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The Effect of Litter and Soil Disturbance on Seed Germination in Upper Montane Rain Forest, Jamaica

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ABSTRACT. – The role of litter and soil disturbance in determining the pattern of germination of dormant seeds was investigated at four understory sites in upper montane rain forest in the Blue Mountains, Jamaica. At each site, soil samples were collected to determine seed bank density and composition by germination under greenhouse conditions. Additionally, at each site, 1 m^2 plots were established with treatments of litter removal, litter addition, soil disturbance, and a combined treatment of litter removal and soil disturbance. The seed bank density was high (1170 seeds/m^2), and was dominated by the exotic species *Pittosporum undulatum*, which constituted 56% of all seedlings that emerged. The combined treatment of litter removal and soil disturbance significantly increased seed germination in the field over undisturbed controls, but only when data were pooled for all species. When disturbance events differ in the range of micro sites they produce (e.g., defoliation caused by moderate hurricane damage, versus uprooting of trees caused by severe hurricane damage), there are implications for the relative contribution of buried seeds to forest regeneration following these disturbances.

INTRODUCTION

The role of leaf litter as a determinant of patterns of seed germination and seedling establishment has been well documented. Effects of litter include an alteration of light and temperature cues to germination (Sauer and Struik, 1964; Vázquez-Yanes et al., 1990; Vázquez-Yanes and Orozco-Segovia, 1992), providing a physical barrier to seedling establishment (Sydes and Grime, 1981; Vázquez-Yanes and Orozco-Segovia, 1993), and possibly affecting rates of seed predation (Shaw, 1968; Sydes and Grime, 1981). At the community level, heterogeneity of litter abundance, and differential abilities of species to germinate and establish in litter potentially maintains seedling diversity (Molofsky and Augspurger, 1992).

The role of soil disturbance, as distinct from the presence or absence of litter, has received less attention, although in general it has been found to promote seedling establishment. Bell (1970) found that soil disturbance was a critical factor required for germination of *Phytolacca icosandra* in Puerto Rico, and Hopkins and Graham (1984) report that some factors associated with disturbing the topsoil in deep shade stimulate germination of a substantial proportion of the seed population in lowland tropical rain forest in Australia. In seasonally moist lowland forest in Panama, seedlings and saplings of pioneer species were found to be concentrated within gaps on the soil disturbed by uprooted trees (Putz, 1983). In Borneo, scarification of soil within artificial gaps resulted in the germination of 2.5 times as many seedlings on average, as in undisturbed (litter covered) controls (Kennedy and Swaine, 1992).

Williams-Linera (1990) further speculated that soil disturbance may be critical for the regeneration of some pioneer tree species. She noted that while the seeds of pioneer trees were abundant in the soil seed bank along forest edges in lower montane rain forest in Panama, and light availability was sufficient for the germination of these seeds in petri dishes placed out along the same edges, saplings and adults of these species were rare at these sites. Artificial scarification of the soil using hand tools clearly increased seedling density and changed floristic composition, so that after

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8 mo. disturbed soil plots had 8 times more seedlings than undisturbed control sites.

Canopy defoliation following hurricanes may have effects akin to those of edge creation reported by Williams-Linera (1990). Damage to the upper montane rain forest of Jamaica by Hurricane Gilbert, and to the low-elevation "tabanuco" forest of Puerto Rico by Hurricane Hugo was largely restricted to canopy defoliation; relatively few trees were uprooted (Bellingham, 1991; Walker, 1991; Bellingham et al., 1992). As a consequence, gap creation occurred with relatively little soil disturbance, but with a large, short-term increase in litter deposition (419-451 times the mean daily input of fine litter for the Bisley watershed forest following Hurricane Hugo; Lodge et al., 1991).

In upper montane rain forests, where rates of litter decomposition are slow, and the standing crop of litter is large (Grubb, 1971; Tanner, 1981), the effects of litter in impeding seedling establishment might be significant. In particular, increased litter fall associated with hurricanes might be expected to strongly diminish the wave of seedling establishment normally associated with gap creation. In a study of seedling responses to litter following Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico, Guzmán-Grajoles and Walker (1991) found that seedling densities were highest in an experimental litter removal treatment; however, species differed in their response to litter removal, with the strongest positive response from early successional species Some support for this view also comes from the observation made in montane forest in Jamaica following Hurricane Gilbert, where the highest densities of the gap-demanding species *Alchornea latifolia* and *Turpinia occidentalis* were observed at sites where litter had been removed and the soil had been disturbed by feral pigs (P. Bellingham, T. Goodland, pers. comm.).

In this study, the effects of both litter and soil disturbance on seedling establishment were investigated in relation to the pool of dormant seeds in the soil at four understory sites in upper montane rain forest in Jamaica. The study was conducted in May 1990, 20 months after Hurricane Gilbert. Specifically the following questions were addressed. i) What was the size and diversity of the soil seed bank? ii) What role do litter and soil disturbance play in limiting seedling establishment? iii) What proportion of the soil seed bank germinates in response to litter removal and soil disturbance? Although this study was carried out more than a year after Hurricane Gilbert, results need to be interpreted with caution since light levels, the standing crop of litter, and turnover of the soil seed bank may still have been affected by the hurricane.

Materials and Methods

The study was conducted in the western Blue Mountains (18°05'N; 76°39'W) between 1460 m and 1770 m in altitude. Annual rainfall averages 2500-3000 mm, with a dry season from June-August; mean monthly maximum and minimum temperatures are c. 20°C and c. 11°C (Kapos and Tanner, 1985). Within this area, four understory sites were chosen, all within the "Wet Slope" forest type (Grubb and Tanner, 1976). All the sites were within old secondary forest, although the history of past disturbance is largely unknown. Canopy dominants at these sites were *Clethra occidentalis, Podocarpus urbanii, Cyrilla racemiflora, Alchornea latifolia,* and the introduced invasive species, *Pittosporum undulatum.* Nomenclature follows Adams (1972).

Four sites were established in May-June 1990; each consisted of one block of six 1 m^2 plots, separated by 0.5 m buffer strips. Individual plots were clearly marked, and care was taken not to disturb them. To determine the composition of the soil seed bank, a 10 cm diameter soil corer was used to take four, 10 cm deep, 785 cm^3 soil samples from the buffer strips between four of the plots at each site. The four soil cores from each site were thoroughly mixed, and the soil was set out in an approximately 1 cm thick layer on top of a 2 cm layer of vermiculite in three, 1000 cm^2 seedling trays. The trays were located randomly in a shade house (walls of double layer shade cloth; roof of single layer shade cloth, and approximately 20% full sun) at the nearby

Cinchona Botanic Gardens at an altitude of 1490 m. An additional four, 785 cm^3 samples of forest soil were autoclave at 110 °C for one hour and used as controls to measure seed rain contamination within the shade house. For the first two months, emerging seedlings were recorded and removed weekly, then monthly for five additional months, until no new seedlings emerged. Seedlings of only two taxa, (*Rhynchospora* spp. and *Viola patrinii)* emerged in the autoclave, control soil samples. These taxa were subsequently excluded from analysis of the seed composition of the soil samples.

After removing soil samples, each of the 1 m^2 plots at each site was assigned to a different treatment to investigate the role of litter and soil disturbance on seedling establishment. The six treatments were:

i) Control with no disturbance (CND). Plots were delineated, but otherwise left untouched.
ii) Control, litter replaced (CLR). All litter was removed from the plot and then replaced evenly over the plot.
iii) Litter removal (– L). All litter was removed from the plot, but the soil was undisturbed.
iv) Litter addition (+ L). Existing litter was removed and replaced, and litter added from the (– L) treatment.
v) Disturbance, litter replaced (DLR). All litter was removed, the soil was "scarified" (loosened to a depth of 2 cm with a fork), and the litter was replaced evenly over the plot.
vi) Disturbance and litter removal (D –L). All litter was permanently removed, and the soil was scarified as above.

Control (CLR) and undisturbed plots (CND) were set up separately, since removal and redistribution of litter could, on its own, affect seedling establishment if the litter layer itself contains large numbers of seeds, and if the distribution of these seeds in the litter is altered by handling. If seedling establishment in CLR and CND plots are not different, however, this indicates that treatment effects are not an artifact of these manipulations.

Fresh litter collected from the CLR, –L, +L, DLR, and D – L plots was separated into leaf litter and woody debris and weighed in the field with a spring balance before being replaced or moved. Samples of litter from the D – L plots were oven dried at 70°C for 72 hr, to calculate a conversion factor for dry weight. Seedlings present in the plots prior to the assignment of treatments were either labelled, or in the case of very small seedlings, removed. Seedlings emerging in the plots were censused and removed weekly for 6 wk, and thence monthly for an additional 3 mo. Since only small seedlings were removed from the plots, it was not anticipated that seedling removal itself could affect the plot treatments. Fresh litter that accumulated in the – L, and D – L plots was removed and discarded at the time of each subsequent census.

Initial seedling numbers within plots, and the total number of emergent seedlings, post experiment, from the litter and soil disturbance experiment were log-transformed. An initial effect of litter quantity on pre-experiment seedling densities was investigated by linear regression. Effects of plot treatments on subsequent seedling emergence were analyzed using a one factor ANOVA. Where treatment effects were found to be significant, post-hoc comparisons were made using Fisher's LSD test. Means are reported with ± 1 S. D.; significance was determined at the 5% level.

Results

A total of 147 seedlings from 18 taxa germinated over the census period (Table 1), representing a terminable seed density of 1170 seeds / m^2 in the top ten centimeters of soil. The seed bank was dominated by the invasive exotic species *Pittosporum undulatum*, which accounted for 56% of seedlings.

The estimated dry mass, standing crop of leaf litter (0.32 kg/m^2 ± 0.08, n = 4), and of woody debris (0.48 kg/ m^2 ± 0.14, n = 4) differed significantly among sites (df = 1,3; F = 5.94; p = 0.006; F = 4.40, p = 0.019 respectively), but regressions between initial (pre-experiment) seedling numbers within the treatment plots, and

TABLE 1. Seed diameter, and number of seedlings that emerged from four 785 cm^3 soil samples taken from four understory sites. Samples were taken with a soil corer to a depth of 10 cm.

Species	Seed size[1]	Site I	Site II	Site III	Site IV	Total
Trees and shrubs						
Pittosporum undulatum	2.5	2	23	43	14	82
Alchornea latifolia	4.4	1	1	2	2	6
Hedyosmum arborescens	—	5	0	0	1	6
Psychotria spp.	—	1	3	0	0	4
Turpinia occidentalis	7.3	1	0	1	1	3
Eugenia virgultosa	—	3	0	0	0	3
Brunellia comocladiifolia	1.2	0	0	2	1	3
Podocarpus urbanii	4.5	2	0	0	0	2
Trema floridanum	2.0	1	0	0	1	2
Myrsinaceae	—	1	0	1	0	2
Melastomataceae	—	0	0	1	0	1
Herbs						
Bocconia frutescent	2.2	4	2	4	10	20
Rubus spp.	—	1	5	0	0	6
Eupatorium spp.	—	0	1	0	1	2
Relbunium hypocarpium	—	0	0	1	1	2
Bidens shrevei	—	0	0	1	0	1
Salmea scandens	—	0	0	0	1	1
Dendropanax spp.	—	0	0	0	1	1
Total		22	35	56	34	147

[1] Mean diameter (mm) measured from herbarium specimens (n = 5 seeds minimum). — No data available.

leaf litter mass (df = 1,19, F = 4.34, p = 0.052) or total litter mass (df = 1,19, F = 3.16, p = 0.093) were not significant. The apparent negative trend between total leaf litter mass and seedling number was largely due to very high numbers of *Pittosporum* seedlings in relatively litter free plots at one site.

Mean seedling emergence for all species combined ranged from 3.3 (± 1.0) seedlings/m^2 to 26.8 (± 16.3) seedlings/m^2 across treatments (Fig. 1). The maximum value, found in the DLR treatment represents only 2% of the of the resident soil seed bank, assuming all seedlings originated from dormant seeds. There was a significant treatment effect on total seedling emergence (d.f. = 5, 23; F = 3.34; p = 0.03). Post-hoc comparisons revealed a significant difference between the – L and the + L treatments, and between CLR and D– L treatments (Fig. 1). Differences between the CLR and CND treatments, and between CLR and –L treatments were not significant, indicating that manipulations of litter, and the litter removal treatment alone, had no effect in this experiment. Treatment effects were not significant for individual species, though sample sizes were only large enough to make comparisons for *Pittosporum undulatum* and *Alchornea latifolia* (n = 211, df 5,23, F = 0.74, p = 0.605; n = 31, df 5,23, F = 2.23, p = 0.096 respectively, Table 2).

DISCUSSION

Densities of dormant seeds in this Jamaican montane forest, (1170 seeds/ m^2; 517 seeds/m^2 excluding *Pittosporum undulatum)* are high in comparison with other montane sites, where seed bank densities have been measured using similar methods (243 seeds/ m^2 for woody species in lower montane forest in Thailand (Cheke et al., 1979); 406 seeds/m^2 in cloud forest in Costa Rica (Lawton and Putz, 1988); and 403 seeds/ m^2 in lower montane forest in Puerto Rico, (Guariguata, 1990). Furthermore, the actual viable seed density reported in these studies was probably underestimated, since soil depths greater than 5 mm strongly inhibit seedling emergence from soil flats (Dalling et al., 1995).

The significantly higher number of emergent seedlings in the litter removal and soil disturbance treatment, than in the control treatment, indicates that the combined effect of litter and soil disturbance could determine patterns of seedling establishment. Indeed, litter removal and soil disturbance do occur in some natural disturbances (e.g. on tip-up mounds produced by tree falls), and seedlings of some species establish preferentially in these sites (Putz, 1983). The effect of litter removal and soil disturbance probably occurs primarily through the removal of physical barriers to seed germination and seedling establishment (e.g., Sydes and Grime, 1981; Carson and Pickett, 1990; Vázquez-Yanes et al., 1990), possibly by removing chemical germination inhibitors (Rice, 1979), and by bringing viable seeds to the soil surface, where, in the absence of litter, they are exposed to germination cues. Conditions favoring seedling emergence and early establishment however, may not be indicative of suitable conditions for long term seedling survival and growth. Guzmán-Grajoles and Walker (1991) noted that

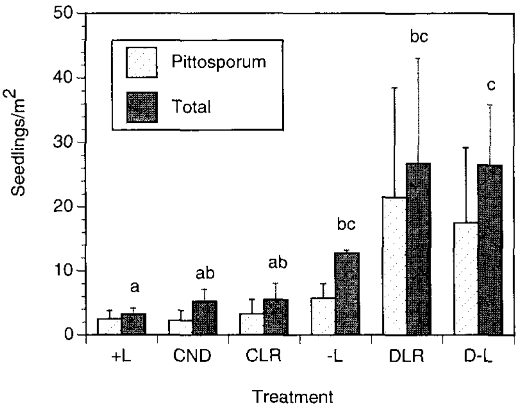

FIG. 1. Seed germination by treatment for i) *Pittosporum undulatum* and ii) all species combined, where + L = litter addition; CND = control undisturbed; CLR = control, litter replaced; –L = litter removed; DLR = soil disturbed, litter replaced; D – L = soil disturbed and litter removed. Values are means (n=4 plots per treatment + 1 S.E.). Treatment bars sharing the same letter were not significantly different ($p<0.05$).

moderate amounts of litter did not adversely affect the emergence of *Cecropia schrebiana* seedlings, and may be beneficial in the longer term because of higher seedling growth rates, and lower mortality rates than in litter free sites.

In comparison with lowland tropical forests, species in montane forests in Jamaica have small seeds, including species present

TABLE 2. Numbers of seedlings that emerged from 1 m^2 treatment plots, summed across the four sites, where + L = litter addition; CND = control undisturbed; CLR = control, litter replaced; – L = litter removed; DLR = soil disturbed, litter replaced; D-L = soil disturbed and litter removed.

Species	Treatment							% of emergents[1]	% of seed bank[2]
	+L	CND	CLR	–L	DLR	D-L	Total		
Pittosporum undulatum	10	9	13	23	86	69	210	66	56
Alchornea latifolia	0	0	0	3	13	15	31	10	4
Psychotria corymbosa	0	5	1	4	1	9	20	6	3
Eugenia virgultosa	1	1	2	8	1	1	14	4	2
Bocconia frutescent	1	2	1	1	2	2	9	3	14
Turpinia occidentalis	0	1	0	4	2	0	7	2	2
Malvaviscus arboreus	0	0	1	4	0	1	6	2	—
Myrsinaceae	0	1	0	1	2	0	4	1	1
Others (10 species)	1	2	4	3	0	9	19		—
Total	13	21	22	51	107	106	320		

[1] Percentage of total seedlings emerging in plots accounted for by each species.

[2] Percentage of the total seedlings emerging in the soil seed bank accounted for by each species (data from Table 1).

in the soil seed bank (Tanner, 1982; Table 1). Since small seed size results in small initial seedling size, litter effects on seedling establishment might be expected to be especially great in this forest. Deep litter layers inhibit emerging radicles from reaching the soil surface, and cotyledons from reaching the light (Molofsky and Augspurger, 1992). At least one canopy dominant species, *Clethra occidentalis,* although absent from the seed bank, is unable to establish in litter in this forest (Newton and Healey, 1989), yet can grow well from 5 cm tall seedlings transplanted into litter-rich understory sites (Dalling and Tanner, 1995). Clearly a more detailed investigation of litter and soil disturbance effects is warranted, with much larger sample sizes that permit the analysis of responses of individual species.

More studies are also needed that investigate how specific disturbance events affect seedling emergence from seed populations in the soil. It is unclear how Hurricane Gilbert, might have affected recruitment to, and release from, the soil seed bank. Certainly inputs into the soil seed bank during the 18 mo post hurricane are likely to have been much below average. With the exception of *Pittosporum undulatum,* seed production within the tree community was greatly depressed as trees continued to refoliate (P. Bellingham, pers. comm.). Recent studies have shown that soil seed bank turnover rates can be much faster than previously supposed, with declines in seed densities of individual species of > 80% within one year (Alvarez-Buylla and Martínez-Ramos, 1990; Chandrashekara and Ramakrishnan, 1993; Dalling et al., unpublished data); consequently years of very poor seed production might strongly affect the ability of gap-demanding species to colonize disturbances. Initial germination of seedlings from the seed bank following Hurricane Gilbert may have been either higher or lower than in average years, depending on the relative importance of light and temperature cues to break dormancy following canopy opening, versus inhibition of germination or lowered establishment success following increased litter deposition.

The dominant species of the soil seed bank, *Pittosporum undulatum,* was also the commonest emergent in the litter removal/soil disturbance experiment (Table 2). The density of seeds of all species germinating in the combined litter removal and soil disturbance treatment (27 seeds/m^2) represented only 2% of those in the soil seed bank (1170 seeds / m^2). Perhaps the light level in the understory of this forest was insufficient to trigger germination (yet emergence was recorded of some apparently gap-demanding species, *Alchornea latifolia,* and *Turpinia occidentalis, sensu* Sugden et al., 1985; Healey, 1990), or perhaps many seeds present in the seed bank were buried too deeply to be able to reach the soil surface after germination, In other studies where seedling emergence in gaps was compared with the pre-gap seed bank, density values are similarly low. Kennedy and Swaine (1992) found that in artificial gaps in lowland rain forest in Borneo, only 5% of the soil seed bank germinated in plots in which the soil was scarified. Similarly, Williams-Linera (1990) found that only 10% of the seed bank germinated in scarified plots along a recently created forest edge, in lower montane forest in Panama.

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