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The Potential Impact of Small-Scale Physical Disturbance on Seedlings in a Papuan Rainforest[1]

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ABSTRACT

Physical disturbance, such as falling debris, is an important cause of mortality to rain forest seedlings. I used artificial seedlings to quantify physical disturbance in a rain forest at the Crater Mountain Biological Research Station in Papua New Guinea. Single (N = 418) and clustered artificial seedlings (N = 428) were placed on eight transects spanning varied topography to assess the area's disturbance regime, to test if ground slope affected disturbance, and to test if clustering affected the incidence of damage.

Two transects showed a significant departure from random in the spatial distribution of damaged seedlings within the transect, suggesting that some areas of experience more disturbance than others. Artificial seedlings on level ground experienced damage less often than artificial seedlings on slopes; disturbance increased with ground slope. Artificial seedlings in dry washes experienced the greatest probability of damage. Artificial seedlings in clusters experienced significantly less damage than single ones, suggesting clustered seedlings might be less vulnerable to damage than lone seedlings. The disturbance rate at this site (34.7% damaged in one year) was markedly lower than that measured at the La Selva Biological Reserve in Costa Rica (82.4%).

Key words: *artificial seedlings; disturbance; ground slope; litterfall; mortality; Papua New Guinea; rain forest; seedling.*

In the years between leaving the parent tree as a seed and maturation as a reproductive adult, individual trees face many potential sources of mortality. Seed predators kill many seeds before germination and herbivores and pathogens kill many seedlings (*e.g.*, Janzen 1983, Augspurger 1984, De Steven & Putz 1984, Howe *et al.* 1985). One important and only recently examined cause of mortality to seedlings of rain forest trees is incidental physical damage.

Studies in Costa Rica (Hartshorn 1972, Vandermeer 1977, Clark & Clark 1987) and Panama (Aide 1987, Augspurger & Kitajima 1992) showed litterfall and animal disturbance are important causes of seedling mortality. Such disturbances are readily assayed using an artificial seedling free of biotic sources of mortality (Clark & Clark 1989). One advantage of the artificial seedling assay is the ease of replication at different localities (*e.g.*, McCarthy & Facelli 1990).

This study of physical disturbance on seedlings was part of a broader investigation of seed dispersal by the Dwarf Cassowary, *Casuarius bennetti,* in the lower montane forest of Papua New Guinea (PNG). Cassowaries disperse large numbers of seeds of many tree and liana species (Stocker & Irvine 1983, Pratt 1983, Coates 1985). Cassowaries range widely, non-randomly dispersing seeds to a variety of sites. Seeds are disproportionately dispersed to level sites and rarely dispersed to steep sites or dry washes (Mack 1995a). Seeds in cassowary droppings usually germinate and form clusters of seedlings (Stocker & Irvine 1983; A. Mack, pers. obs.), a situation that might be disadvantageous to seedlings due to competitive effects (Howe 1989). I undertook this study to assess potential impact of physical damage to seedlings, particularly in relation to ground slope and clustering effects. Furthermore, I examined heterogeneity in the disturbance regime within the study area and compared the disturbance regime to that of another rain forest.

STUDY SITE

This study took place at the Crater Mountain Biological Research Station (6°43.437′ S, 145°05.576′ E) in southwest Simbu Province, Papua New Guinea from February 1991- March 1992. The study area lies in rugged hill forest at 950–1200 m elevation. The area is closed, primary forest with little recent human disturbance. The composition of the forest is extremely diverse, with no markedly dominant species (Wright *et al.* 1997), somewhat resembling the evergreen hill forest to sub-montane forest descriptions of Paijmans (1976).

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METHODS

Artificial seedlings (hereafter abbreviated AS) were made using two clear plastic drinking straws stapled in a cross and wired to a 13 cm thick gauge wire "root" following the design of Clark and Clark (1989). Each artificial seedling had a numbered aluminum tag wired to its base. When positioned, the wire was pushed firmly into the ground until the upright straw was flush with the ground.

TRANSECTS.—In March 1991 I established eight linear transects 120 to 150 m long starting from randomly selected spots (6 on trails, 2 off trails) and following randomly selected compass bearings. It was necessary to bend three of the transects slightly to avoid cliffs. The transects were centrally located in a roughly 400 ha study area. I placed AS at 2 m intervals along each transect. On seven transects I placed a cluster of four AS at every fourth or fifth position (= every 8 or 10 m); all other positions were occupied by single AS. Cluster seedlings were positioned in a square so the arms of each artificial seedling overlapped *ca* 3 cm with its two neighbors. This arrangement was designed to simulate the clusters of seedlings, usually $\gg 4$ seedlings, that emerge from cassowary droppings (Stocker & Irvine 1983; Mack, pers. obs.) a total of 418 single and 428 clustered (in 107 clusters) AS were positioned on the transects.

When positioning the AS, I classified each location by ground slope: class 1 = level ($<10°$ slope), class 2 = gentle slope (11–25°), class 3 = steep (26–40°), class 4 = very steep ($>40°$), class 5 = dry wash. Dry washes were sites without standing or running water but which might have moving water during heavy rains.

TRANSECT CENSUSES.—The transects were censused ten times between March 1991-April 1992. Census intervals were 26–49, days except the last interval which was 92 days. On censuses I walked each transect and recorded whether AS were standing, bent, or damaged. "Standing" AS had no visible change, "bent" seedlings had one arm touching the ground, "damaged" AS had both arms flattened on the ground. "Damaged" single AS were removed. "Damaged" clustered AS were recorded, then repaired or replaced in order to maintain the cluster effect. For data analyses, all cluster AS repaired or replaced were considered damaged at that census, allowing up to four instances of damage per cluster. This enabled me to test if clustering had any effect on "survivorship" without the complication of quartets becoming triplets, triplets becoming doublets, *etc.*, as individuals within clusters were damaged.

I attempted to categorize the cause of damage to those AS classified as damaged as follows: "Debris" if fallen debris was on top of the AS and obviously damaging it; "animal" if the AS was uprooted (which required a strong pull), if the seedling was obviously gnawed upon, or if the area around the seedling was obviously dug up by a ground-foraging animal; "wash" if rain wash had swept the AS over; and "unknown" if the cause could not be confidently attributed to any of the above causes.

DATA ANALYSES.—Damage to AS was considered equivalent to mortality so the data could be treated as right-censored survivorship using the non-parametic Peto and Peto Logrank Test (Pyke & Thompson 1986). Other statistics were calculated with the software SYSTAT (Wilkinson 1990).

RESULTS

SINGLE ARTIFICIAL SEEDLINGS.—After one year, 34.7 percent of the single AS on transects had been damaged and removed. There was not a significant difference in damage among the eight transects (Peto and Peto logrank = 8.787, $0.3 > P > 0.2$ and Kruskal-Wallis ANOVA , $H = 8.147$, df = 7, $P = 0.320$), therefore I pooled all transects for further analyses (Fig. 1a).

To test for heterogeneity on a smaller scale, I performed a Runs test for each transect. Two transects had significant departures from a random distribution of damaged AS ($Z = -3.72$, -3.24 respectively, $P < 0.005$). On these two transects areas of damage were clumped, not due to a few large, single events (*e.g.*, large treefalls), but rather the clumped pattern was due to the accumulation of many independent events that occurred throughout the year.

GROUND SLOPE EFFECTS.—The slope of the ground on which single AS were positioned had a significant effect on the incidence of damage: damage increased with ground slope (Peto and Peto logrank = 10.845, df = 3, $0.02 > P > 0.01$). After one year, the proportions of standing AS from level (class 1) to very steep (class 4) sites were: 0.766, 0.632, 0.624, and 0.548 respectively (Fig. 1b). Those AS in dry washes ($n = 12$) were damaged early in the study: 50 percent were damaged in the first census interval (29 days) and only 25 percent

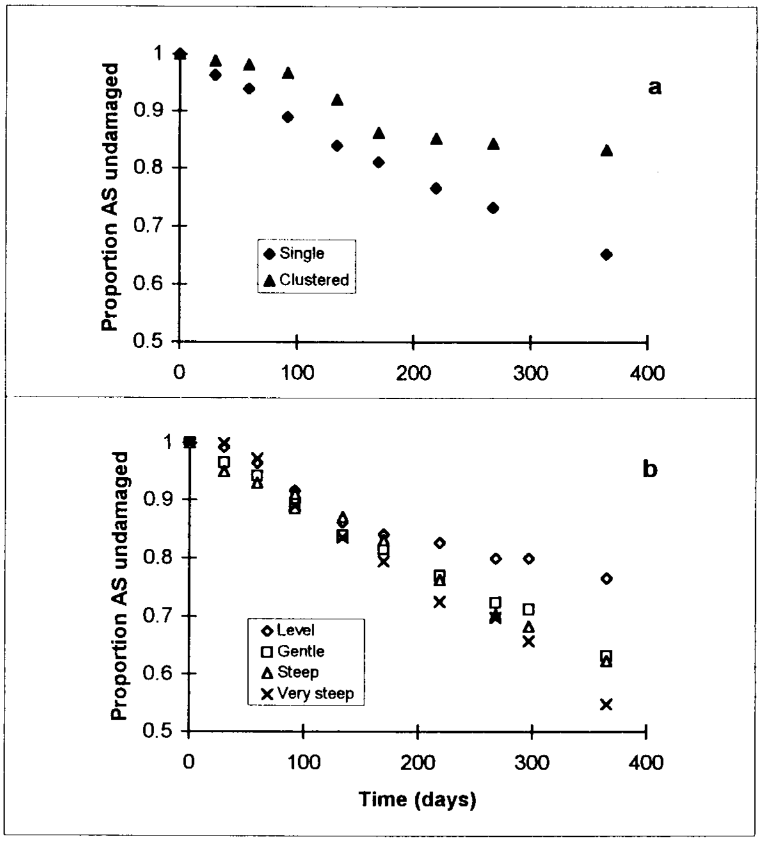

FIGURE 1. **a**: Proportion of all single artificial seedlings ($N = 418$) undamaged after one year compared to artificial seedlings in clusters of four ($N = 428$). **b**: Proportions of single artificial seedlings (AS) undamaged over one year in four different ground slope microsites. See methods for description of ground slope categories. Sample sizes = 145 level, 87 gentle slope, 101 steep, 73 very steep.

remained after one year. The survivorship in all five microsites differed significantly (Peto and Peto logrank = 19.02, df = 4, $P < 0.001$). Lastly, the clumping of damaged AS in transects 4 and 8 that caused the departure from random in the runs test occurred on very steep slopes.

CLUSTER EFFECTS.—Treating all AS in clusters as independent ($N = 428$), there was a significant difference in the incidence of damage to single versus clustered: single AS had a greater probability of experiencing physical damage (Fig. 1a; Peto and Peto logrank = 36.45, df = 1, $P < 0.001$) than single AS in clusters. Using a more conservative approach, treating each cluster as a unit ($N = 107$) and damage to one or more AS in the unit equating a "fatality," there was not a significant difference between clusters and single AS (Peto and Peto logrank = 2.05, df = 1, $P > .1$)

CAUSES OF MORTALITY.—The single AS in this study experienced less damage than AS in a similar assay at La Selva, Costa Rica: 34.7 percent versus 82.4 percent damaged (Table 1). Damage attributed to

TABLE 1. *Causes of damage to single artificial seedlings at two tropical rain forest sites: Crater Mountain, Papua New Guinea (this study) and Finca La Selva, Costa Rica (Clark & Clark 1989).*

	Percent	
Cause	Papua New Guinea	Costa Rica
Unknown	11.0	42.2
Litterfall	13.8	19.2
Animal-digging	7.0	21.0
Water wash	2.9	—
Undamaged	65.3	17.6

animal-digging was roughly a third and damage from unknown causes was roughly one fourth as common as in the Costa Rica study (Table 1). Adding the water wash category (not assessed at La Selva) into the unknown category, causal differences between the two studies were statistically significant (Chi-square test, $\chi^2 = 228$, df = 3, $P < 0.001$). The regression for single AS in this study [ln# undamaged = 6.03 −0.001 (elapsed time); $r^2 = 0.997$] reflects the lower overall damage rate than at La Selva [ln# undamaged = 6.294 −0.005 (elapsed time); $r^2 = 0.99$]; (Clark & Clark 1989).

DISCUSSION

Physical disturbance, as measured by this artificial seedling assay, probably plays an important role in the seedling ecology in Papuan rain forests. Thirty-five percent of the single AS suffered damage in one year that reasonably could be fatal or detrimental, to a real seedling.

Effects of ground terrain.—In this study, the terrain of the AS microsite significantly affected the incidence of damage to AS. Artificial seedlings in dry washes (2.9% of sites) experienced damage rapidly (50% in the first month). Rainfall at the Crater Mountain research station exceeds that of many rain forests and is aseasonal (during this study $\bar{x}$ = 56.8 cm/month, SD = 19.5; D. D. Wright, pers. comm.). During heavy rain, dry washes fill with fast-moving run-off, uprooting new seedlings or burying them under water-borne debris (A. Mack, pers. obs.).

Very steep slopes made up a substantial proportion of the transects; 17.9 percent of the single artificial seedling sites were on class 4 slopes. These sites had significantly higher damage rates than all other (non-dry wash) sites and all sloped sites (62.8% of sites) experienced greater damage rates than the level sites. This was largely due to litter and detritus washing or sliding downhill, flattening and burying AS in the process (A. Mack, pers. obs.). The potential effect of downslope litterwash on seedling survivorship is an important consideration for future studies of seedling demography, particularly in mountainous rain forests as found in much of New Guinea.

Observations of actual seedlings at Crater Mountain corroborate that ground slope affects seedling establishment. Seedlings are often killed when uprooted or bent by debris sliding downhill (A. Mack, pers. obs.). In mountainous areas with high rainfall, such as Crater Mountain, such disturbances might contribute to determining which species establish on steep slopes. Ruxton (1967) described disturbance due to slopewash in PNG and noted that leaf litter depth was greater on level vs. non-level ground. Species with rapid root growth and resilient stems might establish on steep slopes more readily than species with slow root growth and brittle stems.

Cluster effect.—Individual AS in clusters of four had significantly better chances of withstanding damage during the year of this study than did single AS. At the end of the study 65.3 percent (*N* = 418) of the single AS were standing, whereas 82.7 percent (*N* = 428) of the AS in clusters were still standing. However, the sites of clusters (*N* = 107) did not experience less damage than single AS sites. This suggests that clusters were equally as likely to experience disturbance (they did not happen to be in better sites), but that individual AS in clusters did not experience the same probability of damage as the same AS placed by itself.

The clusters were repaired after damage to avoid the complications of quartets becoming triplets. This does not occur in real clusters and could somewhat elevate any potential benefit of clustering. However, in the situation this was designed to mimic, seedlings from cassowary droppings usually contain many more than four seedlings (Stocker & Irvine 1983; A. Mack, pers. obs.). Thus, even though the number in the cluster was artificially held at four, it is still a conservative comparison of real clusters at this site.

Observations of disturbances suggested several possible reasons why AS in clusters were less vulnerable to damage, though quantitative data were not collected. Fallen or sliding debris sometimes bent an AS against others in a cluster without flattening it because the other AS provided support. The sliding debris could be deflected or delayed by some members of a cluster– thus the damage to one AS in the cluster could reduce or delay damage to other members of the cluster. Furthermore, ground-foraging animals (*e.g.*, Megapodidae: Aves, Peroryctidae: Marsupialia) sometimes appeared to have avoided clusters more so than single AS. However, if this were often the case, there would have been a significant difference in the incidence of damage to cluster sites (*N* = 107).

Because only one seedling can attain maturity at any given site, dispersal of seeds in clumps might be considered a liability. Density-related mortality (*e.g.*, pathogens, herbivores, etc.) and competition might be elevated for seeds and seedlings in clumps

(Howe 1989). These data suggest that under some circumstances (*e.g.*, on rain-washed slopes) there might be some advantages to being in clusters, at least in the early stages of seedling establishment. Field testing with larger samples of AS and with real seedlings is needed to confirm any possible benefit to being in clusters.

COMPARISON WITH THE LA SELVA STUDY.—More than three times as many AS at Crater Mountain were undamaged after a year than at La Selva (Table 1). The percentage of damage due to animal activity was three times higher at La Selva. Differences in the terrestrial vertebrate faunas of Costa Rica and Papua New Guinea are probably partially responsible for this difference. The large (>1 kg) terrestrial mammal fauna of Crater Mountain is fairly depauperate: no more than seven species (D. D. Wright, pers. comm.; Flannery 1995) compared with that of La Selva: 15 (Timm 1994) and large mammals are less common at Crater Mountain than at La Selva (A. Mack, pers. obs.). Crater Mountain has several large terrestrial birds suspected of damaging some of the AS (*e.g.*, *Casuarius bennetti, Megapodius freycinet*); however, La Selva also has several species of terrestrial birds capable of damaging AS (Levey & Stiles 1994).

The difference in damage attributed to litterfall was not great between La Selva and Crater Mountain (19.2 vs. 13.9% respectively). However, the incidence of damage attributed to unknown causes was much higher at La Selva and much of this damage was suspected to have been caused by litterfall (Clark & Clark 1989). Many characteristics such as floristic differences, wood strength, crown size, tree stature, windiness, or epiphyte loads could differ between sites and affect litterfall. At Crater Mountain most litterfall damage was due to smaller fallen debris, not entire treefalls. Low vegetation is dense in many parts of the Crater Mountain study area; the understory and low vegetation could break the fall of canopy debris.

Methodological differences could be partially responsible for observed differences between the two sites. Clark and Clark (1989) considered an artificial seedling damaged when it had one or both arms touching the ground. In this study, I considered an artificial seedling damaged only when both arms were touching the ground. Observations of real seedlings at Crater Mountain indicate most seedlings can withstand substantial bending (A. Mack, pers. obs.). The condition of having both AS arms on the ground as the criterion for judging an AS damaged seemed more realistic in terms of what would kill real seedlings. However, I did record when the AS on transects were bent with only one arm touching the ground. Addition of these bent AS to the tally of damaged seedlings reduces the percentage of undamaged AS from 65.8 percent to 58.0 percent, still considerably greater than the value, 17.6 percent, from La Selva.

CONCLUSIONS.—Small scale physical disturbance potentially plays an important role as a determinant of seedling survivorship in rain forests. In this study over one third of the single AS suffered physical damage that probably would kill an actual seedling. A cohort of seedlings would be reduced by an order of magnitude after five years if its annual survivorship was the same as that of the AS in this study. Seedlings of many species in the Crater Mountain study area persist as "dormant" seedlings (<1 m tall) for at least five years with little or no growth (Mack 1995b). For such species the effect of physical disturbance at the rates detected could have important implications to population demography.

The three primary findings of this study are: (1) The chance of a seedling experiencing serious physical damage varies by the microsite of the seedling; the chances of damage increase with increasing ground slope and are greatest in places where runoff occurs during heavy rains; (2) The disturbance regime at Crater Mountain differs substantially from that detected in a similar study at La Selva, Costa Rica; and (3) AS in clusters are possibly less vulnerable to physical damage than lone AS.

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