.R., & L.W. Pratt. 2001. Seedling mortality in Hawaiian rain forest: the role of small-scale physical disturbance. *Biotropica* 33: 319–323.
- Funch, L.S., Funch, R., & G.M. Barroso. 2002. Phenology of gallery and montane forest in the Chapada Diamantina, Bahia, Brazil. *Biotropica* 34: 40–50.
- Gillman, L.N., Wright, S.D., & J. Ogden. 2002. Use of artificial seedlings to estimate damage of forest seedlings due to litterfall and animals. *Journal of Vegetation Science* 13: 635–640.
- Gillman, L.N., Ogden, J., Wright, S.D., Stewart, K.L., & D.P. Walsh. 2004. The influence of macro-litterfall and forest structure on litterfall damage to seedlings. *Austral Ecol.* 29: 305–312.
- Goosem, M. 1997. Internal fragmentation: the effects of roads, highways, and powerline clearings on movements and mortality of rainforest vertebrates. Pp. 241–255 in W.F. Laurance & R.O. Bierregaard (eds.). *Tropical Forest Remnants: Ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago.
- Hewitt, N., & M. Kellman. 2004. Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings. *For. Ecol. Man.* 191: 39–59.
- Howe, H.F., Schupp, E.W., & L.C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781–791.
- Kapos, V., Wandelli, E., Camargo, J.L.C., & G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. Pp. 33–44 in W.F. Laurance & R.O. Bierregaard (eds.) *Tropical Forest Remnants: Ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago.
- Laurance, W.F. 2004. Forest-climate interactions in fragmented tropical landscapes. *Phil. Trans. R. Soc. Lond. B.* 359: 345–352.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., & T.E. Lovejoy. 2000. Rainforest fragmentation kills big trees. *Nature* 404: 836.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., & S.G. Laurance. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79: 2032–2040.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., Hutchings, R.W., & T.E. Lovejoy. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Cons. Biol.* 12: 460–464.
- Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C., & T.E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278: 1117–1118.
- Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., L.H. Harper, L.H., Brown, K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., & M.B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285 in Soulé, M.E. (ed.). *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Inc., Massachusetts, USA.
- Machado, I.C.S., Barros, L.M., & E.V.S.B. Sampaio. 1997. Phenology of Caatinga species at Serra Talhada, PE, northeastern Brazil. *Biotropica* 29: 57–68.
- Mack, A.L. 1998. The potential impact of small-scale physical disturbance on seedlings in a Papuan rainforest. *Biotropica* 30: 547–552.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10: 58–62.

- Scariot, A. 2000. Seedling mortality by litterfall in Amazonian forest fragments. *Biotropica* 32: 662–669.
- Sizer, N.C., Tanner, E.V.J., & I.D. Kossmann-Ferraz. 2000. Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *J. Trop. Ecol.* 16: 853–863.
- Tabarelli, M., Mantovani, W., & C.A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biol. Cons.* 91: 119–127.
- ter Braak, C.J.F., & C.W.N. Looman. 1995. Regression. Pp. 29–77 *in* Jongman, R.H.G., Ter Braak, C.J.F., & O.F.R. Van Tongeren (eds.). *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.
- Vasconcelos, H.L., & F.J. Luizao. 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. *Ecol. Appl.* 14: 884–892.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78: 356–373.
- Williams-Linera, G., Dominguez-Gastelu, V., & M.E. Garcia-Zurita. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Cons. Biol.* 12: 1091–1102.
- Windsor, D.M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. *Smithsonian Contributions to the Earth Sciences* 29: 145.