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Gap phase regeneration of tree species of differing successional status in a humid tropical forest of Kerala, India

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Abstract. Germination, establishment and growth of seedlings of tree species *Palaquium ellipticum* (primary), *Actinodaphne malabarica* (late secondary) and *Macaranga peltata* (early secondary) were studied in a humid tropical forest at Nelliampathy, in the Western Ghats of Kerala. While the primary species completed its germination within a brief period of 1·5 months, at the other extreme, early secondary species showed slow germination extending for about 5 months, the late secondary species falling in between. Although, all the species studied showed higher establishment and growth under gaps, the early secondary species were more responsive compared to the primary species. Primary species showed better establishment in undisturbed sites and natural gaps than under selection felled gaps; the reverse was true for late and early secondary species. Survival of seedlings increased with gap size, but sharply declined with gap age. Shoot/root ratio was consistently higher in the early secondary species than in the primary species.

Keywords. Canopy gaps; humid tropical forest; seed germination; seedling establishment and growth; Western Ghats.

1. Introduction

Recruitment of viable seeds, germination seedling establishment and their growth are indicators of the regeneration potential of a plant community. In tropical forests, many tree species are dependent on canopy openings for germination and seedling growth (Richards 1952; Hartshorn 1978). Bazzaz and Picket (1980) have assigned tropical forest trees into two categories, namely primary species and early secondary species. Primary species germinate under a closed canopy and remain suppressed until a gap is created which then triggers further growth. On the other hand, early secondary species are found only in gaps that too in larger ones (Baur 1964; Whitmore 1984). Furthermore, primary species have a low compensation point, photosynthetic rate and growth rate, in contrast to early secondary species (Lugo 1970; Ashton 1978), with late secondary species falling in between (Swaine and Whitmore 1988; Bazzaz 1990). Brokaw (1985) studied the response of naturally occurring saplings of primary and early secondary species to gap size at different time intervals after gap formation. More precise studies were carried out by Popma and Bongers (1988) on introduced seedlings of ten different tree species in gaps of different sizes but of unspecified age, and they concluded that the growth of all the species is enhanced in gaps, the effect being more pronounced in larger gaps. However, primary species were shown to have a higher relative growth rate

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compared to early secondary species under a closed canopy, the latter doing better than the primary species in the gaps.

The present paper discusses the results of a study on regeneration behaviour of a few tree species in a humid tropical rain forest of the Western Ghats of India. The species examined are *Palaquium ellipticum* (Dalz.) Baill., *Actinodaphne malabarica* Balak. and *Macaranga peltata* (Roxb.) Muell. -Arg. which are the major primary, late secondary and early secondary tree species respectively (Aiyer 1932; Kadambi 1941). We evaluated establishment and growth pattern of these three tree species in non-canopy gap regions of a forest stand and in canopy gaps of different sizes and ages. A further comparison was made between natural canopy gaps and canopy gaps created by selective logging operations.

2. Study area and climate

The study area at Nelliampathy 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 an annual rainfall of 283 cm, 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 is 20·4° C.

3. Methods

The present study is based upon natural canopy gaps formed through branch/ treefall and artificial canopy gaps formed through selection felling operations done during 1977, 1982 and 1986. In the study area 1-, 5- and 10-yr old gaps with the following size categories, each category with three replicates were identified. For 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 selection felled gaps, however, and all the size classes, except the first three. The area of each gap was measured by following mapping procedure, the perimeter of the gap being bordered by the canopy foliage of the vegetation around (Brokaw 1982). Care was taken to select identical gaps with regard to their shape and topography with the north-wardly slope not more than 20°. In the present paper only 100 m^2 and 500 m^2 gaps have been discussed, since 30 m^2 and 60 m^2 natural gaps were similar to the gaps of 100 m^2, and the remaining size classes were similar to 500 m^2 gap, both in terms of structure and functions (Chandrashekara 1991). However, all the gap sizes mentioned above were considered to determine the relation between the gap size and the other parameters of the study.

Age of the natural gaps (time since gap creation) was determined in three steps. First, if the gap created had intact or dried foliage it is suggestive that it was created during the last two years or so. This was followed up by architectural analysis of the regenerated saplings to determine the age of the gap. Such an approach has been successfully employed to determine the age of tree saplings by Ramakrishnan *et al* (1982). After a preliminary screening of a number of late secondary and early secondary tree species, *Clerodendrum viscosum* Vent, and *M. peltata* were found useful for calculating gap age. After production of first-order branches both species terminated annual growth as delimited by very short distance between nodes. This feature helped in aging the sapling and therefore the gap itself. Saplings of known age were used as standards. Further confirmation was made by aging saplings through annual growth rings clearly exhibited by *A. malabarica, Clerodendrum viscosum, Euodia lunu-ankenda* (Gaertn.) Merr., *M. peltata* and *Maesa indica* (Roxb.) DC.

Germination and growth rate were studied in three tree species, *P. ellipticum* (primary), *A. malabarica* (late secondary) and *M. peltata* (early secondary) each in different gaps and in undisturbed forest stands. Seeds of *A. malabarica* and *M. peltata* were collected in the previous winter season (December-January), stored and used at the time of experiment. On the other hand, seeds of *P. ellipticum* were collected a few days before the beginning of the experiment and used. Two hundred seeds of each species were introduced into 500 cm^2 culture pots filled with forest soil and the pots were inserted into the forest floor in such a way that the pot soil was at the same level as soil on the forest floor. The mouth of the pots was covered with a nylon mesh to prevent both loss of seeds from pots and possible entry of seeds from outside. The number of germinated seeds were recorded at monthly intervals and removed. Another experiment was conducted with 200 seedlings introduced into a 2 × 2m quadrat and its survival pattern was observed over a 1 -yr period starting June 1988.

For growth measurements, 200 seedlings were raised in a 2×2 m quadrat at each of the three replicate gaps of a given size class. Five seedlings of each species were randomly harvested from each replicate gap, at monthly intervals from August 1988 to August 1989. After measuring the sapling height, the root, stem and leaf components were separated and dried at 80° C for 24 h and weighed. Leaf area was measured using leaf area-meter. Growth parameters, such as relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were measured based on the methods of Hughes and Freeman (1967) and Radford (1967).

The influence of gap age on different seedling parameters was assessed using one-way analysis of variance: completely randomized without nested design (Snedecor and Cochran 1967). Wherever *F*-value is significant $(P < 0{\cdot}05)$ means were compared using Fisher's least significant difference (LSD) test. To determine the relation between the gap size and the mean values of each parameter studied, correlation coefficients were calculated (Snedecor and Cochran 1967).

4. Results

In a comparative analysis of germination patterns of *P. ellipticum* (primary), *A. malabarica* (late secondary) and *M. peltata* (early secondary), all the 200 seeds of the primary species germinated over a period of 6 weeks, whereas the early secondary species had staggered germination over a period of 20 weeks, the late secondary species falling in between. Since no significant difference in the germination patterns was observed at different sites, the trend in the undisturbed forest site alone is given here (figure 1).

Of the 200 individuals of *P. ellipticum, A. malabarica* and *M. peltata* introduced into the different sites, a substantial number of seedlings died either through collar rot disease or through root exposure (figure 2), and no other type of mortality was noticed. In the case of *P. ellipticum* and *A. malabarica,* death due to root exposure

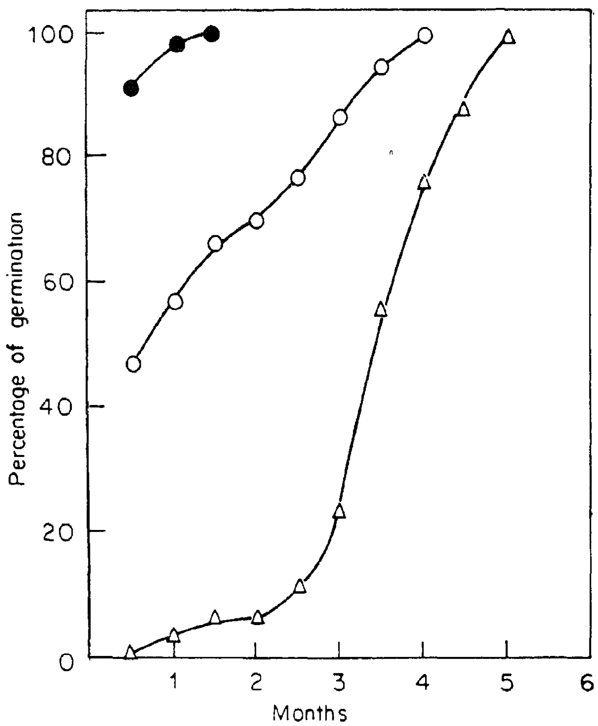

Figure 1. Germination pattern of the seeds of the primary species, *P. ellipticum* (●), late secondary species, *A. malabarica*(O), and early secondary species, *M. peltata* (Δ) in a humid tropical forest at Nelliampathy.

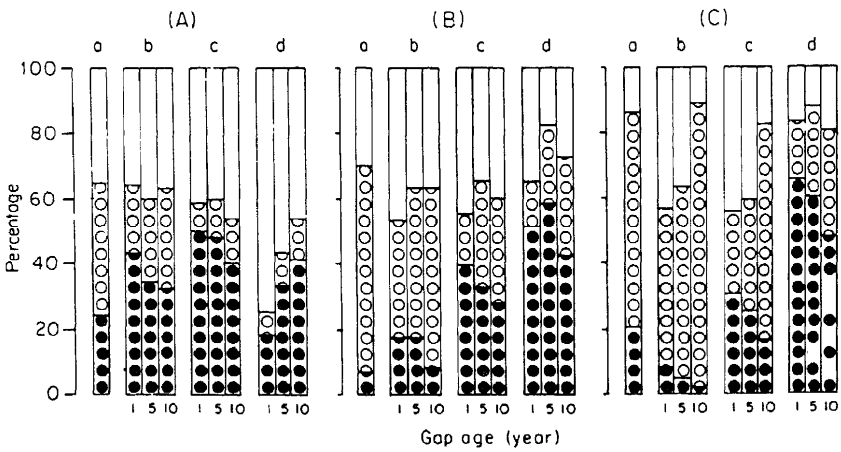

Figure 2. Establishment patterns of the seedlings of the primary species, P. ellipticum **(A),** late secondary species, *A.* malabarica **(B)** and early secondary species, M. peltata **(C)** in a humid tropical forest at Nelliampathy. (●), % survivability; (O), % mortality due to collar rot disease;(□), % mortality due to root exposure. Undisturbed forest (a); natural gaps of 100 m^2 (b) and 500 m^2 (c); selection felled gap of 500 m^2 (d).

was generally higher, but mortality of *M. peltata* was more through collar rot disease. In general, seedling establishment at the end of one year increased due to gap formation for the three species at all sites, except for the decline in establishment of *P. ellipticum* in 1-yr old selection felled gap. Further, in all cases, establishment at the end of one year declined with gap age, except for *P. ellipticum* in selection felled gaps. In natural gaps, the trend in seedling establishment was *P. ellipticum* > *A. malabarica* > *M. peltata,* while in selection felled gaps it was *M. peltata* > *A malabarica* > *P. ellipticum.* Whereas *P. ellipticum* had more establishment in natural gaps compared to selection felled ones, the reverse was the case for the other two species. A positive correlation between survivability and gap size was generally observed for all the species; the exception being *P. ellipticum* in 1-yr old selection felled gaps, where the correlation was negative. *P. ellipticum* in 5-yr old selection felled gaps and *A. malabarica* in 1yr old selection felled gap, did not exhibit significant correlation between survivability and gap size (table 1).

Table 1. Correlation coefficient values (r) between per cent survivability of seedlings versus size of the natural gaps (df = 6) in a humid tropical forest at Nelliampathy.

	Gap age (yr)		
Species	1	5	10
Palaquium ellipticum	0·968** (–0·961**)	0·926** (0·867^{ns})	0·938** (0·918*)
Actinodaphne malabarica	0·970** (0·861^{ns})	0·938** (0·980**)	0·946** (0·912*)
Macaranga peltata	0·983** (0·902*)	0·997** (0·986**)	0·986** (0·958*)

*, $P < 0·05$; **, $P < 0·01$; ns, nonsignificant.
Values in parantheses are for selection felled gaps (df= 3).

For the three species considered here, all growth parameters increased sharply an year after the gap formation, the exception being *P. ellipticum* in selection felled gaps (tables 2 and 3). In natural gaps of smaller size, growth values were the least for *M. peltata,* whereas in larger gaps, the lowest values were obtained for *P. ellipticum.* The exception to this was shoot/root ratio which was consistently higher for *M. peltata* and minimal for *P. ellipticum.* Growth values in the case of *P. ellipticum* were higher in natural gaps compared to selection felled ones and the reverse was true for the other two species. With increased gap size, the growth values increased for the three species (correlation coefficient values (r) ranging between 0·876 and 0·978; P < 0.05-0.001) and this increase was more pronounced for *M. peltata* compared to the other two. Values of all growth parameters studied in the three species decreased with the increase in gap age (tables 4 and 5).

There was. a general increase in ground layer vegetation in the gaps which declined with gap age (table 6). Tree seedlings/saplings of the early/late secondary species came up in large numbers in the gaps when compared to undisturbed sites; primary tree species also increased in the gaps.

5. Discussion

Within the broad generalization that viability of tree seedlings in tropical rain forests is low, ranging from 1 to 5 months, one could find variation in the seed

Table 2. Growth characteristics (mean ± SE., after one year's growth; *n*=3) of different species under undisturbed sites and natural canopy gaps in a humid tropical forest at Nelliampathy.

		Gap size (m^2)					
		100			500		
	Undisturbed	Gap age (yr)			Gap age (yr)		
Species	site	1	5	10	1	5	10
Palaquium ellipticum							
Seedling height (cm)	9·4±0·6	21·5±0·4	20·4±0·2	18·2±0·6	25·3±1·0 (20·1±0·4)	24·2±0·2 (22·1±0·2)	22·1±0·4 (16·2±0·5)
Aboveground biomass (g)	3·9±0·2	7·1±0·3	6·4±0·2	5·4±0·2	9·4±0·2 (4·8±0·7)	8·8±0·1 (5·5±0·2)	7·0±0·5 (6·9±0·2)
Belowground biomass (g)	3·0±0·1	4·2±0·1	3·7±0·2	3·2±0·1	4·3±0·1 (3·1±0·1)	4·1±0·2 (3·4±0·2)	3·4±0·1 (3·8±0·2)
Shoot/root ratio	1·28	1·69	1·76	1·67	2·2 (1·52)	2·16 (1·64)	2·09 (1·81)
Actinodaphne malabarica							
Seedling height (cm)	5·2±0·4	28·1±3·0	20·0±1·8	8·1±1·1	51·4±2·7 (104·6±6·1)	41·2±3·1 (88·1±4·4)	34·0±2·1 (47·1±1·8)
Aboveground biomass (g)	2·2±0·7	11·1±1·0	7·5±0·8	3·1±0·5	19·0±1·8 (37·1±4·2)	14·4±2·1 (29·1±3·0)	12·0±0·7 (16·0±2·8)
Belowground biomass (g)	1·0±0·1	5·0±0·7	3·8±0·4	1·9±0·3	8·5±0·7 (18·0±1·0)	6·5±0·4 (13·0±0·6)	5·3±0·3 (7·1±0·2)
Shoot/root ratio	2·13	2·21	1·98	1·64	2·22 (2·06)	2·20 (2·23)	2·28 (2·25)
Macaranga peltata							
Seedling height (cm)	2·4±0·4	23·8±1·8	18·5±1·0	–	89·3±4·2 (128·3±6·7)	72·3±2·1 (117·0±1·8)	24·0±1·7 (59·5±4·1)
Aboveground biomass (g)	1·1±0·2	3·3±0·2	2·2±0·1	–	15·1±0·5 (29·7±2·1)	11·3±0·4 (24·3±1·7)	3·3±0·2 (7·1±0·6)
Belowground biomass (g)	0·5±0·1	1·4±0·2	0·9±0·1	–	5·0±0·2 (12·5±1·0)	3·7±0·4 (9·7±0·5)	1·3±0·2 (2·8±0·3)
Shoot/root ratio	2·28	2·44	2·40	–	3·02 (2·38)	3·04 (2·51)	2·60 (2·52)

Values in parantheses are for selection felled gaps.

germination pattern. Thus a primary species such as *P. ellipticum* would complete its germination over a brief time period and at the other extreme, an early successional species such as *M. peltata* may have staggered germination extending for about 5 months. These two extremes in the seed germination patterns have important implications in the gap phase regeneration. In this forest, most of the canopy gaps are formed during monsoon season (Chandrashekara 1992). Since *P. ellipticum* produce seeds during this season, immediate germination of their seeds would help the species to establish well in canopy gaps. On the other hand, *M. peltata* and *A. malabarica* produce seeds during winter (Balasubramanyan 1987). Thus, their extended viability period of about 5 months would help them to regenerate in gaps which would be created in the succeeding year.

Table 3. Growth characteristics (mean ± SE, between August 1988 and August 1989; $n = 3$) of different species under undisturbed sites and natural canopy gaps in a humid tropical forest at Nelliampathy.

Species	Undisturbed site	Gap size (m²) 100, Gap age (yr) 1	100, 5	100, 10	500, Gap age (yr) 1	500, 5	500, 10
Palaquium ellipticum							
Relative growth rate (mg g⁻¹ day⁻¹)	4·9±0·1	6·6±0·0	6·3±0·0	5·9±0·1	7·2±0·1 (5·7±0·1)	7·0±0·1 (6·0±0·1)	6·4±0·1 (6·5±0·1)
Net assimilation rate [mg(cm²)⁻¹ day⁻¹]	0·5±0·0	0·8±0·01	0·8±0·01	0·7±0·01	0·8±0·01 (0·7±0·01)	0·9±0·0 (0·8±0·0)	0·7±0·0 (0·7±0·0)
Leaf area ratio (cm² g⁻¹)	0·2±0·01	0·3±0·01	0·2±0·01	0·2±0·01	0·4±0·01 (0·2±0·01)	0·3±0·01 (0·2±0·01)	0·3±0·01 (0·3±0·02)
Antinodaphne malabarica							
Relative growth rate (mg g⁻¹ day⁻¹)	3·1±0·1	7·6±0·3	6·6±0·4	4·4±0·3	9·1±0·3 (11·0±0·4)	8·3±0·2 (10·3±0·3)	7·0±0·4 (8·6±0·1)
Net assimilation rate [mg(cm²)⁻¹ day⁻¹]	0·4±0·0	0·4±0·0	0·4±0·01	0·4±0·0	0·5±0·0 (0·3±0·02)	0·4±0·0 (0·5±0·0)	0·4±0·01 (0·5±0·0)
Leaf area ratio (cm² g⁻¹)	0·2±0·0	0·8±0·01	0·5±0·01	0·1±0·0	1·4±0·01 (2·5±0·04)	1·1±0·01 (2·3±0·02)	0·8±0·01 (1·2±0·03)
Macaranga peltata							
Relative growth rate (mg g⁻¹ day⁻¹)	1·4±0·1	4·2±0·1	3·1±0·2	–	8·2±0·4 (10·2±0·3)	7·4±0·3 (9·7±0·1)	4·2±0·1 (6·3±0·2)
Net assimilation rate [mg(cm²)⁻¹ day⁻¹]	0·3±0·1	0·4±0·0	0·3±0·03	–	0·5±0·06 (0·5±0·03)	0·5±0·05 (0·6±0·02)	0·4±0·05 (0·4±0·01)
Leaf area ratio cm² g⁻¹)	0·1±0·01	0·2±0·03	0·1±0·01	–	1·0±0·04 (2·4±0·08)	0·7±0·02 (1·6±0·05)	0·2±0·01 (0·4±0·006)

Values in parantheses are for selection felled gaps.

Table 4. ANOVA, F-values of growth characteristics among 1-, 5- and 10-yr old canopy gaps of a given gap size class for different species in a humid tropical forest at Nelliampathy.

	Natural gaps		Selection felled gap
	Gap size (m^2)		Gap size (m^2)
Species	100	500	500
Palaquium ellipticum			
Seedling height	15±13*** (1·50)	6·60* (2·20)	59·76*** (1·34)
Aboveground biomass	12·66** (0·83)	15·50*** (1·10)	6·02* (1·51)
Belowground biomass	12·48** (0·49)	11·15** (0·49)	4·05^{ns}
Shoot/root ratio	0·87^{ns}	0·96^{ns}	3·70^{ns}
Actinodaphne malabarica			
Seedling height	22·54*** (7·34)	10·79* (9·23)	50·34*** (14·60)
Aboveground	25·34*** (2·76)	4·63^{ns}	9·88* (11·75)
Belowground biomass	9·91* (1·72)	10·77* (1·72)	63·79*** (2·37)
Shoot/root ratio	21·06*** (0·24)	1·50^{ns}	0·39^{ns}
Macaranga peltata			
Seedling height	6·61^{ns1}	142·67*** (9·84)	62·92*** (16·12)
Aboveground biomass	23·91**^{1} (0·62)	241·33*** (1·34)	55·30*** (5·49)
Belowground biomass	4·89^{ns1}	44·24*** (0·98)	81·00*** (1·87)
Shoot/root ratio	0·05^{ns1}	0·80^{ns}	1·23^{ns}

[1]df=2,4; ns, nonsignificant; *$P<0·05$; **$P<0·01$; ***$P±0·005$
Least significant difference test values are given in parantheses. df=2, 6.

Effects of man-made disturbance such as selection felling have often been equated with natural gap forming processes (Denslow 1980). However, Mackie *et al* (1986) have shown that altered micro-environmental conditions in selectively logged area are totally different from those prevailing in natural gaps. In addition to this, studies on the ground layer vegetation structure in natural and selection felled gaps of our experimental plot have also demonstrated the existence of difference between these two types of gaps with regard to the density of plants belonging to different categories (table 6; Chandrashekara 1991). Selection felled gaps, involving the destruction of seedlings and sapling vegetation during felling operations and the soil disturbance due to hauling of logs by elephants or mechanical means, show harsher micro-environmental conditions than gaps created by the fall of single or multiple trees. The present study shows that *P. ellipticum* (primary species) recorded more

Table 5. ANOVA, *F*-values of growth characteristics among 1-, 5- and 10- yr old canopy gaps of a given gap size class for different species in a humid tropical forest at Nelliampathy.

	Natural gaps		Selection felled gap
	Gap size (m^2)		Gap size (m^2)
Species	100	500	500
Palaquium ellipticum			
Relative growth rate	38·54*** (0·19)	18·60*** (0·33)	16·96*** (0·34)
Net assimilation rate	25·00*** (0·04)	230·77*** (0·04)	76·92*** (0·04)
Leaf area ratio	25·00*** (0·04)	25.00*** (0·04)	25·00*** (0·04)
Actinodaphne malabarica			
Relative growth rate	23·73*** (1·16)	11·63** (1·08)	17·69*** (1·02)
Net assimilation rate	0	75·19*** (0·02)	125·00*** (0·04)
Leaf area ratio	1370·38*** (0·03)	675·00*** (0·04)	525·00*** (0·11)
Macaranga peltata			
Relative growth rate	23·91**[1] (0·62)	51·99*** (1·02)	16·01*** (1·84)
Net assimilation rate	12·00*[1] (0·08)	1·15[ns] (0·19)	23·08*** (0·07)
Leaf area ratio	10·34*[1] (0·09)	236·71*** (0·09)	243·20*** (0·22)

[1]df=2,4; ns, nonsignificant; *P<0.05; **P<0.01; ***P±0.005
Least significant difference test values are given in parantheses. df=2, 6.

establishment in undisturbed sites and in natural gaps when compared with *A. malabarica* (late secondary species) and *M. peltata* (early secondary species). On the other hand, the reverse was true in selection felled gaps. Collins *et al* (1985) named a category of herbs which are physiologically plastic over a variety of light intensities, with a better response both to shade and canopy gaps, as light flexible herbs. Similarly, in the present study, *P. ellipticum* could be regarded as a light flexible tree species. Further, it may be noted that the comparison of seedling survivability and growth of P. *ellipticum* between 1 -yr old natural gap (500 m^2) and selection felled gap (500 m^2) shows better establishment and growth of the species in the former than in the latter. Thus, *P. ellipticum* is a disturbance intolerant species. Based on this study, *A. malabarica* can be categorised as a shade intolerant, light and disturbance flexible species, while *M. peltata* as a shade intolerant, light and disturbance tolerant one. Furthermore, the differential response of primary *versus* early secondary tree species to natural and man-made canopy gaps in terms of their establishment patterns also clearly indicates that these two types of disturbances are not similar. However, further detailed studies on micro-environmental properties of different disturbance regimes and the response of other tree species are required not

Table 6. Density (mean ± SE, 100 m-2) of different categories of plant in undisturbed sites and in natural gaps in a humid tropical forest at Nelliampathy.

		Gap size (m^2)					
		100			500		
		Gap age (yr)			Gap age (yr)		
Plant categories	Undisturbed site	1	5	10	1	5	10
Herbs	70 ± 5	193 ± 25	185 ± 15	65 ± 5	3123 ± 236 (881 ± 92)	1998 ± 342 (2917 ± 306)	1017 ± 186 (846 ± 78)
Shrubs							
Primary	176 ± 38	362 ± 43	636 ± 64	71 ± 15	350 ± 10 (270 ± 14)	1450 ± 44 (1300 ± 50)	230 ± 25 (290 ± 20)
Early secondary	0	57 ± 17	110 ± 23	42 ± 5	152 ± 12 (290 ± 10)	114 ± 18 (400 ± 26)	78 ± 8 (230 ± 20)
Tree seedlings							
Primary	205 ± 25	490 ± 49	162 ± 23	643 ± 49	510 ± 53 (270 ± 24)	280 ± 24 (180 ± 12)	660 ± 35 (350 ± 25)
Late secondary	0	26 ± 7	31 ± 6	26 ± 10	40 ± 5 (30 ± 4)	20 ± 4 (20 ± 4)	20 ± 5 (30 ± 4)
Early secondary	0	27 ± 5	8 ± 3	1 ± 0	170 ± 14 (230 ± 17)	10 ± 2 (10 ± 3)	10 ± 4 (0)
Tree saplings							
Primary	8 ± 2	21 ± 3	18 ± 3	36 ± 5	21 ± 3 (11 ± 3)	14 ± 2 (6 ± 2)	22 ± 2 (14 ± 2)
Late secondary	1 ± 0	1 ± 0	2 ± 1	5 ± 1	1 ± 0 (1 ± 0)	1 ± 0 (1 ± 0)	3 ± 0 (5 ± 1)
Early secondary	0	0	3 ± 1	6 ± 2	7 ± 2 (24 ± 4)	5 ± 1 (67 ± 10)	3 ± 1 (12 ± 3)

Values in parantheses for selection felled gaps.

only to give an insight into the existence of difference between various disturbance types in the forest but also to understand the species-specific or group-specific response to altered conditions. Rapid decrease in establishment of species with gap age could be related to gap closure.

Establishment of seedlings of *M. peltata* and *A. malabarica* in both natural and selection felled gaps, and *P. ellipticum* in natural gaps increased significantly with the increase in the gap size at each gap age which is suggestive of their response to differential microclimatic conditions prevailing in those two kinds of canopy gaps. A negative correlation between the gap size and survivability of *P. ellipticum* in 1-yr old selection felled gaps may be due to its inability to establish in that gap-size and the related disturbance and harsh microclimatic conditions.

Seedling growth of all categories of species in the forest was a function of light availability. Thus, seedlings grown in a canopy gap environment showed higher values for all growth parameters than under a closed canopy environment. This is in accordance with most other studies on growth of tropical forest tree seedlings; a higher light availability results in larger plants irrespective of the ecological categories (Okali 1972; Fetcher *et al* 1983; Whitmore and Bowen 1983; Oberbauer *et al* 1988; Popma and Bongers 1988). It is also discernible that the early secondary species are more responsive to higher light regime compared to primary species. *M. peltata,* being a shade intolerant species, is expected to fail to establish in undisturbed forest. However, in the present study, no marked difference was observed between *M. peltata* and *P. ellipticum* (shade tolerant species) for the seedling establishment pattern in the undisturbed forest sites. But, while the seedlings of *P. ellipticum* in undisturbed sites were well developed, those of *M. peltata* were poorly developed. Thus, the performance of a species needs to be evaluated not only from its seedling establishment but also by its seedling growth pattern. A higher shoot/root ratio for an early succession al species such as *M. peltata* suggests that the greater allocation to shoot would facilitate faster growth of this category of exploitative species for efficient light capture in a transient early successional environment. This observation is in agreement with earlier studies (Boojh and Ramakrishnan 1982; Shukla and Ramakrishnan 1982). Under the undisturbed condition, one can expect, higher shoot to root biomass ratio in shade tolerant species such as *P. ellipticum* than that in shade intolerant species like *M. peltata.* However, in the present study, the reverse trend has been noticed. This is because, under undisturbed sites, due to equally better aboveground and belowground growth, *P. ellipticum* showed lower shoot to root biomass ratio, while *M. peltata* exhibited higher shoot to root biomass ratio with more biomass contribution to the aboveground portion and poor growth of its roots. As we have already pointed out, not only the light environment but also the type of disturbance determines the growth pattern of a species. Thus in natural gaps, while higher shoot to root biomass ratio of *P. ellipticum* suggests the light flexibility and better growth of the species, low shoot to root biomass ratio of *M. peltata* indicates the poor performance of that species. On the other hand, in selection felled gaps, *P. ellipticum* has higher shoot to root biomass not by allocating more biomass to the aboveground than to belowground parts but due to drying of (and thus loss of) root biomass under harsh micro-environmental conditions of these gaps.

It may be concluded that a variety of patterns of seedling regeneration and establishment occur in gaps of different sizes and ages in a humid tropical forest, depending upon the category of species involved. Further, establishment and growth patterns of primary species like *P. ellipticum* in selection felled area may reach such a stage as those in natural gaps of recent origin only after about 10 years. Thus, their regeneration is not only impaired in selection felled area, but also repeated disturbance in these areas may eliminate these species and thus cause the change in forest structure.

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