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SHORT COMMUNICATION

Soil seed bank from lowland rain forest in Singapore: canopy-gap and litter-gap demanders

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The vast array of species found in the humid lowland tropical forests of the world are frequently divided into two general groups, light-demanders and shade-tolerators (Denslow 1980, Swaine & Whitmore 1988). In this dichotomy the characteristics of the gap-demanders are often given to include small seed size, dormancy mechanisms, potentially rapid growth, and requirement of direct sunlight for germination and establishment. Conversely, shade-tolerators are considered to have large, short-lived seeds, the potential to germinate in canopy shade and an ability to grow slowly in deep shade (Swaine & Whitmore 1988). Failing to conform to either general pattern, small-seeded shade-tolerant species have been documented from both the Central American and South-east Asian tropics (Ellison *et al.* 1993, Metcalfe & Grubb 1995). Some of these small-seeded species have been shown to be able to germinate in filtered light approximating to canopy shade (Metcalfe 1996), and seedlings of other small-seeded species have been recorded growing under a closed canopy (Grubb 1996, Kiew 1988, Raich & Gong 1990). Several taxa shown by Metcalfe (1996) and Metcalfe & Grubb (1997) to be small-seeded and shade-tolerant were found in considerable numbers in the soil seed bank in Sabah by Kennedy (1991), and one (*Urophyllum glabrum*) by Putz & Appanah (1987) in Peninsular Malaysia. Species with small seeds (less than about 1–10 mg) do not have the resources to emerge from underneath a covering of leaf litter, and require litter-free sites for successful establishment (Guzmán-Grajales & Walker 1991, Molofsky & Augspurger 1992, Putz 1983).

The study described here sought to determine the presence or absence of shade-tolerant small-seeded species in the seed bank of primary rain forest in Singapore, and establish their abundance relative to canopy gap demanders. It also sought to make a minimum estimate of the longevity of the seed in the soil, and to find the extent to which scarification of the soil and/or removal of litter would bring about germination under an intact canopy. The small-seeded shade-tolerant species may be regularly seeded into the forest, dependent on arriving at a litter-free site, and/or may form a soil seed bank and await formation of a litter-gap.

The species composition of the soil seed bank and the persistence of seeds within it under an intact canopy were investigated in primary rain forest in Bukit Timah National Park, Singapore (see Corlett 1990 for a description of the site). Five sites were randomly chosen along a belt transect 200 m × 20 m; at each site a 2 m × 2 m area was cleared of litter and a centrally located 20 cm × 20 cm soil sample was taken to 5 cm depth. Around this sample three 50 cm × 50 cm mats were laid on the soil and covered with litter. The mats were made of four layers of fine-meshed shade cloth, capable of preventing passage through to the soil of very small seeds (e.g. *Ficus grossularioides*, 0.8 mm diameter). Centrally located 20 cm × 20 cm × 5 cm soil samples were taken from under these mats 1, 2 and 6 mo after they were put down. Soil samples were spread in basins to a depth of 1 cm on moist sterile soil in a 50% neutral shade house at the National University of Singapore. No contamination was recorded in basins of sterile soil placed amongst the forest samples. Germination was recorded on a weekly basis for 8 wk. Identities of common species were accepted from observation only, voucher specimens of more unusual species have been lodged at SINU. Nomenclature follows Turner (1993).

The effects of litter removal and soil scarification on the soil seed bank were investigated at the same five sites as above. At each site a grid of 25 plots (50 cm × 50 cm) was marked out in five rows of five, rows 1.5 m apart, plots within rows 0.5 m apart. Plots which included large trees, rocks, etc. were moved 0.5 m above the row. All vegetation < 10 cm high was cut at ground level and removed to facilitate observations while not disturbing the soil. No further removal of vegetation took place. One plot in each row was treated in each of the following ways: (i) scarification of the soil plus removal of litter, (ii) scarification of the soil but retention of the litter layer, (iii) litter removal without soil disturbance, (iv) doubling of the litter layer, (v) control. Treatments were haphazardly allocated within rows. Sites were visited every 10 d for maintenance of the litter treatments, and for monitoring germination. Seedlings were identified to the point at which the approximate dry mass of their seed could be established, such that they could be assigned to one of three seed-size classes: < 1 mg, 1–100 mg and > 100 mg. Notes were made on 2–3 times weekly visits of species fruiting in the vicinity of the five sites, and of seeds lying on the soil or litter having recently arrived in the seed rain.

Seeds started to germinate 8–10 d after removal from the forest and continued to germinate over the following 7 wk, peaking after *c*. 2 wk. The mean density of seeds in the soil seed bank remained constant at *c.* 1000 m^{-2} over the 6 mo during which it was sampled, suggesting that it might take several to many years for the seeds of the species concerned to decay completely. It also implies that seed inputs into the soil are low. Enright (1985) found evidence from the depth distribution in the soil, notably for *Pipturus argenteus*, that seeds could persist for long periods in the seed bank in lowland New Guinea. Hopkins & Graham (1987) showed that many secondary forest species retained viability for 2 y of burial in a study in north-eastern Australian rain forest; the same study showed limited viability for primary forest species over shorter periods, but no small-seeded species were considered. Clearly new work is needed to pursue the issues of seed longevity and seed input into the soil seed bank for the small-seeded shade-tolerators.

The soil seed bank contained at least 40 taxa (Appendix 1), 34 being identified to family. Five were confirmed shade-tolerators: *Ficus chartacea*, *Pellacalyx saccardianus*, *Pternandra echinata*, *Urophyllum hirsutum* and *Urophyllum* sp. 2 of Wong (1989). The composition of the seed bank was notable for the large numbers of seedlings belonging to the families Melastomataceae, Moraceae, Rhizophoraceae and Rubiaceae. Mean values indicate a seed bank of approximately 1000 seeds m^{-2}. This value is higher than any of the figures given for Asian studies by Garwood (1989), but is well within the range of densities found for logged forests in Australasia (e.g. Hopkins & Graham 1984). High densities of canopy-gap demanding species may build up under closed canopy primary forest under two different circumstances, either where that forest is close to extensive secondary forest (Graham & Hopkins 1990, Putz & Appanah 1987), or where the primary forest suffers frequent disturbance, for example on steep slopes liable to landslides or where strong winds are common (e.g. Hopkins & Graham 1984). The latter point is exemplified by the contrast between the primary forest on steep slopes in Brunei which contains abundant *Macaranga* in the soil (Mitchell 1994) and the primary forest in the Danam Valley of Sabah where the slopes are gentle and very strong winds are rare, and *Macaranga* is almost absent from the seed bank (Kennedy 1991, Kennedy & Swaine 1992). The primary forest at Bukit Timah might be expected to have in its soil a considerable number of seeds coming from secondary forest species which are abundant in its surroundings. This is indeed true, as judged by *Ficus grossulariodes* and *Melastoma malabathricum*, but there is an almost total absence of *Macaranga* and *Trema*.

In the forest plots 511 seedlings germinated over the study period of 120 d, including at least 41 different species (Appendix 2). Almost all of the species germinating from the largest seeds (>100 mg) arrived in the seed rain. Altogether 171 seedlings in the very small-seeded category were recorded; the only treatment having a significant promotory effect on their germination was the combination of soil disturbance and litter removal ($P < 0.05$, ANOVA, Fisher's LSD).

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More seedlings were recorded from that treatment for seeds <1 mg than from all the others together (mean 4.0 seedlings per plot). Doubling the litter thickness reduced the number of seedlings recorded (0.1 per plot) compared to removing litter from the soil surface (1.9 per plot). Scarifying the soil and replacing the litter had no significant effect on germination (0.4 vs 0.6 per plot for control).

The variability in the distribution between plots of the 177 large seeds (> 100 mg) and 163 seeds of intermediate size made all comparisons between treatments not significant ($P > 0.05$, ANOVA; mean seedlings per plot 1.4 (> 100 mg) and 1.3 (1–100 mg)), but for both these seed class categories there are trends: removing litter tended to enhance germination, while disturbing the soil and replacing the litter had little effect. The large-seeded species also appeared to be favoured by increasing the depth of the leaf litter, while smaller seeds were inhibited or smothered by deeper litter.

Both experiments revealed that the soil seed bank contains a number of very small-seeded species which are favoured by closed canopy conditions, such as species of *Pternandra* and *Urophyllum*. These species germinated when soil was removed from the forest, and were almost certainly amongst the Melastomataceae and Rubiaceae which germinated in response to scarification of the soil and removal of the litter under a closed canopy. Others too have found that this sort of treatment can promote germination of many seeds (Dalling 1992, Hopkins & Graham 1984, Kennedy & Swaine 1992). In experiments with seeds in petri dishes, Raich & Gong (1990) showed that *Pternandra coerulescens* and *Urophyllum glabrum* exhibited high percentage germination under a forest canopy (27–67%) and more than in a large clearing. A wider range of species in *Pternandra* and *Urophyllum*, also in *Ficus* and inland Rhizophoraceae, was shown by Metcalfe (1996) to be daylight-demanding immediately after dispersal but able to germinate after 3–6 mo in light with a high far-red component and a peak in the green. Some of the species tested also became able to germinate in darkness. It seems likely that removing the leaf litter exposed seeds to promotory wavelengths (cf. Vázquez-Yanes *et al.* 1990), and that scarification of the soil brought buried seeds to the surface. In the treatment where scarified soil was covered by leaf litter the litter could either have maintained dark-controlled dormancy, or suppressed any tiny seedlings which did germinate.

In conclusion, the primary forest at BTNR was found to have a considerable soil seed bank, the majority being of secondary forest species, but a significant number being of plants which are not favoured by canopy gaps but by gaps in the litter under a closed canopy. Many seeds of a number of species were capable of germinating in response to disruption of the overlying litter layer and disturbance of the soil without simultaneous opening of the canopy. Evidence has been obtained that the litter gap demanders last for at least 6 mo in the soil, and suggests that they may last much longer.

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LITERATURE CITED

CORLETT, R. T. 1990. Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *Journal of Tropical Ecology* 6:55–63.

DALLING, J. W. 1992. *Regeneration on landslides in the Blue Mountains, Jamaica*. PhD dissertation, Department of Plant Sciences, University of Cambridge, UK.

DENSLOW, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12 (supplement): 47–55.

ELLISON, A. M., DENSLOW, J. S., LOISELLE, B. A. & BRENÉS M. D. 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology* 74: 1733–1749.

ENRIGHT, N. 1985. Existence of a soil seed bank under rainforest in New-Guinea. *Australian Journal of Ecology* 10:67–71.

GARWOOD, N. C. 1989. Tropical soil seed banks: a review. Pp. 149–209 in Leck, M. A. & Parker, V. T. (eds). *Ecology of soil seed banks*. Academic Press, San Diego.

GRAHAM, A. W. & HOPKINS, M. S. 1990. Soil seed banks of adjacent unlogged rainforest types in north Queensland. *Australian Journal of Botany* 38:261–268.

GUZMÁN-GRAJALES, S. M. & WALKER, L.R. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo experimental forest, Puerto Rico. *Biotropica* 23:407–413.

GRUBB, P. J. 1996. Rainforest dynamics: the need for new paradigms. Pp. 215–233 in Edwards, D. S., Booth, W. E. & Choy, S. C (eds). *Tropical rainforest research: current issues*. Kluwer, Dordrecht.

HOPKINS, M. S. & GRAHAM, A. W. 1984. The role of soil seed banks in regeneration in canopy gaps in Australian tropical lowland rainforest – preliminary field experiments. *Malaysian Forester* 47:146–158.

HOPKINS, M. S. & GRAHAM, A. W. 1987. The viability of seeds of rainforest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* 12:97–108.

KENNEDY, D. N. 1991 *The role of colonising species in the regeneration of dipterocarp rain forest*. PhD thesis, Department of Plant and Soil Science, University of Aberdeen, UK.

KENNEDY, D. N. & SWAINE, M. D. 1992. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society of London*, series B 335:357–366.

KIEW, R. 1988. Herbaceous flowering plants. Pp. 56–76 in Cranbrook, Earl of (ed.). *Malaysia*. Pergamon Press, Oxford.

METCALFE, D. J. 1994. *Seed size, litter and regeneration in tropical rain forest trees.* PhD dissertation, Department of Plant Sciences, University of Cambridge, UK.

METCALFE, D. J. 1996. Germination of small-seeded tropical rain forest plants exposed to different spectral compositions. *Canadian Journal of Botany* 74: 516–520.

METCALFE, D. J. & GRUBB, P. J. 1995. Seed mass and light requirement for regeneration in South-East Asian rain forest. *Canadian Journal of Botany* 73:817–826.

METCALFE, D. J. & GRUBB, P. J. 1997. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. *Functional Ecology* 11:215–221.

MITCHELL, T. C. 1994. *The ecology of* Macaranga *(Euphorbiaceae) trees in primary lowland Mixed Dipterocarp forest, Brunei*. PhD dissertation, Department of Zoology, University of Cambridge, UK.

MOLOFSKY, J. & AUGSPURGER, C. K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77.

PUTZ, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64:1069–1074.

PUTZ, F. E. & APPANAH, S. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19:326–333.

RAICH, J. W. & GONG, W. K. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* 6:203–217.

SWAINE, M. D. & WHITMORE, T. C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.

TURNER, I. M. 1993. The names used for Singapore plants since 1900. *Garden's Bulletin, Singapore* 45:1–287.
VÁZQUEZ-YANES, C., OROZCO-SEGOVIA, A., RINCÓN, E., SÁNCHEZ-CORONADO, M. E., HUANTE, P., TOLEDO, J. R. & BARRADAS, V. L. 1990. Light beneath the litter in a tropical rain forest: effect on seed germination. *Ecology* 71:1952–1958.
WONG, K. M. 1989. Rubiaceae. Pp. 324–425 in Ng, F. S. P. (ed.). *Tree flora of Malaya* Volume 4. Malayan Forest Records 23. Yau Seng Press, Kuala Lumpur, Malaysia.

APPENDIX 1

Species germinated from the soil seed bank

Species with asterisks are shade-tolerant species. Voucher numbers represent species lodged at SINU. Araceae (*Homalomena* sp., unidentified sp. [D392]), Compsitae (*Mikania micrantha*), Cyperaceae (*Cyperus* sp.), Dioscoreaceae (*Dioscorea bulbifera*), Euphorbiaceae (*Macaranga heynei*), Gramineae (*Digitaria longiflora*), Melastomataceae (*Clidemia hirta*, *Melastoma malabathricum*, *Pogonathera pulverulenta*, **Pternandra echinata*), Moraceae (*Ficus aurantiacea*, **F. chartacea*, *F. fistulosa*, *F. grossularioides*, *F. laevis*, *Ficus* sp. [D354], *Ficus* sp. [D381]), Olacaceae (*Strombosia javanica*), Palmae (unidentified sp. [D393]), Rhizophoraceae (**Pellacalyx saccardianus*), Rubiaceae (*Borreria* sp., *Nauclea officinalis*, *Pertusadina eurhyncha*, *Psychotria helferiana*, *Psychotria* sp. [D360], *Psychotria* sp. [D361], **Urophyllum hirsutum*, **Urophyllum* sp. 2 of Wong (1989), unidentified sp. [D380]), Taccaceae (*Tacca integrifolia*), Theaceae (*Adinandra dumosa*), Ulmaceae (*Trema tomentosa*).

APPENDIX 2

Species germinating in understorey plots

Identities of species recorded germinating in all soil scarification/litter treatment plots in descending order of frequency. Species asterisked were observed in the seed rain during the course of the experiment (for *Ficus* only one sp. detected in seed rain). Voucher numbers represent species lodged at SINU.

>100 mg: *Aporusa* sp. [D353] (Euphorbiaceae) 140*, *Horsfieldia polyspherula* var *sumatrana* (Myristicaceae) 13*, *Uvaria leptopoda* (Annonaceae) 8*, *Willughbeia coriacea* (Apocynaceae) 2*, *Garcinia* sp. [D344] (Guttiferae) 1*, *Litsea* sp. [D339] (Lauraceae) 1*, *Ochanostachys amentacea* (Olacaceae) 1*, *Oncosperma horridum* (Palmae) 1*, (unidentified) 10*. **1–100 mg:** *Dischidia ?albiflora* [D355] (Asclepiadaceae) 109*, *Aspidopteris concava* (Malpighiaceae) 5*, *Dioscorea bulbifera* (Dioscoreaceae) 5*, *Fissistigma* sp. [D341] (Annonaceae) 4*, *Zingiber griffithii* (Zingiberaceae) 2, *Curculigo latifolia* (Hypoxidaceae) 1, *Koompassia malaccensis* (Leguminosae) 1*, *Rinorea anguifera* (Violaceae) 1*, (unidentified) 35. **<1 mg:** Melastomataceae (probably including *Clidemia hirta, Dissochaeta* spp., *Melastoma malabathricum, Pogonathera pulverulenta* and *Pternandra* spp.†) and Rubiaceae (*Nauclea officinalis, Psychotria* spp., *Uncaria* spp., *Urophyllum* spp. †) 111, *Ficus* spp. (Moraceae; possibly *Ficus aurantiacea*, *F. aurata*, *F. botryocarpa*, *F. chartacea*, *F. fistulosa*, *F. grossularioides*, *F. laevis* and three unidentified *Ficus* spp.†) 34*, (unidentified) 18.

† from Metcalfe (1994).