GENERAL INTRODUCTION

The tropical rainforest is chiefly restricted to the equatorial zone from about 10°N to 15°S covering an area of about 830x10^6 ha. Until 150 to 200 years ago the greater part of the land surface in the humid tropics was covered with forests, much of it least disturbed by man. But the old view that these virgin forests had maintained themselves with little change since the time they came into being in the late Cretaceous more than 60 million years ago is no longer taken seriously. Instead, rainforests have probably been alternatively advancing and retreating in response to successive waves of wet and dry periods during major climatic changes resulting in contraction, fragmentation and recovery. Besides, the climax forest is always in a state of flux due to gap formation and the consequent succession initiated in these gaps. Thus at a given point of time three phases of community development: (a) the gap phase, (b) the building phase, and (c) the mature or climax phase forming a mosaic with obvious difference in community structure can be recognised (Watt, 1947; Richards, 1952; Whitmore, 1978; Ramakrishnan, 1985). The gap phase represents the structural changes produced by disturbance; colonization and growth of tree seedlings form an immature forest or the building phase consisting of poles and saplings; these grow on and develop into the mature phase. Since the regeneration pattern in the canopy gaps determines the future vegetation structure.
and composition in the forest, Whitmore (1989) considered the canopy gaps as the driving force in the forest regeneration cycle.

CANOPY GAP REGIMES

Gap creation in the forest

The processes by which canopy gaps in the tropical rainforest are formed can be natural or man-made. The most common type of creation of natural gaps in the rainforests is through branchfall, crownfall, single or multiple treefall and standing dead trees (Brokaw, 1982b; Riera, 1982; Putz et al., 1983; Arringa, 1988). Large canopy gaps are also naturally formed due to some cataclysmic causes such as windstorms or cyclones (Whitmore, 1974; Crow, 1980), drought (Woods, 1989) and fire (Malingreou et al., 1985).

Various ways of human influence on the forest ecosystem lead to canopy gap formation. Monocyclic and polycyclic felling systems adopted in various countries (FAO, 1985; Nair, 1990) lead to the formation of big canopy gaps (Whitmore, 1990). The principle of monocyclic system is to remove the complete stock volume of a given area of forest, whereas polycyclic system involves selective removal of a few trees in a cycle of 30- to 40- years. Tree felling and log removal create canopy gaps and so mimic natural gap formation processes and the forest responds by its natural process (Denslow, 1987; Whitmore, 1990). However, according to
Mackie et al. (1986) felling may disturb sites in ways that differ from the natural disturbances that cause treefall. Therefore they suggested detailed studies of gaps formed due to natural events versus felling activities.

Slash and burn agriculture is another mode of canopy gap formation in the tropical rain forest (Ramakrishnan, 1980; Jordan, 1989). In India as elsewhere (Bartholomew, 1953; Nye and Greenland, 1960; Ewel, 1976; Ramakrishnan et al., 1981), slash and burn agricultural system involves the management by fire for temporary improvement of soil fertility for mixed cropping (Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983b), before the land is abandoned for natural regeneration of plant communities through secondary succession. The patterns and processes involved during secondary succession, therefore, is dependent upon perturbation due to fire and that due to cropping procedures. The traditional agriculturists know the value of the fallow period of secondary forest which could allow the successful regrowth of the forest in the disturbed forest (Ramakrishnan, 1984). However, the present system of slash and burn agricultural system with short fallow cycle could cause desertification and invasion of exotic species which change the vegetation structure permanently (Kushwaha et al., 1981; Saxena and Ramakrishnan, 1984a).
Periodicity in natural gap formation

Natural gap formation through treefalls, branchfalls and crownfalls are often found to be significantly higher in the middle of the wet season (Oldeman, 1972; Brokaw, 1982b). Heavy rain and gusty wind together appear to be responsible for the peak gap formation during the mid-wet season. Rain may encourage gap formation, by loosening the hold of roots, by increasing the weight of limbs and trunks and by reducing the ability of the tree to assume "stream lining" (Gloyne, 1968). Apart from this, fungal, insect, and other damage to stems and roots accumulate all the year long until seasonally proximate causes such as wind and water, provide the final impetus to bring damaged trees down (Brokaw, 1982b).

Croat (1978) and Foster (1986) observed that the major peak of fruit dispersal by trees on Barro Colorado Island occurs during the premonsoon period and this peak is followed by a peak by seedling emergence in the early part of the wet season among some tree species that can germinate under the intact canopy but must subsequently be in a lighter gap for initial establishment (Garwood, 1982). Thus for the light flexible species, a peak of treefalls during the mid-wet season could strengthen selection for dispersal and seedling emergence near the start of the wet season.

Gap size

The gap size has an important influence on species
composition and spatial distribution in the forest (Hartshorn, 1978; Whitmore, 1984) and it determines the resource and microclimate of that part of the forest. Brokaw (1982a) considers the aerial projection of any canopy opening reaching within 2 m of the ground as a gap. However, since gap formation alters the resource availability in the expanded gaps, i.e., that area of surrounding understory affected by it, Runkle (1981) defined a gap to include the ground area under a canopy opening extending to the bases of the canopy trees surrounding the canopy opening. The former definition seems to be a more realistic approach in studying the canopy gap dynamics.

The type of disturbance is a major factor in determining the size of the gaps. Over 76 to 95% of the gaps created due to natural treefall at La Selva and on Barro Colorado Island are <200 m² in size (Hartshorn, 1978). At San Carlos de Rio Negro, Venezuela, most gaps are <100 m² (Uhl and Murphy, 1981). In Mexican tropical cloud forests about 74% of the gaps formed are smaller ones (Arringa, 1988). Brokaw (1982b) demonstrated that in the older forest on Barro Colorado, a greater number of larger gaps (>150 m²) are created when compared to that in the younger forest. This is because the younger forest has few larger canopy trees or emergents.

The size of the canopy gaps created by human activity would be much larger than that of natural gaps (Whitmore, 1974). The gap area may extend up to 1ha or more.
Gap age

The study of late secondary succession in tropical forests is beset with the generally poor records on the history of forest disturbance. In order to predict the future dynamics of the forest communities, historical analysis of disturbance and successional events that have occurred in the past are needed (Harper, 1977). Although several studies on gap phase dynamics are based on the long term monitoring in permanent plots (Hartshorn, 1978; Brokaw, 1982b; Lang and Knight, 1983; Whitmore, 1989b), such an approach is difficult in most of the cases such as a scarcity of forest preserves where long-term observation can be made. Thus, some of the attempts to overcome this problem have been tried. Veblen (1985) suggested that in simpler situations, based on annual observations for a few years, the presence of dried foliage on the gap creator tree would indicate that the gap has been created in the last one or two years. Martinez-Ramos et al (1988) reported that in the tropical rainforest at Los Tuxtlas, Mexico, most individuals of Astrocaryum mexicanum, a monopodial neotropical understorey palm, endure treefalls that form gaps in the forest by bending under falling trees and limbs. After one year, a bent palm recovers vertical growth at its terminal meristem and forms a permanent kink in its stem. Previous detailed demographic studies on the age-constant rate of stem elongation of the palm would help in determining the gap age indirectly.
Gap turnover rate

Gap turnover rate or the mean time interval between successive gaps gives an idea of the mean continuance of the regeneration cycle (Arringa, 1988). The turnover rate depends upon the size of the gap and the type of disturbance. Long-term monitoring of gap formation in permanent plots (Hartshorn, 1978; Brokaw, 1982b; Rollet, 1983), one-time survey of gap size distribution (Poore, 1968; Uhl and Murphy, 1981; Riera, 1985; Sanford et al. 1986), and permanent plot data on tree mortality (Leigh, 1975; Putz and Milton, 1982; Lang and Knight, 1983; Swaine and Hall, 1986) are the methods followed to estimate gap turnover rate. In the tropical rainforests, thus, these studies show that the gap turnover rate ranges from 62 years to 138 years and in the younger forest the turnover rate is slow.

MATURE RAINFOREST ECOSYSTEM

Vegetation, biomass and productivity

One of the most famous features of tropical rainforests is their extreme species richness. According to Whitmore (1990), in the richest rain forests every second tree on a hectare or so is a different species; even disregarding the trees some rainforests are richer in species than any other vegetation on earth. Such a high species diversity has been attributed to genetic drift (Fedorov, 1966), habitat specialization and spatial heterogeneity (Ashton, 1969) and repeated geographic isolation followed by the remixing of
species during the Pleistocene period when drastic climatic fluctuation occurred (France, 1982). However, the above said evolutionary hypotheses do not explain the coexistence and continuation of higher species diversity in the tropical rainforests. Thus, recently, considerable interest to develop an ecological approach for higher species diversity has developed (Ricklefs, 1977; Hartshorn, 1980; Denslow, 1980). Such an approach is also important to understand and develop better management strategies as well as to adapt ecologically sound harvesting procedures in the tropical rainforest ecosystem. While studying the treefall and canopy gap dynamics at La Selva, Costa Rica, Hartshorn (1978) observed that over 75% of the tree species are gap-dependent for seed germination or growth beyond sapling size. Similar observation were also made in the Western Ghats of India (Aiyer, 1932 and Lasrado, 1938). Further, interaction among establishing saplings in the understorey and within the gaps for the canopy space occupancy (Whittaker and Levin, 1977; Orians, 1982), and the recruitment of seedlings and the growth of already existing saplings will determine the community composition and structure (Horn, 1974; Hubbel and Foster, 1983). Thus, due to the combined effect of all these features the tropical rainforest is characterised by having a high species diversity.

The biomass value in the mature tropical rainforests of the world ranges from 170 to 650 t ha$^{-1}$ (Folster et al., 1976; Edwards and Grubb, 1977; Singh and Ramakrishnan, 1982a;
In relatively favourable environments, forest biomass in tropical regions is generally similar to that in temperate regions, with the exception of that of the giant sequoias (Whittaker, 1975). Due to the general closed canopy nature of the forest, the ground vegetation is sparse (Richards, 1952) and the biomass of shrubs and herbs is as low as 5.9 and 1.3 t ha\(^{-1}\) as in the evergreen forests of Karnataka (Rai and Proctor, 1986a).

Litterfall is the major pathway for the return of dead organic matter to the surface of the soil. It also represents the productivity pattern of the forest ecosystem. The tropical rainforest is characterised by having more annual litter production than the temperate forests (Bray and Gorham, 1964). The reason for this increased litter production in the tropical rainforests is the increased light availability combined with warm temperature and sufficient rainfall which enhance the fast rate of nutrient turnover through litterfall and nutrient uptake from the plants. In the tropical rainforests the annual litter production ranges from 3.6 to 14.6 t ha\(^{-1}\) (Hopkins, 1966; Bernhard, 1970; Cornforth, 1970; Edwards, 1977; Singh and Ranakrishnan, 1982b).

Studies on the net primary productivity in tropical rainforest ecosystems are limited. The net primary productivity in the wet tropics is usually higher than in any other region of the world (Whittaker and Marks, 1975).
Medina and Zewler (1972) gave a value of 23.9 to 31.5 t ha$^{-1}$ for the net primary productivity for a rainforest in Congo. However, Rai (1981) recorded a lower net primary productivity value (15.4 t ha$^{-1}$yr$^{-1}$) for a tropical wet evergreen forest of Karnataka. The studies of the net primary productivity of ground layer vegetation in the mature tropical forest is total absent.

**Nutrient cycling**

Nutrient cycling in the tropical rainforests have rates on an annual basis, which are much higher than the rates in other regions of the world (Jordan, 1985). The reason is that, in the humid tropics, the processes go on all the year-round, due to continual warm temperature and abundant moisture. According to Edwards and Grubb (1982), a larger proportion of the elements accumulate in the vegetation and this avoids the nutrient loss out of the system. The high rate of productivity and decomposition in the wet tropics also result in high potential for weathering of parental material (Stumm and Morgan, 1972) and leaching of nutrients held in the mineral soil (Johnson et al., 1977). As long as the forest is undisturbed serious nutrient losses do not occur because the native forest has evolved nutrient conserving mechanisms which counteract the leaching and weathering process (Vitousek, 1982).
Soil seed bank

The limited investigations on seed banks beneath tropical forests indicate the prevalence of seeds of species characteristics of secondary species (Symington, 1933; Keay, 1980; Guevara and Gomez-Pompa 1972; Liew, 1973; Hopkins and Graham, 1983; Enright, 1985). However the importance of viable soil seed banks in forest regeneration has been questioned by Whitmore (1983) and Putz (1983) in view of the reported absence of a soil seed bank in many tropical rainforest (Ng, 1983; Ladbrach and Humberto Mazuera, 1985). Apart from this, there are many reports of tropical tree species lacking dormancy (Ng, 1980; Bazzaz, 1990) often with short viability (Ng, 1980; Appanah and Nor, 1990); many early secondary species are also suggested to have similar properties as climax species with no dormancy (Augspurger, 1984).

Seed germination and establishment

Seed germination characteristics, requirements and establishment patterns have been extensively studied in many rainforest locations. Especially prominent and comprehensive among these are studies in Mexico (Vazquez-Yanes and Orozco Segovia, 1984), in Malaysia (Ng, 1983), and in tropical forests of the Far East (Whitmore, 1984). Some of the important conclusions drawn out of these, as well as other studies (Bazzaz and Pickett, 1980; Augspurger, 1984) are:
i. Seed longevity is generally low in tropical trees. Advanced regeneration (suppressed seedlings) may be more important than the seed bank as a source of regeneration of some tropical trees.

ii. Germination is generally rapid in tropical trees, but there is also a within-species variation in the speed of germination.

iii. Seeds of many primary species except for emergents, are able to germinate in the shade, whereas the germination of many early and secondary species is triggered by disturbance.

Secondary successional patterns

Perhaps, the most important effect of canopy gap opening is an increase in the duration and intensity of direct sunlight reaching the lower strata of the forest (Chazdon and Fetcher, 1984). Apart from this, the root competition decreases significantly (Richards, 1952) and the nutrient availability increases considerably (Schulz, 1960). Depending upon the degree of disturbance the vegetation structure alters significantly. Based on the response of species to the canopy gaps, they have been categorized into three groups (Whitmore, 1984). In any tropical forest, a large group of species - variously termed as "shade tolerant", "persistant", "climax" or "primary forest species" - germinate in the closed forest understory and exist as
suppressed juveniles until a gap opens above them, permitting accelerated growth. A group of species which require light gaps for their regeneration are termed "light demanding", "shade-intolerant", "secondary", "nomadic" or "pioneer species". This group is further subdivided into species which are truly shade intolerant and short-lived (early secondary species), and species which may be intermediate in shade tolerance and long-lived (late secondary species).

The pattern of secondary succession and the rapidity with which a forest community reaches the mature phase depends upon the degree of destruction. The pattern of secondary succession in slash and burn agriculture system varied depending upon the fallow cycle and the intensity and duration of cropping. Thus, Toky and Ramakrishnan (1983a) reported four types of early succession where herbaceous communities dominate. In Type I, *Eupatorium* (Chromolaena) or *Imperata* or both dominate the fallow. *Eupatorium odoratum* (Chromolaena odorata) dominates under a 5-yr fallow cycle, particularly where the rhizomes of *Imperata cylindrica* and *Saccharum spontaneum* are removed by constant hoeing; otherwise *Imperata cylindrica* may exist alone or may co-exist with *Eupatorium odoratum*. In Type II, *Melania micrantha* dominates the fallow under a 10-yr cycle. In Type III, *Saccharum spontaneum* dominates the fallow under a 5-yr cycle where cropping is usually for not more than one year and, therefore its rhizomes have not been destroyed. In Type IV, *Borreria hispida* dominates the fallow under a 30-yr cycle.
This herbaceous phase is then replaced gradually by bamboo and shrubs and trees.

Finegan (1984) recognised two models of successional pattern in the canopy gaps. In bigger gaps, a set of invading early secondary species dominate first and is later replaced by shade-tolerant primary species. This model is called 'relay floristics' and has also been discussed by Clements (1916) and Odum (1969). As an alternative, species with a range of shade tolerances sometimes all colonize simultaneously, this kind of succession is termed as 'simultaneous colonization' as observed at Kada, Ghana (Swine and Hall, 1983) and on Barro Colarado Island (Brokaw, 1987). 'Simultaneous colonization' model of secondary succession is similar to Connell and Slatyer's (1977) 'tolerance pathway' which assumes that late secondary species to be successful, whether or not early successional species have preceded them.

The two successional models - relay floristics and simultaneous colonization are not always mutually exclusive. Uhl and Jordan (1984) observed that in the South Venezuela terre firme forest, forbs dominated in the first year then in second year Cecropia ficifolia. Many Cecropia died in year three and the vacant space was invaded by many other pioneer and climax species (i.e. relay floristics). By the fifth year, there was little more invasion, 56 species were present, over half of them climax species, but mainly in the under canopy below faster growing pioneers (i.e. simultaneous colonization).
Most of the studies on post-fire succession support the 'initial floristic composition' model of Egler (1954) according to which it is the species present before the burn which re-establish after the burn (Purdie and Slatyer, 1976) and this is in contrast to the classical 'relay floristics' model. Saxena and Ramakrishnan (1984) show that under short slash and burn agriculture cycles of 4 and 6 years where the disturbance of fire is more frequent, early succession following fire conforms more closely to the 'initial floristic composition' model. In contrast, the 'relay floristics' model was only found to operate with the long cycles of 10 and 20 years with a comparatively low frequency of fire disturbance.

Increased resource availability and the open space in the canopy gaps allow many species to recruit themselves depending upon their light and spatial requirements (Hartshorn, 1989). According to him, the canopy gap formation plays an important in maintaining high species diversity. In the north-eastern India case study of shifting agriculture system (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983a) species diversity was very low in the first 5 years; it increased considerably between 5- and 10-years, and showed further but less increase in the next 10-years.

Biomass and productivity patterns

Though the biomass, litter production and productivity
patterns have been studied in greater detail in connection with secondary succession under clear felled areas and in slash and burn agriculture systems, such studies in natural canopy gaps are almost absent (Whitmore, 1990). However, the studies on the secondary succession pattern in the forest suggested a sharp increase in the aboveground biomass during secondary succession. According to Lugo (1973) maximum biomass value for tropical forests is approached in about 30 years at a level of 250 m.ton ha\(^{-1}\), whereas, in the temperate forests in the northern hardwoods of USA, after clear-cutting the living biomass rises to a peak of 490 m.ton ha\(^{-1}\) only after about 170 years (Bormann and Likens, 1979). Further, a steady-state for biomass is reached over a shorter time period in the tropics than in the temperate forests. The rate of accumulation of biomass is faster in the early stages of succession but may decline in subsequent years. Toky and Ramakrishnan (1983a) reported a maximum rate of 9 t ha\(^{-1}\)yr\(^{-1}\) in 15 year old successional forests; it then declined slightly. However, the rate of biomass accumulation during succession also depends upon the type of disturbance, vegetation established and other environmental conditions (Jordan, 1971; Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983a).

Comparisons of soil nutrient availability in recent gaps and under intact canopy have not demonstrated a strong pulse in nutrient enrichment in gaps smaller than 300\(^2\) (Vitousek and Denslow, 1987). However, the nutrients in soil
water samples from larger gaps (<500m²) in Costa Rican forests showed an increase in the nutrient level (Parker, 1985). Rapid nutrient uptake by intact roots of standing vegetation may account for the absence of an important nutrient pulse in small gaps; in large gaps, only a small portion of the gap area is reached by the fine roots from surrounding vegetation, and more of the nutrients may be washed through the upper soil layers.

During development of vegetation, a part of the nutrient pool is stored in the vegetation and a part is returned to the surface soil by rain wash from leaves and twigs, by litter and twigfall, and in the form of dead roots and root exudates. The soil humus is increased as succession proceeds, chiefly as a result of litterfall. High litter production during secondary successional stages compared to the mature stage was reported by many workers (Ewel, 1976; Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983c; Uhl and Jordan, 1984; Swamy and Ramakrishnan, 1987a).

Nutrient cycling

Vegetation regrowth following disturbance eventually reduces soil temperature and run-off and reestablishes relatively closed nitrogen and phosphorus cycles (Marks and Bormann, 1972), and the forest floor eventually becomes a net sink of organic matter and nutrients (Covington, 1981). A rapid biomass and nutrient accumulation occurs relatively...
early in succession (Vitousek and Reiners, 1975; Toky and Ramakrishnan, 1981b; Mishra and Ramakrishnan, 1983a). Nutrient limitation can occur as a result of (a) decreased supply of nutrients, (b) increased demand for them, and (c) accumulation of nutrients in the biomass (Aber et al., 1982; Fisher et al., 1982). In the later phases of succession the growing plants become more conservative in their use of limiting nutrients and such plants either operate with lower nutrient concentrations in active leaves (Birk, 1983) or retranslocate nutrients more effectively from senescing leaves (Miller et al., 1976; Turner, 1981). This relatively efficient use of nutrients of trees causes litter produced by such trees to have a high carbon/nitrogen ratio (Vitousek, 1982). High ratios, in turn, cause increased nutrient limitation to decomposers, immobilization of nutrients, decreased nutrient availability to plants, and decreased losses from the whole system (Vitousek et al., 1982). Thus, in general, during secondary succession the nutrient availability decreases with period and the nutrient use efficiency of the vegetation increases, as also observed by Grime (1979) and Miller (1981).

Marks (1974) investigated the functional role of a successional species such as the pin cherry (*Prunus pensylvanica*) in disturbed areas of northern hardwood forests. Pin cherry is a fast growing species which often forms dense stands in disturbed sites. It appears to be effective in preventing nutrient loss by rapid accretion of
elements into its biomass. Thus, this species promotes ecosystem stability by biotic regulation of ecosystem functions. Such biotic regulation of nutrients so that critical elements are conserved through key species has also been shown by others. Under slash and burn agriculture system in north-eastern India, the early successional weeds were shown to drastically check run-off and infiltration losses of nutrients and sediment losses in the very first year of the fallow phase of cropping (Toky and Ramakrishnan, 1983b; Mishra and Ramakrishnan, 1983a). An exotic weed such as Mikania micrantha which dominates in the first few years of the fallow growth under shifting agriculture in north-eastern India was shown to conserve potassium in the system under short fallow cycles (Swamy and Ramakrishnan, 1987b). Under longer cycles of 10-25 years the same function is done by the bamboo Dendrocalamus hamiltonii which dominate the fallow phase of 10-30 years (Toky and Ramakrishnan, 1982; Rao and Ramakrishnan, 1989; Ramakrishnan, 1989).

The present study

In the humid tropical forest of the Western Ghats of India canopy gaps are formed through natural events and through the silvicultural practice of selection felling. Although the importance of canopy gap formation in the rainforests have been emphasized repeatedly by many workers (Kadambi, 1942; Richards, 1952; Brokaw, 1982a; Denslow, 1987), detailed studies on the soil seed bank dynamics,
regeneration patterns of species, biomass and productivity patterns, litter dynamics and nutrient cycling patterns have not received adequate attention. Further, the influence of gap size and age affecting these ecosystem properties are poorly understood. Evaluation of the ecosystem functions between gaps derived through natural and man-made causes is important to evaluate the impact of disturbances and to evolve ecologically sound forest management procedures. The present study at Nelliampathy rainforest reserve in the Western Ghats in India (altitude 950 m) attempts to understand some of the patterns and processes involved in ecosystem regeneration in the gaps of different ages and size categories, considering both natural and selection felled ones.