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Germinable soil seed bank dynamics during the gap phase of a humid tropical forest in the Western Ghats of Kerala, India

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ABSTRACT. The present study showed that the density of germinable seeds in the soil of a humid tropical forest ecosystem at Nelliampathy, in the Western Ghats of Kerala in India, fluctuates sharply at different times of the year. There were more germinable seeds in the soil during the monsoon season. Regeneration was activated after canopy gap formation and thus a decline in the soil seed density in 1-year-old gaps was recorded. However, soil seed density increased with gap age. Differences were found between primary, late secondary and early secondary categories of species with respect to their soil seed bank. There were more seeds of primary species in the soil of natural gaps than in selection felled ones, while the seeds of early secondary shrubs and herbs were more in the soil of selection felled gaps than in natural gaps. The soil seed banks of the primary forest species, being transient, are not an important conservation tool for these species.

KEY WORDS: forest canopy gaps, humid tropical forest, soil seed bank, Western Ghats of India.

INTRODUCTION

Recruitment of viable seeds and their germination, and seedling establishment and their growth are indicators of the regeneration potential of a plant community. It is widely believed that in tropical forests, canopy gap formation plays an important role in natural regeneration (Richards 1952, Whitmore 1984). During gap formation in a forest canopy, a variety of micro-environmental changes occurs (Fetcher *et al.* 1983, Jordan 1985). Increased insolation, more light penetration to the ground level, changes in soil moisture characteristics, faster decomposition of the larger organic matter accumulated on the soil surface and increased disturbance of the surface soil are some of the important changes that could have an effect on regeneration. While there are many reports suggesting that a soil seed bank is an important source for forest regeneration (Enright 1985, Kellman 1970, Liew 1973, Symington 1933, Vazques-Yanes & Orozco-Segovia 1984), other studies have demonstrated the absence of it (Ladrach &

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Humberto-Mazuera 1985, Ng 1983). Indeed, there are many reports of tropical tree species lacking dormancy (Bazzaz 1983, Ng 1980, Whitmore 1984) often with short viability (Appanah & Nor 1990); even many early secondary species are suggested to have similar properties with no dormancy (Augspurger 1984). In view of the conflicting reports regarding the soil seed bank in tropical rain forest ecosystems, it was considered useful to monitor germinable seeds in the soil during the gap, aggrading and mature phases of the ecosystem. In fact, only a few studies (Saulei & Swaine 1988) are available where the dynamics of the soil seed bank has been investigated during all these phases (Garwood 1989). The present study looks at these aspects.

METHODS OF STUDY

The study area at Nelliampathy (Figure 1), of the Western Ghats in Kerala State (10° 30′ N and 76° 40′ E), is located at an altitude of 950 m. The climate is typically monsoonic with a mean rainfall of 2830 mm, most of which (78%) falls during June to September. The mean monthly maximum temperature during the monsoon season is 23.8°C and the mean minimum is 20.5°C. During the dry season, the mean maximum is 25.2°C and minimum 20.4°C.

The forest vegetation in the study area as a whole is a wet evergreen type with at least three tree layers, and shrub, seedling and herb strata. Among the top canopy species (more than 25 m height), *Palaquium ellipticum* (Dalz.) Baill., *Cullenia exarillata* Robyns and *Mesua nagassarium* (Burm.f.) Kostermans are the most important. *Drypetes oblongifolia* (Bedd.) Airy Shaw and *Polyalthia coffeoides* HK.f. & Thoms. are the two dominant mid-canopy species (15–25 m height). *Meiogyne pannosa* (Dalz.) Sincl. and *Antidesma menasu* Mig. & Tul. are the two important understorey species (4–15 m height). Though the trees are mostly primary species, a few late secondary species such as *Actinodaphne malabarica* *Balak*. and *Agrostistachys meeboldii* Pax. & Hoffm. are also present. The shrub and herb layers are generally sparse. While *Tabernaemontana caudata* Gamble and *Nilgirianthus ciliatus* (Nees.) Bremek. are the most dominant shrubs, *Pellionia heyneana* Wedd. and *Ammomum cannicarpum* (Wt.) Benth. dominate the herb layer.

The present study is based upon undisturbed natural forest sites (non-gap regions), natural gaps formed through branch/treefall and artificial gaps formed through selection felling operations carried out during the years 1977, 1982 and 1986. In the study area, 1-, 5- and 10-year-old gaps of various size categories, with three replicates of each age within each size category, were identified. For the natural gaps, the following size classes were considered: 30 ±5, 60 ±5, 100 ±10, 150 ±10, 200 ±10, 300 ±20, 400 ±20 and 500 ±50 m^2. The gaps created by selection felling, however, were all at least 150 m^2 in area, so only the five largest of these sizes could be considered. Thus, in total, 72 natural canopy gaps and 45 selection felled gaps were studied. The natural gaps were either branchfall gaps as in case of the size class 30 ±5 m^2, or single or multiple treefall gaps in the rest. A gap was defined as a vertical opening in the forest

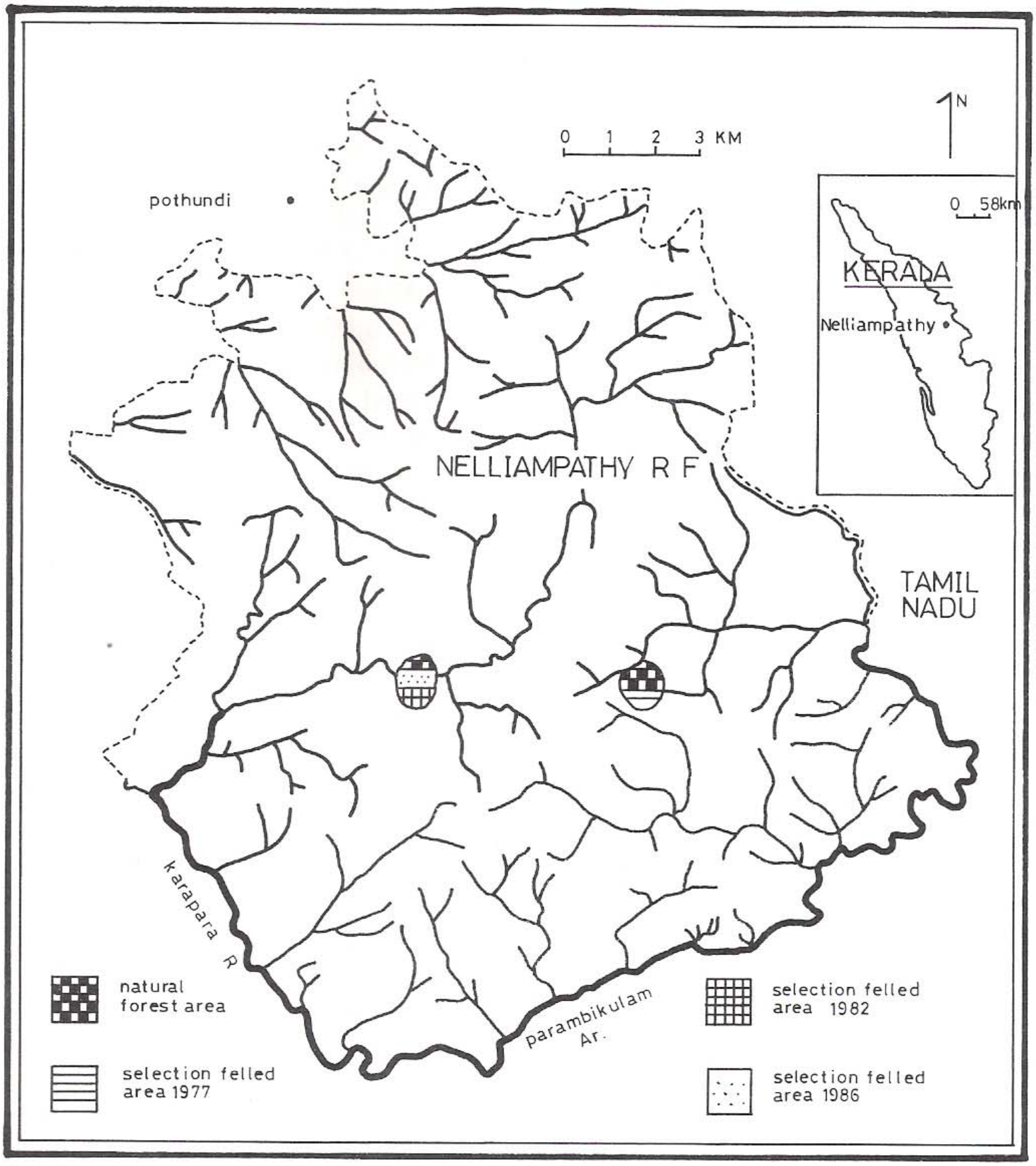

Figure 1. Map showing the study areas in a humid tropical forest of Nelliampathy, Kerala, India.

extending through all foliage levels to within 2 m of the ground (Brokaw 1982). The area of each gap was measured from a scale map drawn with at least eight coordinates of direction and distance to the edge of the surrounding foliage, recorded from a central point within the gap. Care was taken to ensure similarity in shape and comparable topography during gap selection. In the present paper only the 100 m^2 and 500 m^2 gaps are discussed, since the 30 m^2 and 60 m^2 natural gaps were similar to the 100 m^2 gaps and the remaining size classes were similar to 500 m^2 gaps, in terms of both ground flora vegetation structure and effects on regeneration (Chandrashekara 1991).

The age of each natural gap (time since gap creation) was determined in three steps. Firstly, if the tree branch which created the gap had intact or dried foliage it was assumed that it was created during the last two years or so. This was followed up by architectural analysis of the regenerated saplings to determine their age (an approach successfully employed by Ramakrishnan *et al.* 1982). After a preliminary screening of a number of late secondary and early secondary tree species *Clerodendrum viscosum* Vent. and *Macaranga peltata* (Roxb.) Muell.-Arg. were found useful for calculating gap age. In both of these species, after production of first-order branches, the termination of annual growth is delimited by very short nodes. This feature helped in ageing the saplings and therefore the gap itself. Saplings of known age were used as standards. Further confirmation of the reliability of this method was obtained by ageing the saplings through annual growth rings that were clearly exhibited by *Actinodaphne malabarica* Balak., *Clerodendrum viscosum*, *Euodia lunu-ankenda* (Gaertn.) Merr., *Macaranga peltata* and *Maesa india* (Roxb.) DC.

The litter and soil layer (to a depth of 25 cm) were sampled at two-monthly intervals from October 1987 to September 1988. On each occasion, eight quadrats (25 cm × 50 cm) were laid at random in each of the three replicate gaps of a given size and a given age class and in each of the three replicate non-gap regions, avoiding the previously disturbed sample sites. The collected sample from each quadrat was spread out in sufficient metal trays (10 cm × 15 cm size), to give a uniform depth of 3 cm in each tray. Soils were kept moist by hand-spraying with water as required. The top soil in each tray was occasionally disturbed, but without damaging the seedlings, to promote seed germination. Weekly observations of the germinated seeds were made over a 4-month period and seedlings were removed after identification. Unidentified seedlings were labelled and transplanted into soil-filled polythene bags for further observation and identification. The identified seedlings were assigned to one of the following categories: primary trees, late secondary trees, early secondary trees, primary shrubs, early secondary shrubs, primary herbs, early secondary herbs and climbers. The species which regenerate well both in closed canopy forest stands and in the gaps were considered as primary. Late secondary species are those which will not regenerate beneath a closed canopy but will do so in small gaps, whereas early secondary species would regenerate only in larger gaps.

Species diversity of the soil seed bank was calculated using a formula given by Margalef (1968) as:

$$\overline{H} = -\sum (n_i/N)\log(n_i/N)$$

where $\overline{H}$ = Shannon index of general diversity, n_i = soil seed density of species i, N = soil seed density in the community.

To determine the influence of canopy gap formation on regeneration, the density of herbs, shrubs and tree seedlings as estimated in undisturbed forest sites and 1-year-old canopy gaps; sites were then compared for the density values of each category of plants. In each selected experimental plot the density estimation was done based on 25 quadrats (1 m × 1 m) for herbs and trees seedlings, and five 2 m × 2 m quadrats for shrubs.

The influence of gap age on the soil seed bank density and species diversity values was tested using ANOVA and means compared using Fisher's least significant difference test. To compare the undisturbed forest sites and 1-year-old gaps, and natural and selection felled gaps of a given age category, for density and species diversity values in the soil seed bank, Student's t-test was used.

RESULTS

The plant density of herbs, shrubs and tree seedlings increased significantly soon after gap formation ($P < 0.05$) (Table 1). The density was higher in the larger gaps than in smaller ones. The herbs had the highest density followed by tree seedlings and shrubs. The number of germinable seeds in the undisturbed forest soil fluctuated sharply at different times of the year (Table 2). On a seasonal basis, the density of seeds in the soil was greater during the monsoon season (June–September) ($F = 3.6$; df = 5,12, $P < 0.05$). The proportional contribution of different categories of plants to the total seed bank also varied. A similar fluctuation occurred in the gap soils (not presented here).

Some dominant species from different plant categories were studied for their germinable seed density in undisturbed forest soil seed bank (Table 3). These species showed considerable variation in density of germinable seeds in the soil between different times of the year. While each species had a characteristic time when soil seed density was greater, any given species also showed an absence of seeds in the soil at other times.

The species diversity of the soil seed bank in the undisturbed forest was calculated for the bi-monthly samples (Table 4). ANOVA indicated no significant difference in the species diversity value between different seasons ($F = 2.31$; df = 5, 12, $P > 0.05$).

Table 1. Density (mean number of plant m^{-2} ±SE, $N = 3$) of different categories of plants growing in undisturbed forest and in 1-year old natural gaps in a humid tropical forest at Nelliampathy. Values in parentheses are for selection felled gaps (500 m^2)

Categories	Undisturbed forest	Small gap (100 m^2)	Large gap (500 m^2)
Herbs	6 ±0	60 ±2	90 ±2 (101 ±3)
Shrubs	2 ±0	3 ±0	5 ±0 (6 ±0)
Tree seedlings	2 ±0	5 ±0	7 ±0 (6 ±0)
Total	10 ±0	68 ±2	102 ±2 (113 ±3)

Table 2. Bi-monthly variations in the mean density (seeds m^{-2} ±SE, N = 3) of the soil seed bank in an undisturbed humid tropical forest at Nelliampathy. Values in parentheses are percentages.

	Months of sample collection						
Categories	Oct 1987	Dec 1987	Feb 1988	April 1988	June 1988	Aug 1988	Mean value
Trees							
Primary	21 ±6	9 ±3	22 ±5	19 ±6	54 ±10	60 ±8	31 ±5 (19.7)
Late secondary	29 ±8	8 ±2	31 ±4	12 ±4	21 ±3	12 ±2	19 ±2 (12.1)
Early secondary	30 ±6	16 ±2	7 ±0	5 ±1	15 ±3	37 ±6	18 ±3 (11.5)
Shrubs							
Early secondary	4 ±1	17±2	36 ±5	12 ±2	2 ±0	7 ±1	13 ±3 (8.3)
Herbs							
Primary	32 ±5	25 ±3	41 ±7	29 ±7	47 ±9	31 ±8	34 ±2 (21.7)
Early secondary	42 ±4	39 ±2	25 ±4	46 ±5	49 ±4	16 ±4	36 ±3 (22.9)
Climbers	—	—	—	7 ±2	15 ±3	12 ±4	6 ±1 (3.8)
Total	158 ±8	114 ±8	162 ±5	130 ±8	203 ±16	175 ±14	157 ±7

Table 3. Bi-monthly variations in the mean density of seed of some dominant species (seeds m^{-2}, N = 3) in the soil seed bank in an undisturbed humid tropical forest at Nelliampathy. P, primary species; LS, late secondary species; ES, early secondary species.

		Months of sample collection					
Categories	Type	Oct 1987	Dec 1987	Feb 1988	April 1988	June 1988	Aug 1988
Trees							
Actinodaphne malabarica Balak.	LS	20	2	—	—	—	5
Agrostistachys meeboldii Pax. & Hoffm.	LS	—	—	14	7	6	—
Clerodendrum viscosum Vent.	ES	1	—	—	2	5	6
Cullenia exarillata Robyns.	P	—	1	6	5	—	—
Euodia lunu-ankenda (Gaertn.) Miq.	LS	—	—	8	2	5	—
Macaranga peltata (Roxb.) Muell.-Arg.	ES	22	13	6	—	—	14
Mesua nagassarium (Burm.f.) Kostermans	P	—	3	—	—	13	8
Palaquium ellipticum (Dalz.) Baill.	P	5	—	—	14	10	—
Shrubs							
Dendrocnide sinuata (Bl.) Chew.	ES	—	—	5	4	2	—
Leea indica (Burm.f.) Merr.	ES	2	2	5	2	—	—
Solanum wightii Nees.	ES	2	9	12	3	—	—
Herbs							
Acanthosperum hispidum DC	ES	12	10	20	—	—	1
Adenostemma lavenia (L.) O. Ktze.	ES	10	—	—	16	30	5
Cyrtococcum oxyphyllum (Steud.) Stapf.	ES	12	20	—	28	17	9
Elettaria cardamomum (L.) Maton.	P	5	5	29	5	—	6
Hydrocotyle javanica Thunb.	P	—	7	8	4	2	3
Pellionia heyneana Wedd.	P	18	2	—	10	28	14

Table 4. Bi-monthly variations in the mean species diversity value ($\bar{H}$ ±SE, N = 3) of the soil seed bank in an undisturbed humid tropical forest at Nelliampathy.

	Months of sample collection					
Categories	Oct 1987	Dec 1987	Feb 1988	April 1988	June 1988	Aug 1988
Species diversity value ($\bar{H}$)	0.480 ±0.003	0.482 ±0.003	0.480 ±0.002	0.470 ±0.002	0.527 ±0.003	0.515 ±0.001

Table 5 shows the germinable seed density of each category of plants in undisturbed and disturbed forest soil seed bank. Student's t-test revealed that the density of germinable seeds of each category of plants present in the soil is significantly lower in 1-year-old gaps compared with that in soil of undisturbed sites. An exception to this, however, was the soil seed bank of the early secondary herbs in the selection felled gaps, which had increased significantly ($P < 0.05$) by the end of one year. At each gap age, while the seed density of primary trees in the soil was more in natural gaps than in selection felled gaps, that of early secondary shrubs and herbs was more in selection felled gaps (Table 6). However, no significant difference was found for late secondary trees and early secondary trees between natural and selection felled 1- and 5-year-old gaps.

The density of germinable seeds of different categories of plants in the soil tended to increase significantly with gap age (Figure 2). However, primary herbs in natural gaps and early secondary herbs in larger gaps (both natural and selection felled) had maximal density in 5-year-old gaps rather than 10-year-old ones. Since the germinable seeds of climbers were recorded only in certain gaps no statistical comparison was made for their density in gaps of different ages of a given size class.

Table 5. Density of seeds (seeds m^{-2} ±SE, N = 3) of different plant categories in the soil seed bank in an undisturbed forest site and 1-year old canopy gaps in a humid tropical forest at Nelliampathy.

		Natural gap		
Categories	Undisturbed forest	Small gap (100 m^2)	Large gap (500 m^2)	Selection felled gap (500 m^2)
Primary trees	31 ±5	20 ±2*[a]	10 ±2*	4 ±1*
Late secondary trees	19 ±2	4 ±1*	9 ±1*	8 ±1*
Early secondary trees	18 ±3	13 ±1*	11 ±1*	12 ±1*
Early secondary shrubs	13 ±3	8 ±1*	4 ±1*	12 ±2 NS
Primary herbs	34 ±2	8 ±1*	25 ±4*	13 ±3*
Early secondary herbs	36 ±3	13 ±2*	23 ±3*	65 ±8*

[a] For all data, df = 4.

NS: $P > 0.05$, within a plant category, mean value in a gap type does not significantly differ from that in the undisturbed site.

*$P <= 0.05$, within a plant category, mean value in a gap type differs significantly from that in the undisturbed site.

Table 6. Density of seeds (seeds m^{-2} ±SE, N = 3) of different plant categories in the soil seed bank in 1-, 5- and 10-year old natural canopy gaps (large, 500 m^2) and selection felled gaps (500 m^2) in a humid tropical forest at Nelliampathy.

	Gap age (years)		
Categories	1	5	10
Primary trees			
Natural gap (large, 500 m^2)	10 $\pm 2^a$	13 $\pm 2^a$	28 $\pm 3^a$
Selection felled gap (500 m^2)	4 $\pm 1^b$	3 $\pm 1^b$	8 $\pm 1^b$
Late secondary trees			
Natural gap (large, 500 m^2)	9 $\pm 1^a$	10 $\pm 1^a$	20 $\pm 2^a$
Selection felled gap (500 m^2)	9 $\pm 1^a$	9 $\pm 1^a$	8 $\pm 1^b$
Early secondary trees			
Natural gap (large, 500 m^2)	11 $\pm 1^a$	16 $\pm 2^a$	24 $\pm 3^a$
Selection felled gap (500 m^2)	12 $\pm 1^a$	20 $\pm 2^a$	37 $\pm 5^a$
Early secondary shrubs			
Natural gap (large, 500 m^2)	4 $\pm 1^b$	12 $\pm 2^b$	15 $\pm 2^b$
Selection felled gap (500 m^2)	12 $\pm 1^a$	21 $\pm 2^a$	40 $\pm 5^a$
Primary herbs			
Natural gap (large, 500 m^2)	25 $\pm 4^a$	50 $\pm 6^a$	38 $\pm 6^b$
Selection felled gap (500 m^2)	13 $\pm 3^b$	38 $\pm 6^a$	50 $\pm 3^a$
Early secondary herbs			
Natural gap (large, 500 m^2)	23 $\pm 3^b$	57 $\pm 7^a$	26 $\pm 3^b$
Selection felled gap (500 m^2)	65 $\pm 8^a$	82 $\pm 10^a$	65 $\pm 6^a$

Within each gap age and plant category, means in the same column with the same superscript are not significantly different ($P < 0.05$, Student's t-test; for all data df = 4).

The species diversity of the soil seed bank in 1-year-old gaps was significantly lower (Student's t-value = 5.55, 4.74 and 5.55 for small natural gaps, large natural gaps and selection felled gaps respectively ($P < 0.005$)) than in undisturbed sites (Table 7). In smaller gaps the species diversity of the soil seed bank was greater in 5-year-old ones than 1-and 10-year-old ones ($F = 51.32$; df = 2,5, $P < 0.00017$), whereas in larger gaps (natural and selection felled) the species diversity values did not show any significant change with gap age ($F = 2.88$ and 3.04 for natural gaps and selection felled gaps respectively, $P > 0.05$, df = 2,6).

DISCUSSION

In this study, it was not surprising to find that the plant density of ground layer vegetation (herbs, shrubs and tree seedlings) of the site increased during the first year after gap formation, and that the increase was greater in larger gaps than in smaller ones. As disturbance is a major factor determining regeneration processes, it is also reasonable to expect more regeneration in selection felled gaps than in natural gaps of the same size, as was found here, because

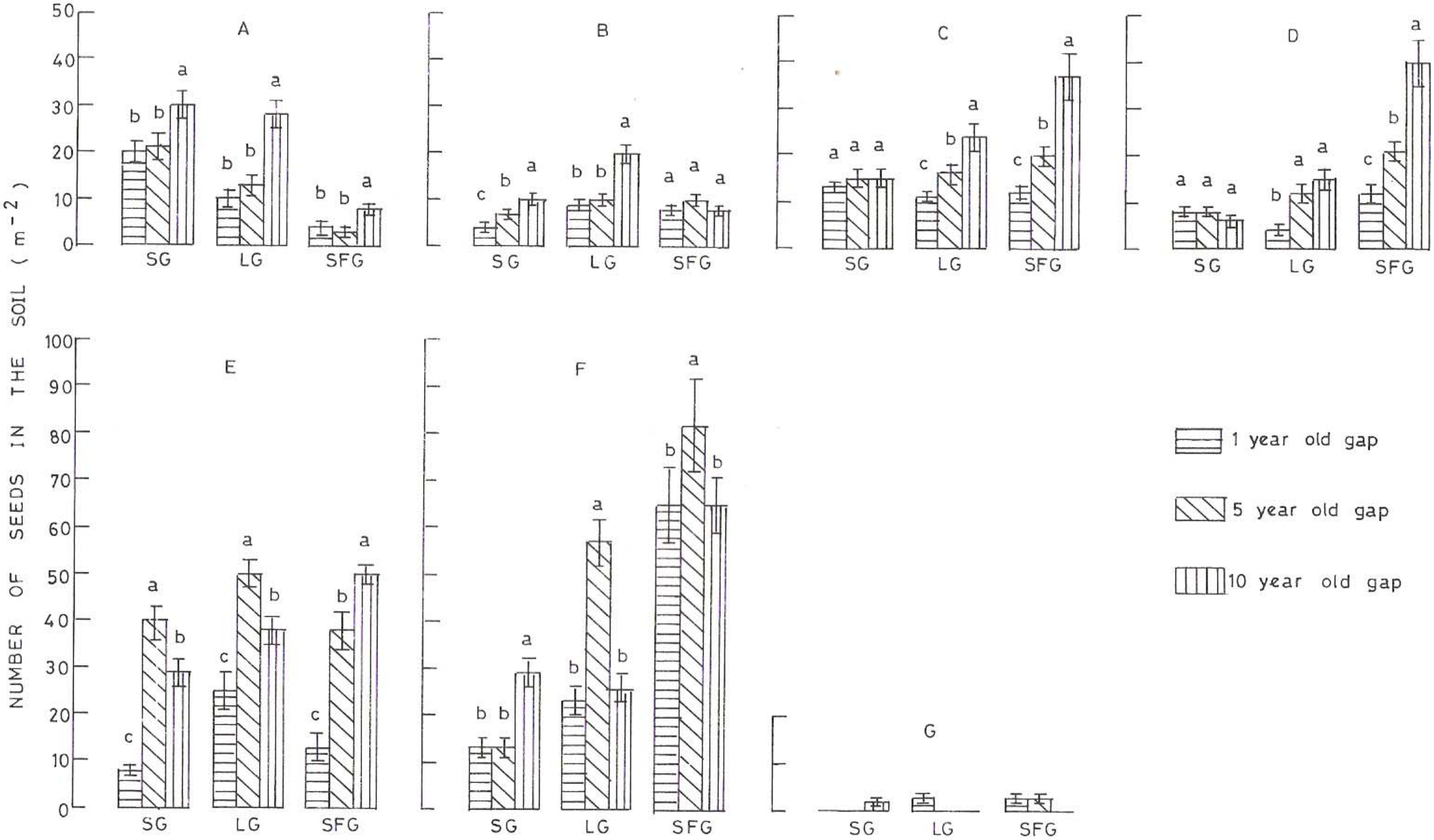

Figure 2. Density of soil seed bank of different plant categories in undisturbed forest and canopy gaps in a humid tropical forest at Nelliampathy, Kerala, India. (A) Primary trees; (B) Late secondary trees; (C) Early secondary trees; (D) Early secondary shrubs; (E) Primary herbs; (F) Early secondary herbs; (G) Climbers. SG (Natural gaps of 100 m^2: Small gap); LG (Natural gaps of 500 m^2: Large gap); SFG (Selection felled gaps of 500 m^2). Bars represent standard error. Within each plant category and gap type, means sharing the same letter do not differ significantly ($P < 0.05$, df = 2,6, ANOVA/LSD-test).

Table 7. Species diversity ($\bar{H}$) (mean value ±SE, N = 3) of the soil seed bank in undisturbed forest and in canopy gaps of a humid tropical forest of Nelliampathy.

Sites	Species diversity value ($\bar{H}$)
Undisturbed forest	0.490 ±0.012
Small natural gaps (100 m^2)	
1-year old	0.398 ±0.010
5-year old	0.496 ±0.016
10-year old	0.404 ±0.008
Large natural gaps (500 m^2)	
1-year old	0.412 ±0.004
5-year old	0.443 ±0.010
10-year old	0.452 ±0.008
Selection felled gaps (500 m^2)	
1-year old	0.397 ±0.006
5-year old	0.416 ±0.010
10-year old	0.427 ±0.008

of crown damage to trees around the edges of the gaps and the consequent better light penetration. These overall figures may, however, vary among different categories of species, for example, some primary species (e.g. *Palaquium ellipticum*, *Mesua nagassarium* and *Cullenia exarillata*) which regenerate less under selection felling (Chandrashekara 1991). Because germination is activated as a consequence of gap formation, it was reasonable to find a decline in the soil seed bank, a year after gap formation, as shown in this study. An initial depletion in soil seed bank after clearance of the Gogol forest in Papua New Guinea (Saulei & Swaine 1988) agrees with the present results. As a corollary to this, the observed significant increase in soil seed bank with gap age over the longer term was also to be expected because of the input of seed rain from surrounding trees and from ground vegetation in the gap itself. Closure of the gap with time would also reduce light availability at the ground level and alter the surface soil micro-environmental conditions so as to reduce seed germination.

If the different categories of plants (primary, late secondary and early secondary species) are considered separately, some significant patterns are observable in their seed bank characteristics in gaps of different sizes and ages and in the undisturbed site. During selective logging operations, generally, not only seed-producing primary trees are felled but also many surrounding trees are damaged, unlike in natural gap formation processes where such damage is minimal (Chandrashekara 1991). Furthermore, greater disturbance in selection felled gaps than in natural gaps adversely affects the germinability of the seeds of primary tree species. Thus, it is reasonable to expect generally a lower seed density of primary tree species in the soil of selection felled gaps than that of natural gaps. In any case, primary tree species in general have little capacity for seed dormancy. After gap formation, the size of the soil seed bank of a given category of plants is also related to its altered population size. For example, in the present study area, while primary herbs had larger numbers of individual plants in 5-year-old natural gaps than in selection felled gaps of the same age, early secondary shrubs and herbs showed a higher plant density in selection felled gaps at each gap age (Chandrashekara 1991). Consequently, a higher rate of local reproduction occurs for primary herbs in 5-year-old natural gaps than in selection felled gaps of the same age and for early secondary herbs and shrubs in selection felled gaps of each gap age. Thus, a denser soil seed bank of these categories of plants in the corresponding gaps could be expected. This agrees with the results obtained by Saulei & Swaine (1988) for the rain forests of Papua New Guinea.

The greater density of seeds beneath undisturbed forest during the monsoon period may be related to maximal seed input at that time of the year. However, such a within-year variation in size of the seed bank was not observed in a Costa Rican forest (Young *et al.* 1987). During the monsoon period more gaps are formed (Chandrashekara 1991) and these gaps could be filled up quickly from germination of the large soil seed bank of the year. However, species such as *Actinodaphne malabarica* and *Macaranga peltata* have a higher germinable seed bank outside the monsoon period during October–December, because these species produce more seeds at this time than at other times of the year. Change in the dominance of species in the soil seed bank during the year was also reported from a Mexican forest (Guevara & Gomez-Pompa 1972), where, while the tree *Robinsonella mirandae* was dominant in five of eight months sampled, three different herbs and shrub species were dominant in other months. Hence, we should be wary of characterizing a soil seed bank by one species or one life-form if it is sampled only once during the year (Garwood 1989). While the individual species patterns may easily arise by chance, the replicate samples for each species considered here show strong agreement. This needs further investigation since temporal patterns of abundance in species soil seed banks in tropical forests have not yet received adequate attention. The size of the soil seed bank in the undisturbed sites of this forest is within the range (55–243 seeds m^{-2}) reported for many other tropical forests of Asia (Ashton 1978, Cheke *et al.* 1979, Putz & Appanah 1987), but smaller than those recorded from the tropical forests of the Neotropics, Africa and Australia (200–4700 seeds m^{-2}; Alexandre 1980, Guevara & Gomez-Pompa 1972, Hopkins & Graham 1983, Soderstrom 1986). Low density in this forest could be attributed to the germination of seeds in canopy gaps and/or to the transformation of the soil seed bank into the seedling bank in closed canopy regions. The absence of any significant difference between seasons for species diversity in the soil seed bank may be because of certain species being present in a given season but absent in another season and vice versa.

Many reports suggest that early secondary categories of species contribute more (60–90% of seeds) to the soil seed bank than the late secondary or primary species (Enright 1985, Guevara & Gomez-Pompa 1972, Liew 1973). This is obviously not true in the present case because of the low density or absence of the early secondary species in the undisturbed stands. The reduced availability of early secondary trees/shrubs in the soil seed bank would, however, be compensated for by the sporadic flowering and fruiting nature of species such as *Macaranga peltata*, *Clerodendrum viscosum* and *Boehmeria glomerulifera*, the seeds being brought in from adjoining areas by dispersal. Furthermore, the hard seed coat found in many of the early secondary species may be a mechanism to prevent seed damage during the dispersal (Holmes 1989) rather than a feature for building up a persistent soil seed bank as suggested by others (Hopkins & Graham 1984a,b, Liew 1973).

The present study thus shows that the soil seed bank size in this humid tropical forest depends upon the season of the year, gap age, the type of disturbance (natural or selection felled), and the categories of plant species involved. It is also worth emphasizing that the soil seed banks of the primary forest species being of a transient type would not be important conservation tools for these species.

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