Dormancy and Dispersal of Seeds of Secondary Forest Species under the Canopy of a Primary Tropical Rain Forest in Northern Thailand

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ABSTRACT

Surface soil in five different habitats contained a stock of viable seeds awaiting suitable conditions for germination. Samples from under a mixed evergreen rain forest canopy included seeds of seral species not represented at the collection site. Seeds of species of *Aralia*, *Macaranga*, *Mallotus*, *Melastoma*, and *Trema*, all seral trees, germinated in soil samples from up to 175 m from the nearest source tree, and from as much as 20 cm below the soil surface. The amount of seed in the soil was much greater than the annual rate of seed rain measured, and indicated that a store of seral tree seed can be built up over several years under primary forest.

THE QUESTION of how the pioneer species of the secondary succession colonize newly cleared areas of primary forest has long been debated but little studied. In temperate zones it is clear that there is an accumulation of dormant seeds in the soil over long periods of time (see refs. in Guevara and Gomez-Pompa 1972), but the question has remained relatively open in the tropics, although Symington's work (1933) suggested that the process was the same in the Malayan rain forest. More recently, in Nigeria (Keay 1960) and tropical Mexico (Guevara and Gomez-Pompa 1972), it has been shown that seeds of seral species are already present in soil under the primary canopy. Further studies in Mexico (Guevara and Gomez-Pompa 1976) have shown a strong seasonality in the appearance of seral tree seedlings in soil samples, but have not clarified whether this is due to seasonal in-seeding or seasonal germination. Castro and Guevara (1976) have shown that many seeds can survive for two and a half years (some for 3 years) in stored soil; however, they dried the soil rather than attempting to simulate the natural conditions of the forest floor. Kellman (1970), working in the Philippines, inferred from his observations that both dormancy and rapid immigration were important in the colonization of clearances. Whitmore (1975: 71) pointed out that critical experiments had yet to be done in the Far East, but added that from his own observations he favored the hypothesis that rapid seeding-in was the more important process.

The study described here was an attempt to elucidate some of the dynamics of secondary species in tropical forest, and was carried out at the University of Chiang Mai, Thailand, in 1970-1972. The work was done in two parts, each being a final-year student project under the guidance of the senior author. The first part was a preliminary survey of the viable seed content of soils in different habitats (Yankoses 1971), while the second investigated one site in greater detail (Nanakorn 1972).

THE STUDY AREA

Chiang Mai, 18°47′N 98°59′E, is in an area of strongly seasonal, hot monsoon climate in northern Thailand. The wet season normally lasts from May to October, but is variable from year to year; the months November to April are usually very dry. The town itself is on an alluvial plain, with gneiss and mica-schist mountains of Palaeozoic age rising to the west. Further details of the area are available in Küchler and Sawyer (1968).

The preliminary survey was done in five vegetation types ranging from mid-level forest on Doi Suthep mountain (7 km west of Chiang Mai town) to relict woodland on the university campus, which adjoins its lower slopes. The highest and least humanly disturbed site on the mountain was chosen for the more detailed investigation.

The vegetation of Doi Suthep has been described in detail, and mapped, by Küchler and Sawyer (1968), and their classification will be referred to throughout (abbreviated to 'K&S' followed by a number). In brief, the mountain stands at the western edge of the floodplain of the Maenam Ping river (300 m above sea level), and rises rather abruptly to twin peaks of 1610 and 1685 m. The plain, now largely cultivated, supports remnant pockets of Teak *Tectona grandis* L.f. forest (K&S types A1, B3 & B4), which gives way to an open, dry dipterocarp forest, locally known as pah daeng (K&S B5), on the lower eastern slopes. The dry forest is dominated

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by *Diperocarpus tuberculatus* Roxb. and *D. obtusifolius* Teysm., and is subject to annual ground fires in the dry season. There is much bare ground and little soil development. Above this, at a variable altitude depending on aspect and incidence of fires, there is a sharp change to wetter closed forest characterized by *Castanopsis acuminatissima* (Bl.) A.DC, *Anthocephalus cadamba* Miq., *Lithocarpus garrettianus* (Craib.) A. Camus, *Schima wallichii* Choisy, and, in places, mostly below 1000 m, *Dipterocarpus costatus* Gaertn.f. (K&S C7 & C11 (part)); this is a tropical lower montane rain forest, *sensu* Whitmore (1975:199ff.). On other parts of the mountain the altitudinal succession is different, but this does not concern us here.

Sawyer and Chermsirivathana (1969) have listed the species found on Doi Suthep during Küchler and Sawyer's study. This publication is the only convenient published list of plants found on the mountain, but is rather incomplete. In relation to our study we would note the absence of any mention of *Macaranga* in either this list or K&S, whereas we found two species, *M. denticulatus* (Bl.) Muell. Arg. and *M. kurzii* (Kuntze) Pax & Hoffman. They also name only one *Mallotus* (*M. barbatus* Muell. Arg.) whereas *M. paniculatus* (Lam.) Muell. Arg. (perhaps their unidentified species) is much commoner, and report *Trema orientalis* Bl. to be "infrequent in phytocenose 11," when we found it to be common in clearings in the *Castanopsis acuminatissima* forest at all levels (K&S C7 & C11).

THE STUDY

In the first part of the study, a square metre of topsoil 5 cm deep was taken in July 1970 from five sites and put in a shade house (approx. 50% full sunlight) at the university biology department. A box of autoclaved sterilized soil from each sample was included as a control for contamination by immigrating seeds. Each box was covered by 2 mm mesh aluminum mosquito netting to reduce the impact of heavy rain. The boxes were regularly watered, and kept clear by hand picking of snails and caterpillars.

Seedlings that emerged were monitored as they grew, and when large enough (woody spp.) were transferred to individual bamboo tubs for further growth. Herbarium specimens were made of representative examples of each species if and when they flowered or showed sufficient characters for identification. When this part of the study had to be terminated after eight months in February 1971, many of the woody species in the evergreen forest samples were still too small to identify.

A quarter of the soil from each sample was analyzed for seed content by passing it in aqueous suspension through sieves of, respectively, 7, 2, and 1 mm mesh, and extracting seeds at each stage. Seeds were sorted into apparently homogeneous taxa, and sown in sterilized soil for identification by germination. Unfortunately, possibly due to the effects of wetting and drying in the extraction process, none germinated, so no identifications were obtained at this stage.

THE SITES.—1) Tall, closed *Castanopsis acuminatissima* forest (K&S:C11) at 1350 m altitude by the principal dam of Kog Ma watershed research project operated by Kasetsart University, Bangkok. The sample site was under the canopy 25 m from a clearing where mature seral species of five trees, *Aralia* cf. *armata* (Wall.) Seem., *Macaranga denticulata*, *Mallotus paniculatus*, *Melastoma malabathricum* L., *Trema orientalis*, and a herb, *Polygonum chinense* L., were growing. Seedlings of *Castanopsis* sp., *Lithocarpus* sp., unidentified woody species, and *Curculigo* were growing at the spot where the sample soil was removed, and those of *Aralia* cf. *armata*, *Macaranga denticulata*, and *Polygonum chinense* were nearby, though slightly nearer the clearing. 2) Forest similar to site 1, but at 1000 m altitude on a ridge, with a lower canopy (K&S:C7), near the Royal Thai Forest Department local headquarters. The sample soil was taken from under canopy about 100 m from a large colony of mixed seral trees of the same *Macaranga*, *Mallotus*, and *Trema* species; some isolated individuals were nearer. Seedlings of *Lithocarpus* sp. and unidentified woody plants and Compositae were growing where the soil sample was taken. 3) Dry dipterocarp forest at 550 m altitude, with an open canopy (K&S:B5), by the reservoir on the Doi Suthep road; soil very poor and stony. Most of the understory was destroyed by human activity before it was assessed. 4) A dense copse of relict teak forest (K&S:A1/B3) on the university campus, set in parkland dominated by lawns, isolated trees, buildings, gardens, and waste ground; altitude 350 m. Most of the understory was destroyed before we were able to assess it. 5) An open area of waste ground on the campus, altitude 350 m. The vegetation consisted of *Eupatorum odoratum* L., *Mimosa pudica* L., *Jussiaea suffruticosa* L., *Sida* spp., *Tridax procumbens* L., *Urena lobata* L., *Cyperus* sp., and various grasses.

Around the shade house itself the following species were particularly common, and were a source of contamination in the trials: *Erechtites valerianifolia* DC, *Oldenlandia corymbosa* L., *Peperomia pellucida* H, B & K., and *Phyllanthus niruri* L. *Ageratum conizoides* L. was common on the campus and also turned up in the sample trays.

Seedlings that emerged from the soil samples and seeds recovered from the soil are enumerated in table 1. It has not been possible to give full details of these data here, but a fuller table will be supplied by the senior author on request.

The important outcome of the first part of the study was to reveal that soil under forest cover contains a large store of viable seeds, many from species not found growing on the site. The second part of the study investigated this matter further at site 1, near the Kog Ma watershed research dam.

The principal feature of site 1, situated in a fairly uniform stand of *Castanopsis acuminatissima* forest (K&S C11), was a small clearing (turning area and car park) about 50 m across, around the edge of which grew a number of mature seral species not found growing within the surrounding primary forest.

The distribution of selected species was mapped (fig. 1), and a 175 m transect chosen through adjacent forest, along which positions were marked at different distances from the edge of the clearing. The transect was chosen through the most uniform part of the surrounding forest, and consisted largely of *C. acuminatissima* canopy.

Three questions were asked. 1) What is the relationship of viable seed density in the soil to distance from the nearest source? 2) To what depth in the soil are viable seeds found (depth can be taken as an indicator of time elapsed since the seed arrived)? 3) How does the observed seed store relate to the rate at which new seeds disperse into the area?

At each position on the transect, a square metre of ground was marked out, and topsoil removed to a depth of 5 cm. At the 25 m position an additional surface soil sample was taken, together with four more samples down to 25 cm under the surface. The soil was treated as in the first experiment, with some sterilized soil as a control. The samples were collected in early July 1971, and the emerging seedlings were monitored until March 1972.

Over each square metre of removed soil, a galvanized steel tray of the same size was placed to catch falling seeds. The trays had a 5 cm high rim all round, were covered with half-inch (12.7 mm) galvanized steel welded mesh to keep out rodents and birds, and supported on water-traps at the corners to keep out ants and other ground insects. Small holes in the trays allowed rain to drain without loss of seeds. The trays were monitored monthly over a period of seven months; it was unfortunately not possible to continue sampling for a full year. At each visit, seeds were collected for examination, the trays cleaned and the water-traps topped-up. In order to be

TABLE 1. *Seeds and seedlings in soils from different habitats near Chiang Mai.*

Site No.	Numbers of species germinating in soil samples: Tree & shrubs	Climbers & lianes	Weedy herbs & subshrubs	Grasses & sedges	other monocotyledons	Total species	Total individuals	Seeds found in soil: No. of species	No. of individuals
1	*Macaranga denticulata* (8)[a] *Mallotus paniculatus* (1) *Melastoma malabathricum* (22) *Trema orientalis* (12) unidentified: 16 spp.	2	4(3)[b]	1	3	30(27)	187(182)	25	99
2	*Macaranga denticulata* (2) *Mallotus paniculatus* (1) *Trema orientalis* (7) unidentified: 14 spp.	1	5(2)	1	0	24(22)	128(121)	18	243[c]
3	unidentified: 1 sp.	0	16(3)	2	0	19(16)	107(103)	16	40
4	unidentified: 2 spp.	0	8(3)	2	0	13(10)	49(43)	11	33
5	none	0	12(3)	0	0	14(11)	44(40)	11	68[d]
Control	none	0	2[e]	0	0	–	–	–	–

[a]The number of individuals is in parentheses.
[b]The number of species thought to be contaminants are in parentheses; these are then deducted from the numbers given in the totals columns, where the figures in parentheses are the net numbers of species and individuals originally in the soil, and can be compared directly with the figures for seeds found in the final columns. The correspondence is extremely close, showing the reliability of the germination method as a means of assaying soil seed stocks.
[c]161 seeds contributed by one species.
[d]46 seeds contributed by one species.
[e]These were *Ageratum conizoides* and *Jussiaea suffruticosa*.

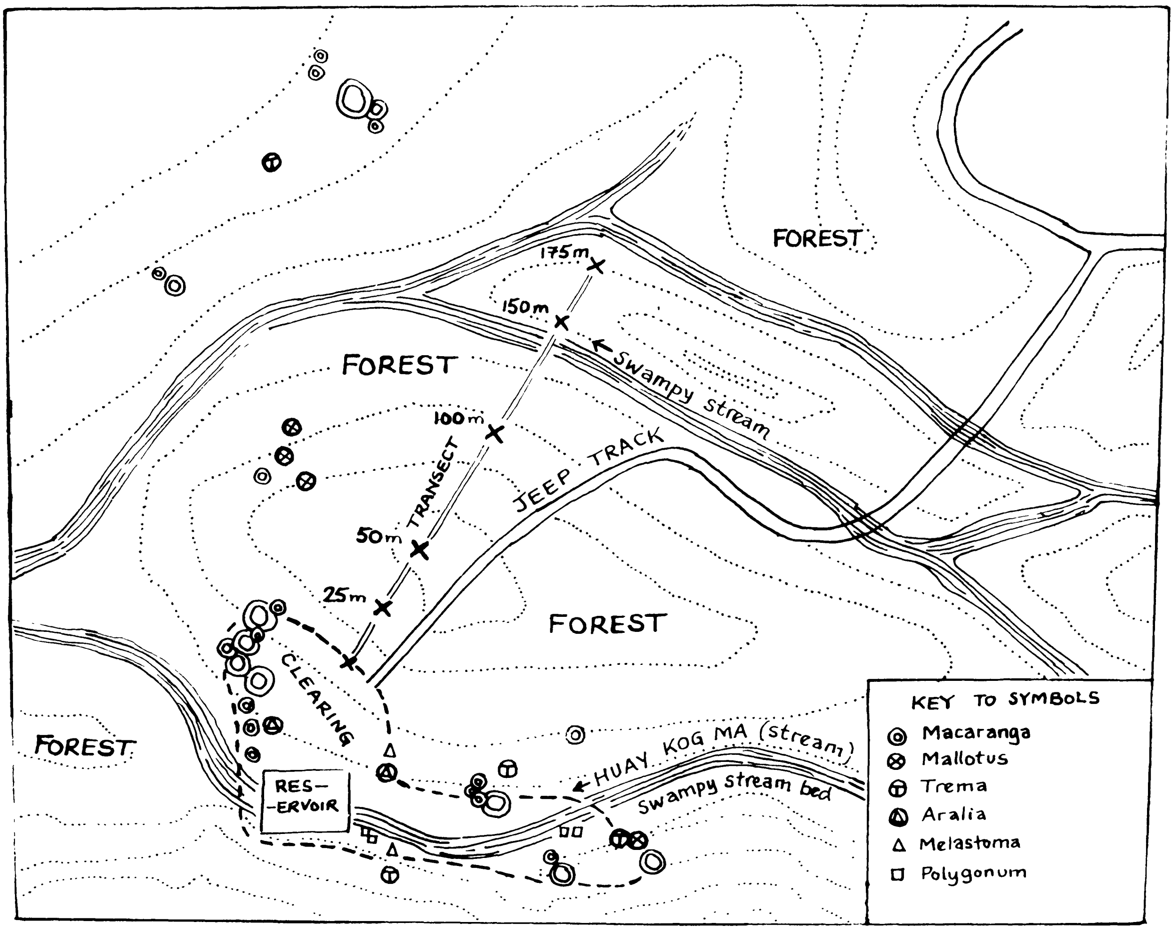

FIGURE 1. The study area at the Kog Ma watershed research dam. The dashed line marks the approximate boundary of the clearing, and the fine dotted lines are contour lines at 4 m vertical interval (redrawn from Nanakorn (1972), whose map was derived from the 3-dimensional model of the watershed at the Kasetsart University field station, Doi Pui).

sure of identifying seeds of the study species that might appear in the trays, reference samples were taken from fruiting specimens.

On Doi Suthep, the study period spanned the main fruiting seasons of all the seral species under consideration except the *Macaranga* and, possibly, the *Melastoma*. The normal flowering seasons, followed by fruiting a few weeks later, are as follows: *Aralia* cf. *armata*, August to October, *Macaranga denticulata*, January to February, *Mallotus paniculatus* September to November, *Melastoma malabathricum*, April-May, *Trema orientalis* and *Polygonum chinense*, throughout the year, though the latter has a peak from September to November. Fruiting specimens of both the *Macaranga* and the *Melastoma* were in fact present in the clearing at the beginning of this part of the study (July). All these species appear to be principally bird-dispersed, probably largely by bulbuls (Pycnonotidae, of which there are many species on Doi Suthep) and laughing-thrushes *Garrulax* spp.

The results of the second part of the study are shown in tables 2 to 4.

DISCUSSION

Certain clear inferences can be drawn from the data: 1) Viable seeds of secondary forest trees are present in considerable quantity in soil up to 175 m or more from the nearest source (table 2). The more distant sites (150 and 175 m) were shadier than the nearer ones, and might have inhibited the germination of freshly arrived seeds more effectively. This effect could account for the increasing number of *Trema* seedlings with increasing distance, the failure to record *Aralia* at the closer sites, and the absence of tree seedlings in one of the 25 m samples. As noted earlier, seedlings of several seral species, as well as those of the local dominants, were present under the canopy up to nearly 25 m from the clearing, though none were recorded at greater distances; at this distance there was more illumination from the side (i.e., from the clearing) than through the canopy. 2) Viable seeds of seral trees are found buried up to 20 cm deep in the soil (table 3). At the study site the transition to subsoil began at about 20 cm. 3) The observed input rate of fresh seral tree seeds is very low compared with the stock of viable seeds in the soil, suggesting that the latter has built up over a period of years (tables 2 and 4). This observation is not substantially diminished by the fact that the seed-collection data were taken over only seven months, as this period covered the main fruiting season of most of the indicator species (see above). 4) The seed fall of the dominant tree *Castanopsis acuminatissima* is extremely high, but no seedlings of this species grew in the shade house. These seeds presumably have a very short period of viability, though in the forest predation by wild pigs (*Sus scrofa*) and birds is no doubt also important. However, some seedlings were present under the canopy in the forest, as already noted. 5) A special watch was kept throughout the study for the two very widespread wind-dispersed invasive species, *Eupatorium odoratum* (Compositae) and *Imperata cylindrica* (L.) Beauv. (*Gramineae*), neither of which was present in the clearing, nor indeed within about half a kilometer of the study site. A few *E. odoratum* seedlings were recorded (part 1, unlisted; table 2), but the presence of others of similar size in the shade house argues for local contamination rather than efficient long-distance dispersal and dormancy. No seeds of this species were found in the trays, but the principal flowering season in Chiang

TABLE 2. *Germination of seeds present in soil samples taken at different distances from the nearest source of indicator species.*

Distance from source	Indicator species: Trees *Aralia* cf. *armata*	*Macaranga denticulata*	*Mallotus paniculatus*	*Melastoma malabathricum*	*Trema orientalis*	Herb *Polygonum chinense*	Other species[a]
25 m (1)[b]	–	–	–	–	–	–	*Ageratum conizoides** (2)
(2)	–	1	2	4	4	–	*Begonia* sp. (1)
(3)	–	8	1	22	12	–	*Eupatorium odoratum** (1) *Peperomia pellucida** (3) *Thunbergia* sp. (1)
50 m	–	–	–	5	3	1	*Curculigo* sp. (2) unidentified (Meliaceae) (2) unidentified (Convolvulaceae) (2) unidentified, other. 3 spp. (3)
100 m	–	1	–	–	12	1	*Erechtites valerianifolia** (1) *Lagerstroemia* sp. (1) unidentified. 2 spp. (2)
150 m	2	3	–	–	34	3	*Arisaema* sp. (3) *Erechthites valerianifolia** (1) unidentified (Cucurbitaceae) (1) unidentified, other. 3 spp. (3)
175 m	1	3	–	2	23	–	*Arisaema* sp. (2) *Erechtites valerianifolia** (1) *Eupatorium odoratum** (2) *Globba* sp. (2)
Control (sterilized soil)							Ferns. 2 spp. (many) unidentified tiny plant (1)

[a]Name, followed by number of individuals in parentheses; possible contaminants are starred (*).

[b]The three sets of figures given for the 25 m site are as follows: 1) this experiment, 2) the soil depth experiment (see table 3), and 3) the first part of this study (see table 1). They are given for comparison, and to balance the anomalous null result of this experiment.

TABLE 3. *Germination of seeds present in soil taken at different depths below the surface* (sample site 25 m from the nearest source of indicator species).

	Indicator species						
	Trees					Herb	
Depth below surface (cm)	*Aralia* cf. *armata*	*Macaranga denticulata*	*Mallotus paniculatus*	*Melastoma malabathricum*	*Trema orientalis*	*Polygonum chinense*	Other species[a]
0-5	–	1	2	4	4	–	*Ardisia* sp. (2) *Cassia nodosa* Buch.-Ham. (1) *Phyllanthus* sp.* (2) unidentified (Commelinaceae) (2) unidentified (Graminae) (1)
5-10	–	1	–	2	5	–	unidentified (Commelinaceae) (1) unidentified (Orchidaceae) (1) unidentified, other (1)
10-15	–	2	–	1	3	–	*Curculigo* sp. (1) *Globba* sp. (1) unidentified, 1 sp. (1)
15-20	–	1	–	1	3	–	*Curculigo* sp. (1) unidentified (Graminae) (1) unidentified, other (1)
20-25	–	–	–	–	–	–	unidentified (Graminae) (1) unidentified, other (tiny plants; 2 spp.) (2)
Control (sterilized soil)							unidentified tiny plants, 2 spp. (2)

[a]Name, followed by number of individual in parentheses; possible contaminants are starred (*).

TABLE 4. *Numbers and species of seeds collected on seed trays at different distances from the nearest source of indicator species.* (Key to indicator species recorded: A=*Aralia* cf. *armata*, M=*Mallotus paniculatus*, P=*Polygonum chinense*, T=*Trema orientalis.*)

Distance from source	Taxon	Date								
		30.VII.71	24.VIII.71	12.IX.71	28.IX.71	31.X.71	21.XI.71	19.XII.71	16.I.72	3.II.72
25 m	*Castanopsis*	50	c.170	c.140	c.25	c.550	c.450	c.70	7	–
	indicator spp.	–	1P	–	–	1M	–	–	–	–
	grasses	1	–	2	2	–	4	3	3	1
	other spp.	1	2	–	–	1	–	–	–	4
50 m	*Castanopsis*	c.75	c.140	c.175	c.130	c.580	c.475	c.75	21	3
	indicator spp.	–	1A	–	–	1P;2T	2P	1T	–	–
	grasses	5	2	2	6	6	3	4	1	3
	other spp.	–	–	–	–	–	–	–	–	–
	Loranthus fowers	16	12	5	–	–	–	–	–	–
100 m	*Castanopsis*	9	c.15	c.12	c.15	c.130	c.125	11	–	–
	indicator spp.	–	–	–	–	1T	–	–	–	–
	grasses	–	1	1	4	6	1	3	1	2
	other spp.	2	1	3	1	–	–	1	3	3
150 m	*Castanopsis*	9	4	3	3	c.45	c.25	c.15	–	–
	indicator spp.	–	–	–	–	1P	–	–	–	–
	grasses	1	1	1	–	–	3	3	9	5
	other spp.	1	3	3	2	12	9	7	8	2
175 m	*Castanopsis*	10	c.35	c.35	c.25	60	60	c.35	3	–
	indicator spp.	–	–	–	–	–	–	–	–	–
	grasses	12	13	3	8	2	3	5	1	6
	other spp.	2	1	1	2	2	–	–	1	1

TABLE 5. *Delayed germination of seeds from forest soil.*

Taxon	Total No. of seedlings that had appeared: November 1971 (after 4 months)	March 1972 (after 8 months)	% of seed germinating in the second period
Trees			
Aralia cf. *armata*	2	3	33
Macaranga denticulata	8	12	33
Mallotus paniculatus	2	–	–
Melastoma malabathricum	12	15	20
Trema orientalis	76	87	13
Herb			
Polygonum chinense	3	5	40

Mai is in December and January, most seeds being produced after the end of the study. No *Imperata*, an easily recognized grass, was recorded during the study.

The germination of the seral species in the shade house took place over a considerable period of time. Table 5 shows that the proportion of seeds with delayed germination varied widely between species. From this, and the data in the previous tables, some inferences can be drawn about the different dispersal and germination strategies of the species under discussion.

Aralia cf. *armata*, *Macaranga denticulata*, and the herb *Polygonum chinense* were all present as seedlings in the forest at around 25 m from the clearing, so it is interesting to note that no seedlings of either *Aralia* or *Polygonum* were recorded as germinating in soil from that distance at any depth. It may be inferred that these species, and to some extent the *Macaranga* also, can and do germinate at lower light intensities than *Melastoma malabathricum* or *Trema orientalis*, both present as seeds, but not seedlings, at 25 meters. *Mallotus paniculatus* seedlings only emerged from surface soil at the distance nearest to the source of seeds, suggesting a poor dormancy potential but a high light requirement, or, less probably in a seral species, a much poorer dispersal ability. In Mexico, Lopez-Quiles and Vasquez-Yanes (1976) have shown that seeds of the seral tree *Cecropia obtusifolia* Bertol. are ten times more likely to germinate in the open than under forest shade, while another seral species, *Ochroma lagopus* Swartz, which germinated more readily in the shade, only showed a doubling when tested in the open. Soil temperature may also be a significant factor in initiating germination (Lopez-Quiles and Vasquez-Yanes 1976); bared soil is hotter and suffers greater extremes of temperature than soil under forest canopy. This situation could be important for well-buried seeds.

A few comments are necessary on the control procedure, which may not have been fully satisfactory. Our impression was that the sterilized soil presented an unfavorable medium for the establishment of seedlings, and the development of numerous fern prothalli implies poor drainage and water balance. Guevara and Gomez-Pompa (1972, 1976) used plain vermiculite as control, an equally inhospitable substrate! A better solution might be to sterilize, then reintroduce soil microorganisms and worms, etc. from an outside source (avoiding seed contamination) to restore the soil's structure; it would obviously be better still to conduct the trials in a situation that precluded external contamination altogether.

CONCLUSIONS

This study has shown not only that the seeds of secondary forest species are well-distributed through the soil of a tropical evergreen forest, but also that they are present in much greater numbers than can be accounted for by the instantaneous seed rain. There is still much to be discovered about the dynamics of the system, particularly about the time scale of the build-up of seeds in the soil, and their potential for dormancy under natural conditions. The abundance of dispersal agents which inhabit both primary and secondary vegetation, and their mobility, will clearly affect the rate and extent of dispersal. Studies of the appearance and turnover of seedlings at different distances from the forest edge and under differing light and temperature regimes would clarify the way in which different pioneers try to establish themselves.

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