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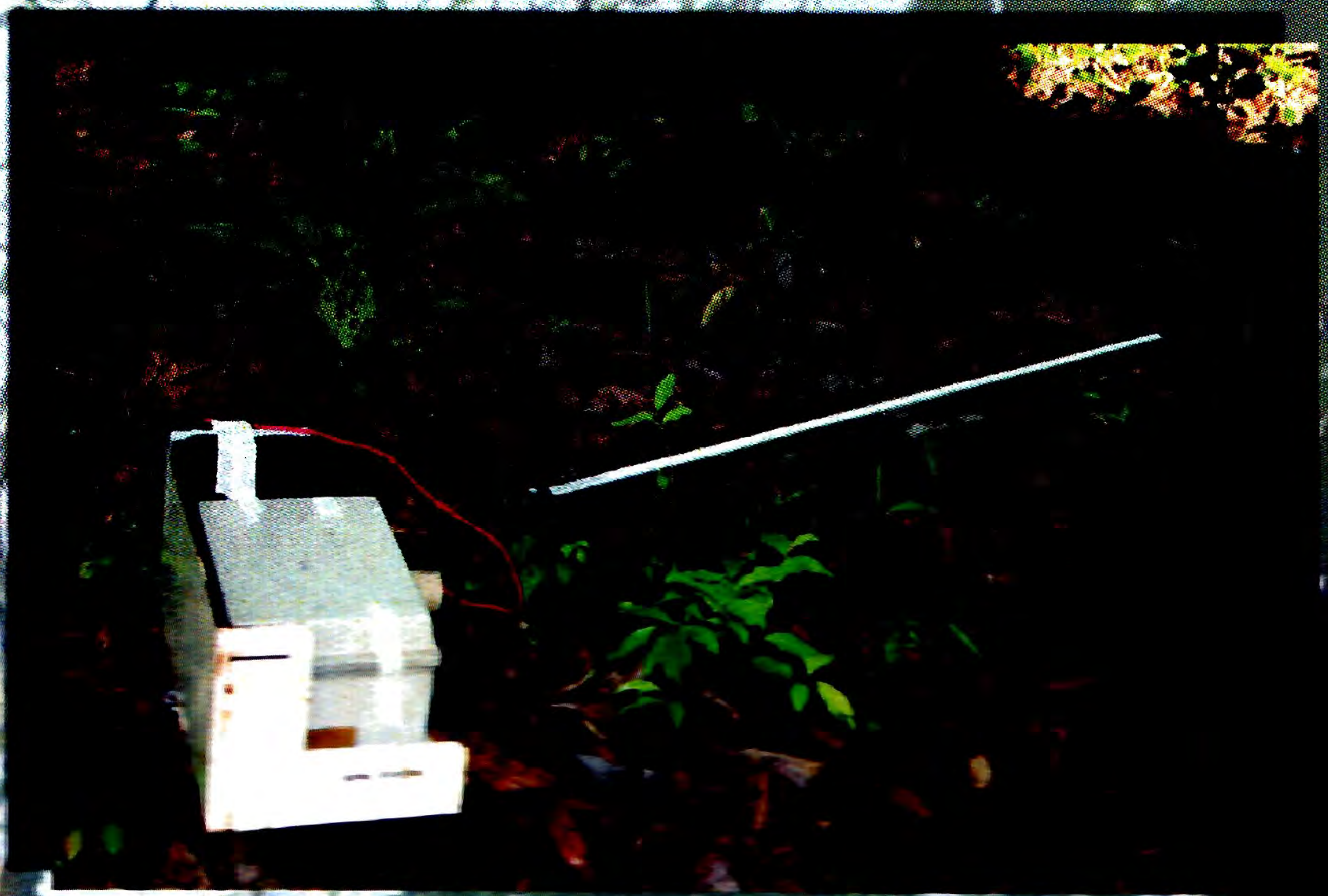
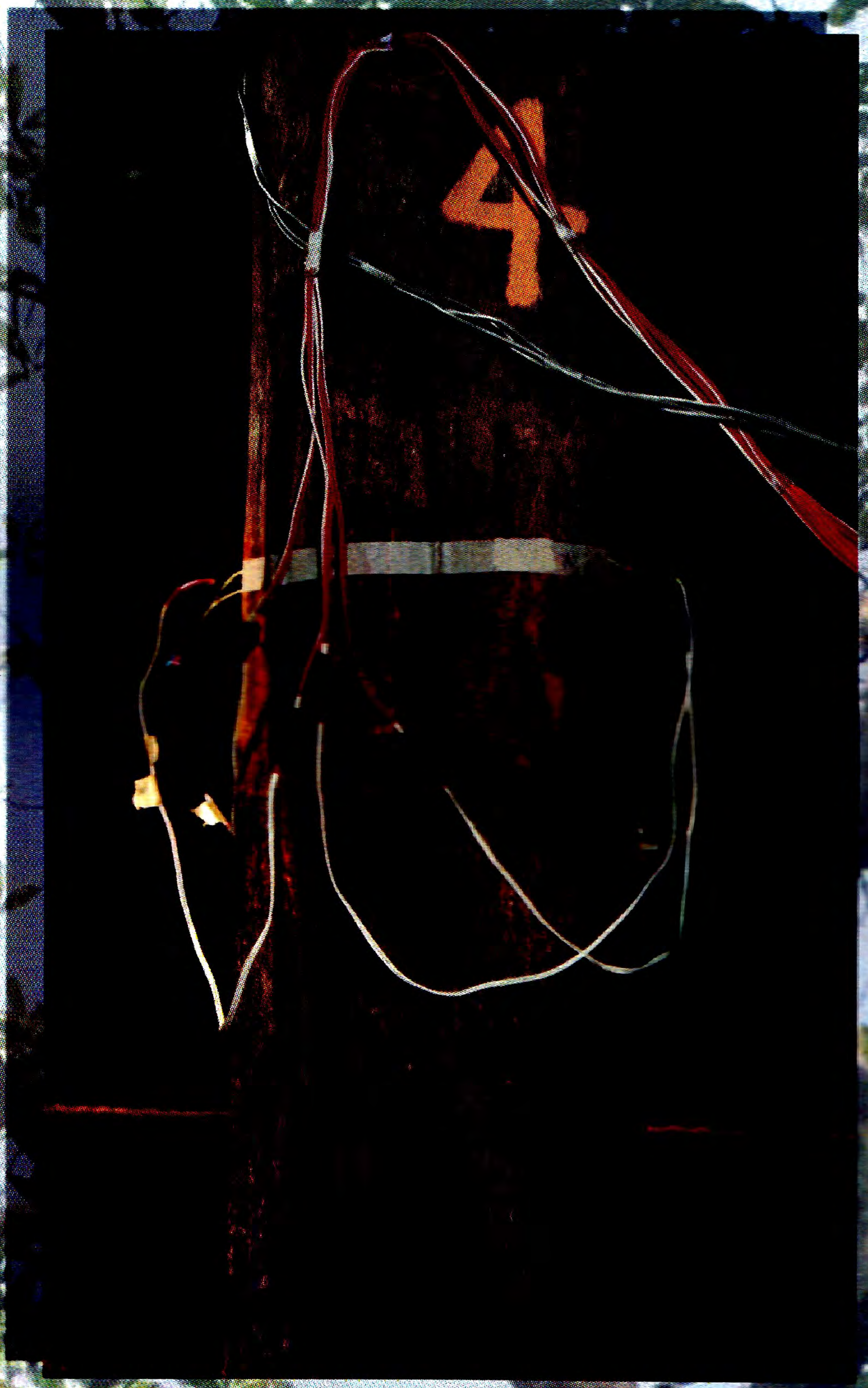
Water and light use characteristics of the vegetation in the different strata of a moist deciduous forest





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Abstract of the Project Proposal

1. *Title of the project* : Water and light use characteristics of the vegetation in the different strata of a tropical moist deciduous forest.

2. *Name of P.I* : Dr. Jose Kallarackal

3. *Coinvestigator* : Dr. U.M. Chandrashekara

4. *Origin and background of the proposal:*

In India, MDFs rank next to the Tropical Dry Deciduous Forests in extent. On the other hand, the MDFs stand first in meeting the requirements of the people, as they yield timber trees of commerce such as Teak, Sal, *Venteak*, Rosewood, etc. Although some ecological research has been conducted in them, most of the studies have been floristic and geographical in nature. The MDFs are commercially much more important, as human dependence on this forest type is greater than that on the evergreens, resulting in a high degree of anthropogenic constraints. Kerala State, at present holds a total of 4100 km^2 of natural MDFs.

The light use characteristics especially the amount of light transmitted and available at the forest floor for the regenerating seedlings need to be studied. Besides the water use by the different species of trees, especially since some of them are used as plantations is interesting to study. The phenological characteristics, leaf area development and litter fall etc. will be also studied in this project.

5. *Project duration* : 3 Years (January 2004 to April 2007)

6. *Objectives:*

   1. To study the availability and efficiency of light usage by the lower strata seedlings in a moist deciduous forest.
   2. To study the water consumption of the different species of trees belonging to the three strata in a moist deciduous forest.
   3. To study the water use by some dominant tree species such as Teak, Terminalia, Xylia etc. that are used in plantations and afforestation programmes.
   4. To study the phenological features of some of the species of trees belonging to the three strata in a moist deciduous forest.
   5. To evolve a model for evapotranspiration from a moist deciduous forest so that it can be used in calculations of the water balance from a catchment.

7. *Study site:* MDF at Pattakarimbu, Nilambur, Kerala (Nilambur North Forest Division)

8. *Total budget:* Rs. 19.20 lakhs

9. *Researach Fellows:* **Mr. K. T. Vivek, Mr. Shajeesh Jan, Mr. Deepak Jolly George and Mr. V. A. Muhammed Nissar**

1 ABSTRACT

The term Moist Deciduous Forests (MDFs) denotes an aggregate forest type. Kerala State, at present holds a total of 4100 km^2 of natural MDFs. These forests hold a complex association of different kinds of habitats like reservoirs, man-made forests and natural forests. The present study was conducted in a moist deciduous forest located at Pattakarimbu, Nilambur North Forest Division, Kerala, India . The climate is typically monsoonal with mean annual rainfall in the study area being 2312mm. This forest area forms part of the Western Ghats range of hills, which is one of the hotspots of biodiversity.

The tree community structure, composition, distribution pattern and diversity were studied in the forest site by laying hundred quadrats, each of 10m x 10 m in size. In the study plot, out of the 33 tree species encountered, *Xylia xylocarpa*, *Terminalia paniculata* and *Grewia tiliifolia* are the most dominant ones. The total tree density in the plot is 415 individuals ha^{-1} with a total tree basal area of 23.2 m^2 ha^{-1}. The crown to land ratio (CLR) was 112.1 ± 6.5 and leaf area index (LAI) was 3.60 ± 0.22. Estimated species diversity index value was 3.49, which suggests that over-dominance of any single or a set of species is absent in this forest.

Phenological studies have shown that duration of the mature leaf phase in the species studied varied from 187 days to 256 days, while yellowing before the abscission takes 12 to 32 days. It was also recorded that the duration between complete leaf-yellowing and leaf abscission ranged from 6 to 16 days. Leaf expansion rates of a few dominant species in the MDF have been also studied. Several deciduous species studied, produced new foliages during early part of the summer season (January-February). The leaf colour variations and the changes in specific leaf area (SLA) have been followed in several species.

The variations in LAI during different months (2004-2005) showed that it started from a higher value (3.60) in June and gradually decreased thereafter up to March (1.57), except a rise (2.89) during December and another rise was noticed during April. The plot-wise production of leaf litter in the nine sample plots analysed is presented. Similarly the month-wise production of leaf litter in each of the plot is also given. Wide variations in leaf litter production can be found between plots. Species associations and their interactions are probably responsible for such behaviour. The variations in SLA of three-age classes, viz., very young, young and mature leaves of seven MDF species are presented using ANOVA.

Transpiration in 12 different tree species were measured using the sapflow method. The species are – *Wrightia tinctoria, Gmelina arborea, Stereospermum colais, Xylia xylocarpa, Dalbergia latifolia, Tectona grandis, Cleistanthus collinus, Sterculia guttata, Terminalia paniculata, Dillenia pentagyna, Terminalia crenulata,* and *Bauhinia* *malabarica*. The measurements were done during the dry period (premonsoon period), the monsoon period and the post monsoon period. The hourly rate of sap flow shows that leaf area is the most important determinant regulating the water loss due to transpiration. The VPD measurements done simultaneously with the sap flow measurements show that all the species have a marked reduction in sap flux during midday when the VPD reaches values greater than 1.0 kPa. This is a very important water conserving mechanism, which prevent excessive water loss from the forest. *Terminalia paniculata, Tectona grandis* and *Gmelina arborea* were the species that consumed the maximum amount of water on a daily basis. The species to species variation and the seasonal variation were so enormous that it is difficult to model the water use of the entire stand in a meaningful way when we have 33 species altogether.

Predawn water potentials measured in seven tree species in the MDF showed values in the range of –0.45 to –0.60 MPa (Megapascals). In almost all the species, there is partial closure of the stomata from midday. The maximum stomatal conductance values are shown before noon. This is an adaptation for most of the native species to prevent water loss from the plant during the warm sunny days in the tropics.

The light availability above and below the canopy of the MDF was measured continuously using the line quantum sensor. It was found that during the dry season the light availability at the ground level was two-third of the light available above. However, during the postmonsoon period, when the canopy was relatively denser, it was only one-third of that available above the canopy. Chlorophyll fluorescence measurements on the seedling-leaves have helped us to assess the stress undergone by them for growth and regeneration. The F_v/F_m values and the PI values recorded show that some of the seedlings are under severe water stress during the dry season. This could be the reason for the absence of several tree species in the adult stage, but present in seedling stage.

It is the interactive controls such as resources, modulators, disturbance regime, human activities and biotic communities that directly regulate ecosystem processes. Species that alter these controls generally have strong effects on ecosystems. This point has been discussed at length based on the phenological and ecophysiological studies carried out in this project.

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2 INTRODUCTION

The term Moist Deciduous Forests (MDF) denotes an aggregate forest type. This forest type is classified variously and the subdivision has received different names in different systems. In India, MDFs rank next to the Tropical Dry Deciduous Forests in extent. On the other hand, the MDFs stand first in meeting the requirements of the people, as they yield timber trees of commerce such as Teak, Sal, *Venteak*, Rosewood, etc. Although some ecological research has been conducted in them (Lee, 1989; Seth and Kaul, 1978; Singh and Singh, 1991; Vyas et al., 1977), most of the studies have been floristic and geographical in nature (Champion and Seth, 1968; Puri et al., 1983). The MDFs are commercially much more important, as human dependence on this forest type is greater than that on the evergreens, resulting in a high degree of anthropogenic constraints. Kerala State, at present holds a total of 4100 km^2 of natural MDFs. These forests hold a complex association of different kinds of habitats like reservoirs, man-made forests and natural forests. Along the upper reaches they form part of the insulation belt around the Evergreen and Semi evergreen forests. On the lower reaches settlements and agricultural lands surround them. Tree stem density in Moist Deciduous Forests of the State ranges from 190 to 1146 individuals ha^{-1} (Chandrashekara and Jayaramanan, 2002). The MDFs usually occur in places with a seasonal rainfall. They flush soon after the beginning of the showers and become leafless when the soil or atmospheric moisture depletes. Therefore, the water consumption of these forests is very interesting. During the dry period, they are leafless, hence assumed to consume negligible quantity of water. Hence they should be considered good ecosystems for conserving the water in a watershed, although some studied done in Kerala have shown that they do not have any particular advantage over plantations located in similar geographical locations (Muralidharan et al., 2007). During the wet season, because of their thick foliage the MDFs mimic the evergreen forests. During this season their surface morphology is very similar to that of the Evergreen forests.

The present study was conducted in a moist deciduous forest located at Pattakarimbu (11^0 15' 20" − 11^0 18' 12" N and 76^o $22^{'}$ $10^{''}$ – 76^o $24^{'}$ $13^{''}$ E), Nilambur North Forest Division, Kerala, India . The climate is typically monsoonal with mean annual rainfall in the study area being 2312 mm, which ranges from 1621 mm to 3271 mm, and highly seasonal. This forest area forms part of the Western Ghats range of hills, which is one of the hotspots of biodiversity. Except for a brief study not much is known about the species composition and association of tree species in this part of the Western Ghats. Hence an analysis of vegetation in this locality has been done to understand the tree community structure, composition, distribution pattern and diversity.

The quantity and distribution of a tree's foliage, and the shape of its crown, are important factors for determining a tree's potential to utilize solar energy and assimilate carbon through photosynthesis (Shuttleworth et al. 1989). Although a good amount of data is available on the major phenological events from different parts of tropical countries including India, (Santapau 1962; Malaisse 1974; Monasterio and Sarmeinto 1976; Liberman 1982; Rai and Proctor 1986; Stevan et al 1987; Bullock and Solis - Magallanes 1990), there is very little information about the phenology of moist deciduous forests located in the southern parts of Western Ghats in India.

Net primary productivity (NPP) of all forest ecosystems are directly related to their leaf area. In mature stands, plant size and leaf longevity are particularly important. Several traits related to growth rate also strongly influences leaf area and NPP, particularly after disturbance. Plants retain their leaves according to environmental conditions. Persistence of leaves in turn requires an anatomy that resists desiccation and/or freezing and a chemistry that deters herbivores and pathogens. These leaves typically have a low specific leaf area (SLA) (thick or dense leaves) and low tissue nitrogen concentration that in turn constrains photosynthetic rate (Reich et al., 1997). Many of these growth related traits are functionally inter-related; others may be linked through common developmental pathways (Chapin et al., 1993). The leaf area changes throughout the year, the SLA of some dominant species in the vegetation have been studied to understand the variations in the MDF regarding the functionality of the leaves.

Litter from species typical of productive environments, for example, deciduous species typically decompose more rapidly than that from species from less productive ecosystems (e.g. evergreens). The quantity of litter input provides a critical link between NPP and decomposition because at steady state, NPP governs the quantity of organic matter inputs to decomposers. The quantity and quality of organic matter inputs to soils, as determined by plant traits, are the major determinants of decomposition when ecosystems are compared at steady state. Hence the linkage between NPP and litter decomposition is very important for the survival of an ecosystem. In this project, we have studied the leaf area and litter fall relations in the moist deciduous forest to understand the rates of litter fall and the capacity of the ecosystem for NPP.

Evapotranspiration processes greatly determine the energy balance in an ecosystem. Data on the evaporation from the ground and transpiration from the trees and ground vegetation are important in understanding the available energy within an ecosystem (Monteith, 1965). However, transpiration forms the most important component in evapotranspiration, which is much depended on vapor pressure deficit of the air, aerodynamic and stomatal conductance. Since aerodynmic and stomatal conductance for the entire forest are difficult to determine, which can only be estimated, we have used the sapflow method of measuring the transpiration from trees. This method has the added advantage that it is accurate and we get the information on individual trees and species. It is also important to see the differences between trees that form the different layers of the canopy. However, in a forest ecosystem with a number of different tree species occurring in a mixed form, the possibility for scaling up the individual tree measurement of transpiration to stand level is rather complicated.

Due to seasonal rainfall, even the humid tropics are to a great extent subjected to severe water stress at certain parts of the year. Although this may not be very severe as to cause the total desiccation of the trees, the drought conditions can cause severe stress for growth and regeneration of seedlings. Moreover, drought conditions can result in a forest fire which can be devastating especially with a high amount of litter fuel on the ground. At the same time, the litter can act as a mulch in the deciduous forest ecosystems preventing much water loss from the soil. There is not much information on the water potential of the trees in a MDF. This has been measured for a few dominant trees in the present project to understand the extent of water stress suffered by the trees especially during the dry period of the year. The stomatal conductance in the seedlings of the trees is also an important ecophysiological factor determining its survival in the forest floor during stress period. This has been measured in several species to see if there is a stomatal control on water loss.

Light plays a very important role in determining the photosynthetic productivity of the ecosystem. The visible wave lengths, which are important in photosynthesis, has to penetrate through the canopy cover as transmitted light and also as direct light in the form of sun flecks. What percentage of the light reaches the ground level will depend on how deep is the canopy cover. The seedlings that are regenerating in the ground level will need to harvest this light for their growth. In this study we have made an attempt to understand the light availability at the ground level in the MDF under study. Even when the light reaches the forest floor, how efficiently the plants use them will depend on their physiology as well as the environmental stress such as drought, high temperature, etc. Screening the seedlings on the forest floor *in vivo* for their photosynthetic efficiency has now been made practicable by the chlorophyll fluorescence method. This has been used in the present study to screen seedlings of a number of MDF species on site for their photosynthetic performance.

The specific objectives of the project were the following:

1. To study the availability and efficiency of light usage by the lower strata seedlings in a moist deciduous forest.
2. To study the water consumption of the different species of trees belonging to the three strata in a moist deciduous forest.
3. To study the water use by some dominant tree species such as *Tectona, Terminalia, Xylia* etc. that are used in plantations and afforestation programmes.
4. To study the phenological features of some of the species of trees belonging to the three strata in a moist deciduous forest.
5. To evolve a model for evapotranspiration from a moist deciduous forest so that it can be used in calculations of the water balance from a catchment.

3

STUDY SITE AND VEGETATION ANALYSIS

The study was conducted in a moist deciduous forest located at Pattakarimbu (11^{o} 15’ 20” – 11^{o} 18’ 12” N and 76^{o} 22$^{'}$ 10$^{''}$ – 76^{o} 24$^{'}$ 13$^{''}$ E), Nilambur North Forest Division, Kerala, India (Fig. 1 & 2). Soil is acidic (pH 5.2 to 5.5), with fine loam at the surface level, and gravel and red sandy at the sub-surface level.

Fig. 1. Location map of Kerala Forest Divi-sions showing the study site at Pattakarimbu (in circle) in the Nilambur North Forest Division.

The climate is typically monsoonal with mean annual rainfall in the study area 2312 mm, ranging from 1621 mm to 3271 mm. The major portion of the annual rainfall occurs from the southwest monsoon, which starts from June and continues till the end of August. The northeast monsoon sets in October and lasts till the end of November, gives but comparatively less quantity of rainfall. Rainfall occurs almost nine to ten months in a year. The mean annual maximum temperature is 35^{o}C and mean annual minimum is 15^{o}C. The weather data collected at the KFRI Subcentre, Nilambur which is within 10 km of the experimental forest plots is given in Fig. 3. The daily rainfall has been collected using a manual rain gauge. The monthly figures for rainfall during 2004 to 2007, which is the research project period is shown. The total number of rainy days is also shown in Fig. 3.

Fig. 2 . Location map of the study site at Pattakarimbu in the Nilambur Forest Division.

Fig. 3. Rainfall for Nilambur for years starting 2004 to 2007. The number of rainy days for each month is also depicted.

Vegetation analysis

The tree community structure, composition, distribution pattern and diversity were studied in the forest site by laying hundred quadrats, each of 10m x 10 m in size. Trees present in each quadrat were marked, identified, counted and their GBH (girth at breast height, i.e., girth measured at 1.37 m above the ground level) was recorded. Density, basal area, frequency, relative density, relative frequency and relative dominance of individual species were calculated separately. Species Importance Value Index (IVI), the sum of the values of relative density, relative frequency and relative dominance, were calculated for each species.

Results and discussion

In the study plot, out of the 33 tree species encountered, *Xylia xylocarpa*, *Terminalia paniculata* and *Grewia tiliifolia* are the most dominant ones (Table 1). Vegetation analyses done in nearby forest locations in Nilambur have shown different species combinations dominating the MDF (Kallarackal *et al.*, 2005). The total tree density recorded in the plot is 415 individuals ha^{-1} with total tree basal area of 23.2 m^2 ha^{-1}. This falls within the range of 190-1146 trees ha^{-1} previously reported for Kerala (Chandrashekara & Jayaraman, 2002). Based on the measurement of maximum length and breadth of crown of each tree (gbh >10.1 cm) the crown area was calculated. Sum of the crown area of all trees in a unit land area of the study plot was divided by the land area to obtain crown to land ratio (CLR). The value obtained for the plot was 112.1 ± 6.5. Leaf area index (LAI), an important parameter to understand the canopy cover of a forest plot, was analyzed during the south-west monsoon period (June – August 2004) using canopy analyzer (LI-COR, Nebraska, USA). The maximum LAI recorded for the study plot was 3.60 ± 0.22. The CLR and LAI clearly indicated that the forest canopy is not very dense compared to universally reported values (Scurlock *et al.*, 2001). Estimated species diversity index value was 3.49, which suggests that over-dominance of any single or a set of species is absent in this forest.

Density of trees of smaller girth classes is lower than that of larger girth classes, which indicates the forest is highly disturbed (Fig. 4). When the girth class distribution of individual tree species were analysed, it was clear that in majority of the dominant tree species, smaller girth classes were less in number (Table 2). This shows the poor recruitment of seedlings into saplings phase. This may be attributed to grazing, fire, firewood collection and drought conditions, which are prevalent in this location.

Table 1. Density, basal area, frequency and Importance Value Indiex (IVI) of trees (>10.1 cm Gbh) in a moist deciduous forest at Pattakkarimbu

Sl No	**Species**	**Density (individ. ha^{-1})**	**Basal area (m^2 ha^{-1})**	**Frequency (%)**	**IVI**
1	*Xylia xylocarpa*	96	3.48	46	**54.6**
2	*Terminalia paniculata*	67	3.24	55	**49.1**
3	*Grewia tiliifolia*	45	4.21	37	**42.7**
4	*Tectona grandis*	27	2.79	20	**26.1**
5	*Terminalia crenulata*	21	1.73	21	**20.2**
6	*Terminalia bellirica*	7	1.91	7	**13.1**
7	*Dillenia pentagyna*	19	0.62	17	**13.0**
8	*Schleichera oleosa*	23	0.34	13	**11.4**
9	*Stereospermum colais*	17	0.63	13	**11.2**
10	*Mitragyna parviflora*	12	0.55	9	**8.5**
11	*Dalbergia latifolia*	11	0.22	9	**6.7**
12	*Holarrhena pubescens*	10	0.03	6	**4.7**
13	*Bridelia crenulata*	6	0.24	6	**4.5**
14	*Lagerstroemia flos-reginae*	5	0.43	4	**4.3**
15	*Wrightia tinctoria*	7	0.04	6	**4.1**
16	*Wendlandia thyrsodea*	6	0.02	5	**3.2**
17	*Bauhinia malabarica*	4	0.17	4	**2.9**
18	*Phyllanthus emblica*	4	0.15	4	**2.8**
19	*Lagerstroemia microcarpa*	3	0.23	3	**2.6**
20	*Sapindus trifoliata*	4	0.01	3	**1.8**
21	*Mallotus philippinensis*	3	0.03	3	**1.7**
22	*Odina wodier*	2	0.12	2	**1.6**
23	*Cyclostemon confertiflorus*	3	0.03	2	**1.4**
24	*Sterculia guttata*	3	0.03	2	**1.4**
25	*Careya arborea*	2	0.02	2	**1.1**
26	*Haldinia cordifolia*	1	0.13	1	**1.1**
27	*Hardwickia pinnata*	1	0.04	1	**0.7**
28	*Pterocarpus marsupium*	1	0.02	1	**0.6**
29	*Butea monosperma*	1	0.01	1	**0.6**
30	*Cordia dichotama*	1	0.01	1	**0.6**

31	*Aphanamixis polystachya*	1	0.01	1	**0.6**
32	unidentified 1	1	0.003	1	**0.5**
33	*Strychnos nux-vomica*	1	0.001	1	**0.5**
	Total	**415**	**23.19**	**306**	**300.0**

Fig. 4. Girth class distribution (Gbh in cm) of different tree species in a moist deciduous forest at Pattakkarimbu.

Girth Classes: A=10.1-20.0; B=20.1-30.0; C=30.1-40.0; D=40.1-50.0;
E=50.1-60.0; F=60.1-70.0; G=70.1-80.0; H=80.1-90.0;
I=90.1-100.0; J=100.1-110.0; K=110.1-120.0; L=120.1-130.0;
M=130.1-140.0; N=140.1-150.0 and O=150.1 cm above

Table 2. Girth class distribution (gbh in cm) of different tree species in a moist deciduous forest at Pattakkarimbu

Sl No	Species	Girth classes															
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	Total
1.	*Xylia xylocarpa*	8	9	6	13	14	6	13	13	7	5	1	1	0	0	0	96
2.	*Terminalia paniculata*	9	10	4	9	3	5	7	0	4	8	4	0	2	0	2	67
3.	*Grewia tiliifolia*	0	1	0	1	2	2	3	5	8	6	6	1	5	1	4	45
4.	*Tectona grandis*	1	0	0	0	0	0	0	2	5	5	3	6	4	1	0	27
5.	*Terminalia crenulata*	0	0	0	1	1	1	1	1	3	3	4	2	1	2	0	20
6.	*Terminalia bellirica*	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1	7
7.	*Dillenia pentagyna*	3	1	2	2	2	3	3	2	0	0	1	0	0	0	0	19
8.	*Scheichera oleosa*	6	4	4	3	3	2	1	0	0	0	0	0	0	0	0	23
9.	*Stereospermum colais*	0	2	3	1	4	1	3	1	1	0	0	1	0	0	0	17
10.	*Mitragyna parviflora*	1	2	3	0	1	2	2	1	0	0	0	0	0	0	0	12
11.	*Dalbergia latifolia*	2	4	0	1	1	1	1	0	0	1	0	0	0	0	0	11
12.	*Holarrhena pubescens*	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	10
13.	*Bridelia crenulata*	0	1	1	0	1	0	1	0	2	0	0	0	0	0	0	6
14.	*Lagerstroemia flos-reginae*	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	5
15.	*Wrightia tinctoria*	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	7
16.	*Wendlandia thyrsodea*	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	6
17.	*Bauhinia malabarica*	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	4
18.	*Phyllanthus emblica*	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	4
19.	*Lagerstroemia microcarpa*	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	4
20.	*Sapindus trifolia*	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
21.	*Mallotus philippinensis*	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3
22.	*Odina wodier*	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	2
23.	*Cyclostemon confertiflorus*	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	3
24.	*Sterculia guttata*	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	3
25.	*Careya arborea*	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2
26.	*Haldinia cordifolia*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
27.	*Hardwickia pinnata*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
28.	*Pterocarpus marsupium*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
29.	*Butea monosperma*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1

30.	*Cordia dichotoma*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
31.	*Aphanamixis polystachya*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
32.	unidentified 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
33.	*Strychnos nux-vomica*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Total	48	50	30	39	37	25	39	27	31	33	20	11	13	5	7	415

Girth Classes: A=10.1-20.0; B=20.1-30.0;C=30.1-40.0; D=40.1-50.0; E=50.1-60.0; F=60.1-70.0; G=70.1-80.0; H=80.1-90.0; I=90.1-100.0; J=100.1-110.0; K=110.1-120.0 ; L=120.1-130.0; M=130.1-140.0; N=140.1-150.0 and O=150.1 cm above

4

PHENOLOGY OF FOLIAGE

The quantity and distribution of a tree's foliage, and the shape of its crown, are important factors for determining a tree's potential to utilize solar energy and assimilate carbon through photosynthesis (Shuttleworth *et al.*, 1989). Leaf longevity of tropical trees tends to be shorter than those of typical temperate trees; on the other hand, regeneration cycles of new foliage leaves are much shorter. The net primary productivity of a forest would greatly depend on the amount of foliage present at the time of good water availability in the soil and also the sunlight available for photosynthesis.

The phenology of plants such as flushing, flowering, leaf shedding, fruit setting, seed dispersal, etc. has been associated with feeding, movement patterns and sociality of insects, birds and mammals (Foster 1982b; Leigh and Windsor 1982; Prasad 1983; Wada 1983; Appanah 1985; Coates - Estrada and Estrada 1986). Although a good amount of data is available on the major phenological events from different parts of tropical countries including India (Santapau 1962; Malaisse 1974; Monasterio and Sarmeinto 1976; Liberman 1982; Rai and Proctor 1986; Stevan et al 1987; Bullock and Solis - Magallanes 1990), there is very little information about the phenology of moist deciduous forests located in the southern parts of Western Ghats in India. Western Ghats, a hotspot of biodiversity, has a large number of tree species which are relatively unexplored compared to its counterparts elsewhere in the world. Nevertheless, a few studies are available on the subject (Boojh and Ramakrishnan, 1981; Shukla and Ramakrishnan, 1982; Ralhan *et al.*, 1985; Prasad and Hegde, 1986; Kallarackal *et al.*, 2005).

In this study, we have tried to examine the foliage phenology of a number of tree species in the MDF, which includes the leaf longevity, expansion rate of leaves, changes in leaf colour during different stages of maturity and leaf fall, etc.

Methodology

Foliage phenological observations were taken for six species, namely, *Dalbergia latifolia*, *Phyllanthus emblica*, *Terminalia bellirica*, *Terminalia crenulata*, *Terminalia paniculata* and *Xylia xylocarpa*. During the visit, once in three days, 25 marked leaf buds of each species, were qualitatively characterized for the four leaf phenological events, namely, production of leaf buds, development of young leaves from leaf buds, leaf maturation and abscission. Both buds and expanded leaves of each species were monitored for various morphological features such as presence/absence of hairs, margins, venation, colour change, development of certain structures such as extrafloral nectaries (EFNs) on the leaf etc. The rate of leaf expansion of each investigated leaf (leaflet in the case of *Xylia xylocarpa*) was determined by measuring leaf area at every three days until they reached full size. The per cent of daily increase in size during the expansion was calculated using the following formula given by Kursar and Coley (2003):

Expansion rate as per cent per day = $100 * (e^{(\ln(\text{area2}/\text{area1})/\text{time})}-1)$ (1)
where, `area 1’ and `area 2’ are leaf area at different measurement and `time equals’ equals the number of days between measurements. Values of 100% per day indicate that the leaves doubled in size daily. Species that expanded more slowly had lower values of expansion.

Results and discussion

Leaf buds of *Terminalia bellirica*, *Terminalia crenulata* and *Terminalia paniculata* and *Xylia xylocarpa* are brown, while those of *Dalbergia latifolia* and *Phyllanthus emblica* are pale green and red, respectively. Bud phase continues for 9 to 18 days (Table 3) and leaf expansion started when the leaf bud area is between 0.48 and 0.56 cm^2. Except in *Dalbergia latifolia*, buds are pubescent either with villosulous or strillose hairs. It is reported that leaf hairs play important physiological and ecological roles. They often protect leaves, particularly in the bud and expanding phases, from ultraviolet light damages (Skaltsa *et al.*, 1994; Karabourniotis *et al.*, 1995) and by reducing radiation heat load (Ehleringer, 1984). They are also known for their ability to decrease pathogen germination rates by decreasing leaf wetness (Brewer and Smith, 1997) and herbivore damage (Palaniswamy and Bodnaryk, 1994). In fact, in all five species, hairs, though less dense, continued to be present in the leaf expanding phase and gradually falling off. For instance, in *Terminalia bellirica*, leaves become glabrous when they were about 19 days old. However, in the case of *Xylia xylocarpa* leaflets showed quick hair fall (Table 1). Thus, number of days in the leaf-expanding phase when the leaf hairs are seen showed the following trend:

Terminalia bellirica >Terminalia crenulata> Phyllanthus emblica >Terminalia paniculata > Xylia xylocarpa

It may be pointed out here that decrease in hair density may increase photosynthetic capacity by decreasing reflectance (Ehleringer, 1984). Thus it seems that comparatively quick hair fall in *Xylia xylocarpa* is an adaptation to enhance photosynthetic capacity of expanding leaves.

Terminalia crenulata, *Terminalia paniculata* and *Xylia xylocarpa* are characterized by having extrafloral nectaries (EFNs) on the leaves. In case of *Terminalia crenulata* and *Terminalia paniculata*, generally two EFNs are seen on petiole near the leaf base. However, in *Xylia xylocarpa*, one EFN can be seen on the leaf rachis at the juncture of each pair of leaflets. There are reports to indicate the interaction of ants with EFNs and to provide strong evidence supporting the so-called “protectionist hypothesis” (Brown,1960; Bentley,1977). According to this view, ant visitation to EFNs is beneficial to the plant because the ants’ predatory and/or aggressive behaviour toward herbivores reduces significantly the damage caused to the plant by the latter. In the present study, an attempt has been made to monitor the active period (where the secretion of nectar is seen or the EFNs are live) of the EFNs in the above-mentioned three species. In the case of *Xylia xylocarpa*, the EFNs remain red and functional for a longer period (57 days) than in *Terminalia paniculata* (33 days) *and Terminalia crenulata* (21 days). Further studies are required to find the reasons and consequences of variation between species in terms of cessation of the EFN’s activities. The vulnerability of the leaves for herbivores at different age of the leaf could be related to this behaviour.

Variation among six species studied showed their mean leaf expansion rates (Table 1) with significantly higher value for *Terminalia bellirica*, and lower value for *Xylia xylocarpa*. It was also observed that the leaf expansion rate is exponential during the first half of the total number of days they require for complete expansion, with exception being *Xylia xylocarpa* (Figs. 13 & 14). According to McKey (1979), rapid young leaf expansion is a strategy to shorten the period of vulnerability to herbivores. There is a counter-argument indicating that species with rapid leaf expansion suffer higher rates of herbivory apparently because of higher nutritional value and lower secondary metabolites (Kursar and Coley, 2003). However, if the fast expanding leaves have the property of delayed greening they can escape from herbivory with reduced amount of energy and nitrogen content (Kursar and Coley, 1992). In the present study, species such as *Terminalia bellirica* and *Terminalia crenulata* showed a synchrony between complete leaf expansion and greening. However, species like *Terminalia paniculata* and *Phyllanthus emblica* took more time for greening than for complete leaf expansion, when in *Dalbergia latifolia* and *Xylia xylocarpa* opposite trend was observed. Among the species studied, leaf greening patterns are also different. For instance, in case of *Terminalia bellirica* and *Terminalia paniculata,* greening starts at leaf tip and spreads downwards towards the leaf base, while opposite pattern can be seen in *Phyllanthus emblica* (Figs. 5-11). In *Terminalia crenulata* and *Dalbergia latifolia,* greening starts from the leaf centre, particularly around the primary and secondary veins, and spreads to the margin. During the greening of leaflets of *Xylia xylocarpa,* a mosaic of green and red colour throughout the lamina can be seen. Thus further detailed studies on different traits: physical, physiological and chemical, prevailing in each species are needed to fully explore how such traits, either individually or in combination, help the species to escape and/or protect from herbivory.

Duration of the mature leaf phase in the species studied varied from 187 days to 256 days (Fig. 12), while yellowing before the abscission takes 12 to 32 days (Table 3). It was also recorded that the duration between complete leaf-yellowing and leaf abscission ranged from 6 to 16 days.

Foliage phenological studies of tropical species have established that the leaf flush occurs either with the onset of rain after a spell of dry period (Proctor *et. al*., 1983) or early in the dry period (Whitmore, 1984). Deciduous species studied here produced new foliages during early part of the summer season (January-February). During this part of the year, it is known that the temperature and hours of sunshine are at their maximum. These environmental factors have been regarded as suitable for maximizing photosynthesis and vegetative growth (Salisbury and Ross, 1974). It has been also noted (*see* Chapter 6) that the predawn water potentials of the trees do not go below –0.50 Mpa, which probably shows that they are not under severe water stress. Probably, a mulch of fallen leaves helps to retain sufficient soil moisture. Thus the emergence and maturation of leaves in the pre-monsoon period are prominent. The leaf fall patterns that appear to be beneficial adaptations have evolved in response to seasonal climatic changes. A large number of factors have been implicated to trigger leaf shedding in tropical trees, including water and cold stress, photoperiod (Bhat, 1990) and intrinsic factors (Addicot, 1978). In the present study, leaf abscission which occurs during November and December may be an adaptation to avoid water stress and also helping to mulch the soil surface.

Fig. 5. Change in leaf colour at different stages of maturity of *T. bellirica*

Fig. 6. Change in leaf colour at different stages of maturity of *D. latifolia*

Fig. 7. Change in leaf colour at different stages of maturity of *Xylia xylocarpa*

Fig. 8. Change in leaf colour at different stages of maturity of *Terminalia paniculata*

Fig. 9. Change in leaf colour at different stages of maturity of *Terminalia crenulata*

Fig. 10. Change in leaf colour at different stages of maturity of *Holarrhena pubescens*

Fig. 11. Change in leaf colour at different stages of maturity of *Phyllanthus emblica*

Fig. 12. Leaf duration in the several MDF species conducted at Pattakarimbu site.

Table 3. Interphenophase durations and leaf expansion rate in some dominant tree species in a moist deciduous forest at Pattakarimbu, Nilambur, Kerala. (Values are Mean± SE, N= 25 leaves. NA: Not applicable).

Attributes	**Species**					
	Terminalia bellirica	*Terminalia crenulata*	*Terminalia paniculata*	*Dalbergia latifolia*	*Phyllanthus emblica*	*Xylia xylocarpa*
Duration of leaf bud stage (days)	9±1	13±2	9±1	12±2	18±3	12±2
Bud area (cm^2) when the buds started transforming into young leaves	0.52±0.21	0.52±0.03	0.56±0.1	0.52±0.0.5	0.52±0.04	0.48±0.02
Duration of leaf hair presence in young leaves (days)	19±2	11±2	7±1	NA	14±2	2±1
Duration of extrafloral nectaries (EFNs) active in leaves (days)	NA	21±3	33±3	NA	NA	57±3
Time required for complete leaf expansion (days)	21±2	33±3	39±2	27±3	27±3	66±4
Leaf expansion rate (in %)	36.2±1.3	17.9±0.8	14.3±1.2	24.9±1.5	14.8±1.2	6.9±1.0
Time required for complete greening of leaves (days)	24±2	36±3	51±2	18±1	42±5	25±2
Duration of leaf mature phase (days)	224±12	188±15	256±22	236±24	187±12	236±21
Time required complete yellowing of old leaves (days)	21±4	28±5	32±4	26±4	12±3	18±4
Time required for leaf abscission after leaf yellowing (days)	15±3	10±2	16±2	12±2	6±2	6±1

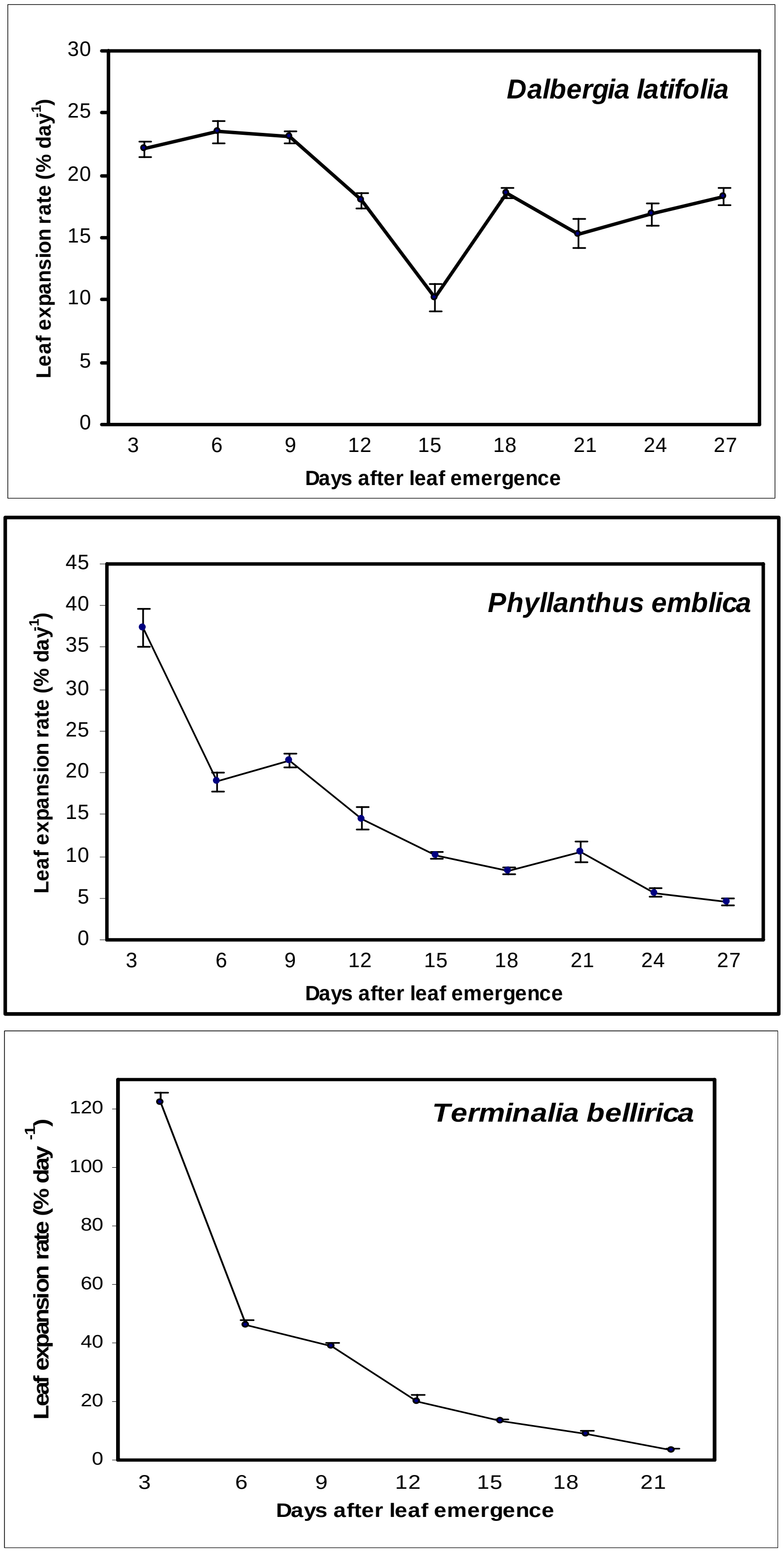

Figure 13. Leaf area expansion rate (% day^{-1}; mean ± SE) in different tree species. N=25 leaves per species.

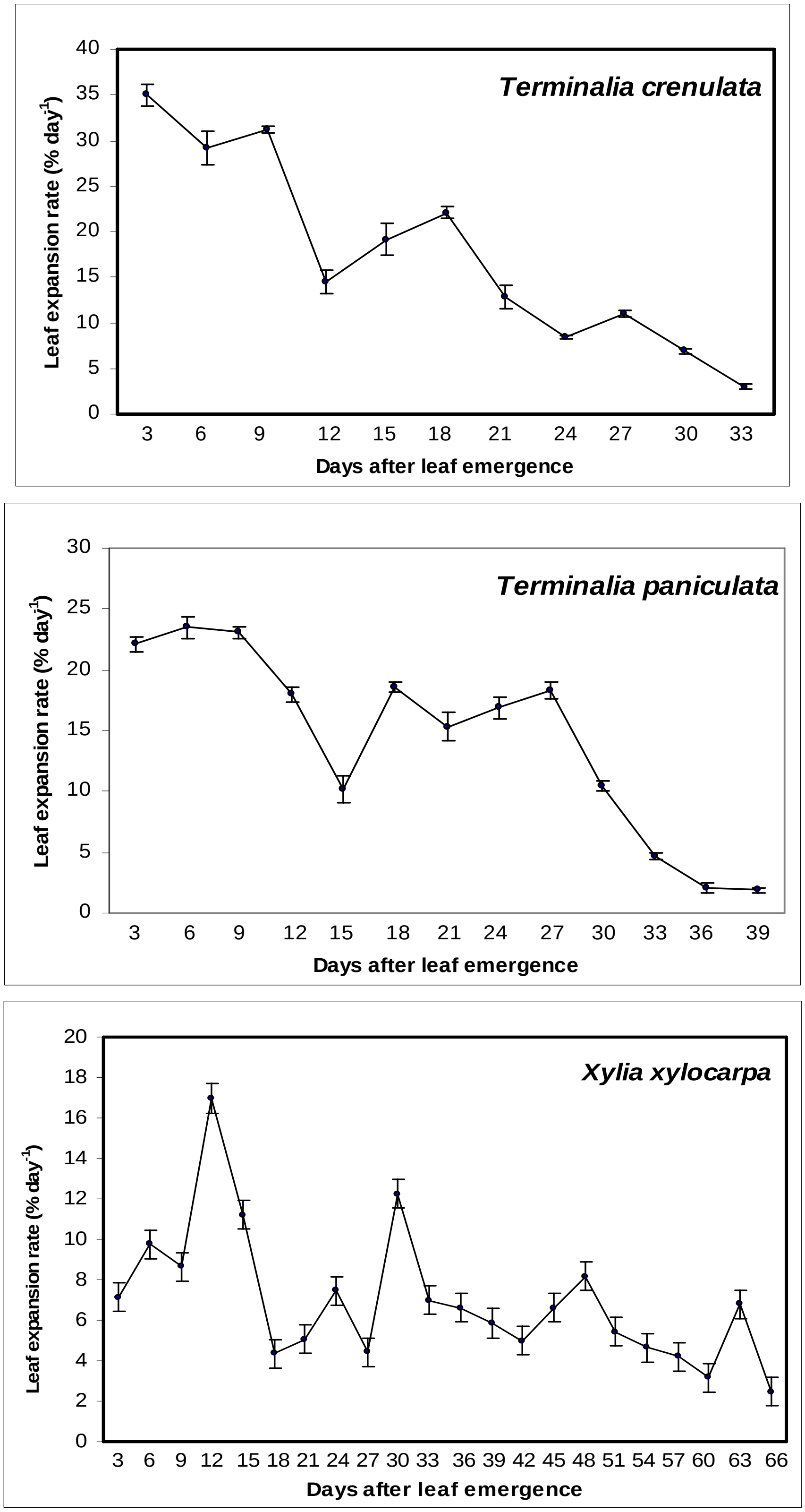

Figure 14. Leaf area expansion rate (% day^{-1}; mean ± SE) in different tree species. N=25 leaves per species.

5 LEAF AREA AND LITTER FALL

Many plant traits directly influence the capacity of plants to produce and maintain leaf and root area, and therefore net primary productivity (NPP). In mature stands, plant size and leaf longevity are particularly important. Large plants such as trees support more leaf area than do smaller plants. Evergreen trees, including conifers, support more leaf area than deciduous trees in the same environment. Several traits related to growth rate also strongly influence leaf area and NPP, particularly after disturbance. Small, slow growing plants commonly dominate environments characterised by low availability of water and nutrients (Chapin, 1980; Lambers and Poorter, 1992). These species minimize their resource requirement by retaining leaves for a long time (Berendse *et al.*, 1987). Persistence of leaves in turn requires an anatomy that resists desiccation and/or freezing and a chemistry that deters herbivores and pathogens. These leaves typically have a low specific leaf area (SLA) (thick or dense leaves) and low tissue nitrogen concentration that in turn constrains photosynthetic rate (Reich *et al.*, 1997). Many of these growth related traits are functionally inter-related; others may be linked through common developmental pathways (Chapin *et al.*, 1993).

When plant leaves senesce, they resorb approximately half of their nitrogen and phosphorus pool and very little of the initial carbon pool, regardless of the environment in which thy grow (Chapin and Kedrowski, 1983). Litter from species typical of productive environments, for example, deciduous species typically decompose more rapidly than that from species from less productive ecosystems (e.g. evergreens). In a leaf litter decomposition study conducted in Kerala, consisting of the leaf litter of *Terminalia paniculata, Dillenia pentagyna, Grewia tiliifolia, Wrightia tinctoria* and *Xylia xylocarpa,* it was noted that 90 per cent of the litter decomposed within 3-10 months (Swarupanandan *et al.*, 2001).

The quantity of litter input provides a critical link between NPP and decomposition because at steady state, NPP governs the quantity of organic matter inputs to decomposers. When biomes are compared, heterotrophic respiration is approximately equal to NPP. This means that net ecosystem production (NEP), the rate of net carbon sequestration, is approximately zero regardless of the climate or ecosystem type. This indicates that the quantity and quality of organic matter inputs to soils, as determined by plant traits, are the major determinants of decomposition when ecosystems are compared at steady state. Hence the linkage between NPP and litter decomposition is very important for the survival of an ecosystem.

In this project, we have studied the leaf area and litter fall relations in the moist deciduous forest to understand the rates of litter fall and the capacity of the ecosystem for NPP.

Leaf area in a forest is usually measured as the Leaf Area Index (LAI), which is the ratio of the foliage area to the ground area. The measurement of LAI is of fundamental importance in agricultural and ecological research because LAI is a measure of leaf area, plant growth and productivity. It directly affects the interception and absorption of light by the canopy and it influences the heat balance and evaporation from the landscape.

Materials and Methods

Leaf area index (LAI)

LAI of the study site was taken at monthly intervals by the light interception method using a Canopy Analyser (LAI-2000, Li-COR, Nebraska, USA). Four measurements were done in each of the sample plots and the values were averaged. The precautions according to the manufacturer's instruction manual were followed during the measurements.

The LAI-2000 calculates Leaf Area Index (LAI) and other canopy structure attributes from radiation measurements made with a fish-eye optical sensor. Measurements made above and below the canopy are used to compute canopy light interception at five angles, from which LAI is computed using a model of radiative transfer in vegetative canopies.

Leaf litter fall measurements

For the litter fall measurements, in each experimental sample plot an area of 1.5 m x 1.5 m (2.25m^2) was marked using bamboo splits. The leaf litter, which falls into the marked area were collected at fortnightly intervals and air dried. This is weighed separately and pooled to get the monthly total from each plot. Five leaves taken from the above sample is cut into 10 cm^2 size using a template and weighed separately. From these values the mean sample weight is calculated. The mean values for each plot was used to extrapolate the total litter area, from which the monthly weight was calculated.

Results and Discussion

Leaf area index (LAI)

The LAI variations in the nine sample plots is depicted in Fig. 15. Although they follow the same pattern, there are wide variations in the LAI in different plots. This is due to different combination of species in each plot and the difference in timing for the leaf fall in the different species.

Fig. 15. Monthly variation in LAI in the 9 plots at MDF, Pattakarimbu.

Fig. 16. Mean LAI for different months for the MDF, Pattakarimbu.

The variations in LAI during different months (2004-2005) showed that it started from a higher value (3.36) in August and gradually decreased thereafter up to March (1.57) except a rise (2.89) during December and again an increase was noticed during April (Fig. 16). The LAI was lowest during March and highest (3.60) in June. In Northern parts of India, the leaf renewal occurs between the months of February and June (Newton, 1988), whereas, in the present site it occurred mostly between February and April.

Leaf litter production

Table:4. Species-wise leaf litter production in the sample plots in MDF at Pattakarimbu

Month	**Plots with**			**Dominant species (Based on IVI)**	**Main contributing species during litter collection**
	Maximum	**Minimum**	**Intermediaries**		
September	1	9	6,7,8,5,4,2,3	*T.crenulata,* *T.paniculata*	*T. paniculata*
October	5	1	9,4,2,3,6,7,8	*G.tiliifolia,* *T.paniculata*	*G. tiliifolia*
November	5	1	6,9,7,2,3,4,8	*G.tiliifolia,* *T.paniculata*	*G. tiliifolia*
December	3*	1	9,8,5,4,2,7,6	*X.xylocarpa,* *T.paniculata,* *T.crenulata*	*X. xylocarpa,* *T. crenulata*
January	3*	1	7,4,2,9,6,8,5	*X.xylocarpa,* *T.paniculata,* *T.crenulata*	*X. xylocarpa,* *T. crenulata*
February	7	3	4,2,6,1,5,8,9	*T.grandis,* *D.pentagyna*	*T. grandis*
March	4	3	7,8,9,1,5,2,6	*Xylia xylocarpa*	*Xylia xylocarpa*

* In these plots, most of the leaves fell during the months of December and January irrespective of species. This might be attributed to the commencement of early soil moisture stress due to its higher elevation compared to other plots.

Based on the above table, the dominant species represented in each monthly collection of leaf litter in descending order is as follows: *Terminalia paniculata* > *Grewia tiliifolia* > *Schleichera oleosa* > *Dillenia pentagyna* > *Terminalia bellirica* > *Tectona grandis* > *Terminalia crenulata* > *Xylia xylocarpa.*

In general, taking all the plots together, monthly variation in leaf litter production (m²/ha) was 1989 in November and reached a peak in February (20597) (Fig. 17). The total leaf litter production for the entire year amounts to 10.07 tonnes ha^{-1}, which is very near the value obtained by Swarupanandan *et al.* (2001) for similar MDF in Kerala. The LAI and leaf litter area from the different plots shows an inverse relationship.

Fig.17 . Average leaf litter production in the nine sample plots expressed month wise (m^{2}plot^{-1}).

The month-wise average production of leaf litter in each of the plot is given in Fig. 18. The plot-wise production of leaf litter in the nine sample plots is given separately in Fig. 19. The variations noticed in each plot are due to the different combinations of species and the interactions between them. This graph also indicates the variations that occur within an MDF at different locations with regard to leaf fall. Species associations and their interactions are probably responsible for such behaviour. The ecological significance of such interaction need further studies.

LAI vs. leaf litter production

The relation between LAI and leaf litter production plotted in Fig. 20 shows that there is a linear relation between the two. Although the correlation coefficient is not very high, which may be due to some experimental error, the non-invasive and fast method of LAI measurement can be very well used to estimate the litter fall in a MDF. The relationship between mean LAI and mean monthly leaf litter production showed that it assumes an R² value of 0.6732.

Specific leaf area (SLA)

Specific leaf area (SLA), the ratio of leaf area to leaf dry matter (expressed as $m^2 kg^{-1}$) is an important ecological parameter. It is considered as a good indicator of the strength of photosynthetic tissue which can be modified by leaf age, environmental conditions especially temperature, water, irradiation and nitrogen supply. Leaf area and leaf mass are closely related to light interception, photosynthesis, transpiration, growth rate and furthermore to NPP. SLA is used in many ecological models to calculate either leaf area or leaf dry weight. In this study, our aim was to determine the changes of SLA during the maturation of leaf in a few dominant tree species of the MDF.

The variations in SLA of three-age classes, viz., very young, young and mature leaves of seven MDF species are presented using ANOVA. The results of the study are given in the Table 5. Among the three maturity stages (very young, young and mature) the mean SLA was maximum in very young leaves in the case of *Holarrhena pubescens, Dalbergia latifolia, Emblica officinalis* and *Terminalia paniculata* while it was in young leaves in *T. bellirica, X. xylocarpa* and *T. crenulata*. A smaller value for SLA indicates thick or dense leaves. The lowest SLA values noted in mature leaves of all the seven species compared to their juvenile can be attributed to high drymatter accumulation in mature leaves when compared to very young as well as young leaves. The study also showed that mean SLA was significant at 1% level in all the species except *T. paniculata* in which, it was not significant. Among the mature leaves measured, *T. paniculata, E. officinalis* and *D. latifolia* showed the lowest values for SLA compared to other species. Low values for SLA indicates low tissue nitrogen content and this in turn constrains photosynthetic rate (Reich *et al.,* 1997).

Fig. 18 . Monthly averages of leaf litter production expressed plot-wise ($m^2 plot^{-1}$)
Fig. 19 . Plot-wise averages of leaf litter production expressed month-wise ($m^2 plot^{-1}$)

Fig. 20. Relation between leaf litter production regressed against LAI showing the correlation coefficient.

Table.5. SLA values ($m^2 kg^{-1}$) measured in some dominant species of the MDF.

Species	**Very young**	**Young**	**Mature**
Terminalia bellirica	$18.7^{\mathbf{B}}$	$22.7^{\mathbf{A}}$	$17.7^{\mathbf{C}}$
Holarrhena pubescens	$21.3^{\mathbf{A}}$	$20.6^{\mathbf{B}}$	$14.3^{\mathbf{C}}$

Xylia xylocarpa	20.9^{B}	30.1^{A}	20.0^{C}
Dalbergia latifolia	27.0^{A}	22.6^{B}	11.4^{C}
Emblica officinalis	15.5^{A}	14.9^{B}	9.6^{C}
Terminalia paniculata	13.6^{A}	11.3^{A}	9.8^{A}
Terminalia crenulata	21.2^{B}	25.0^{A}	19.9^{C}

Note: Values with the same alphabet as the superscript are not significantly different within a species.

It has been shown that SLA reflects previously captured resources and indicates that species with high SLA exhibit high productivity (Poorter and Van der Werf, 1998; Van der Werf *et al.*, 1998; Wilson *et al.*, 1999). Therefore, species with high SLA do better in resource-rich environments while species with low SLA do better in resource-poor environments. Many of these growth related traits are functionally inter-related; others may be linked through common developmental pathways. Thus it can act as a guide in determining the possible success of certain species over others in an ecosystem. It may be noted that *Xylia xylocarpa*, which is having the highest SLA value, is the species showing the maximum IVI in the present study site.

6

TREE TRANSPIRATION

Evaporation from forests is studied within the research fields of forest hydrology, meteorology, and plant ecology. According to their specific objectives, information on evaporation and transpiration is provided on various temporal and spatial scales based on different methodology, which may be broadly classified into three – water balance methods, microclimate methods and ecophysiological methods. Conceptual frameworks of evaporation processes regarding vegetation as a "big-leaf" are helpful to understand controls on evaporation and transpiration such as available energy, vapor pressure deficit of the air, aerodynamic and stomatal conductance (Monteith, 1965). However, the average stomatal conductance of a whole canopy (canopy conductance, g_c) is not easily determined, because it depends on species physiology, seasonal or site specific adaptations of the vegetation, distribution of nitrogen within the canopy, and the canopy structure (Field and Mooney, 1986; Shuttleworth, 1989; Monteith, 1995; Whitehead, 1998). Therefore, g_c is often empirically estimated from evaporation measurements (Kelliher *et al.*, 1995).

The relationships between evaporation components and forest structure are difficult to establish. These shortfalls may be overcome by interdisciplinary ecosystem research focusing on investigations of both plant and soil properties as well as on material fluxes between soil, vegetation and atmosphere (Tenhunen *et al.*, 1998; 2001b). Forest structure refers to the number and size of plant parts or individuals as well as to age and species composition (Oliver, 1992). In a tropical moist deciduous forest, the association of species and their interaction with the physical environment essentially determine these factors. In order to describe relationships between tree structure and tree water use, sapflow measurements became a key-instrument in forest ecosystem research bridging leaf-to-stand level processes and monitoring water fluxes through trees in the long-term (Granier *et al.*, 1996a; Köstner *et al.*, 1998b). It was shown that tree sapflow rates scaled to the stand level plus evapotranspiration from soil and understory agreed with water vapor fluxes measured above the forest canopy by eddy-correlation techniques (Diawara *et al.*, 1991; Kelliher *et al.*, 1992; Köstner *et al.*, 1996b; Granier *et al.*, 1996b). Sap flow measurement is probably the only technique providing water fluxes at the whole-tree level under natural atmospheric conditions, discerning tree water fluxes from other sources, and directly enabling its analysis with respect to tree species, size and age.

Principle and method of sapflow measurement

At appropriate time-scales (≥1 day) changes in tree water storage are low and water flux through the sapwood (water conducting tissue or xylem) equals tree canopy transpiration (cf. Schulze *et al.*, 1985). Depending on the water conducting system of species and on forest structure, various approaches can be used to scale from individual measurements in trees to the stand. In most cases tree sapwood area, which is closest related to water transport in the tree, is used as a structural scaling factor. From sapflow density (flow rate per sapwood area) of individual sensors and the related sapwood area (A_s), canopy transpiration (E_c) is determined as follows:

$$E_c=J_{\mathrm{mean}}*\mathrm{A}_{\mathrm{s}}^{\text{-stand}}, \qquad (2)$$

where, J_{mean} = mean sapflow density of sample trees (kg m^{-2} s^{-1}) and $\mathrm{A}_{\mathrm{s}}^{\text{-stand}}$ = cumulative sapwood area per ground area (m^2 m^{-2}).

In homogenous stands, the coefficient of variation (CV) for estimates of $\mathrm{J}_{\mathrm{rnean}}$ is usually less than 15% using approximately 10 sample trees (Kostner *et al*., 1996b) but variation may increase in older less homogenous stands requiring a larger number of sample trees (Kostner *et al.*, 1998a). Estimates of $\mathrm{A}_{\mathrm{s}}^{\text{-stand}}$ can be derived with relatively high accuracy from regression curves between stem diameter at breast height (dbh) and sapwood area of a subsample of trees applied to all trees within the patch (cf. A1sheimer *et al.*, 1998). In forest stands composed of different canopy layers or tree species, *Ec* is summed up from several equations of type (2) representing different subsamples E_{ci} *(i* = layers, species, etc.) of the patch. Scaled sapflow rates provide an independent estimate of tree canopy transpiration as compared to total water vapor flux above the forest (Granier *et al.*, 1996a, Kostner *et al.*, 1998b).

The total water vapor transfer conductance (g_t) accounting for conductances from height of the "average" stomata in the tree canopy to the height of measurement of vapor pressure deficit of the air *(D;* Thorn, 1972) can be estimated from *Ec* (Kostner *et al.*, 1992):

$$g_t=E_c/D*P_w*G_v*T_K \qquad (3)$$

where, *Ec* = canopy transpiration (mm s^{-1}); D = vapor pressure deficit of the air (kPa), *Pw* = density of water (998 kg m-3), *Gv* = gas constant of water vapor (0.462 m^3 kPa kg^{-1} K^{-1}), T_K = air temperature (Kelvin).

The total conductance includes components of both stomatal (g_c) and aerodynamic conductance (leaf boundary layer and eddy diffusive conductance, g_a). Typically, g_a is more than an order of magnitude higher than g_c in rough forests, where g_t approximates g_c ($\mathrm{l}/g_t = \mathrm{l}/g_c + \mathrm{l}/g_a$). Estimates of g_c derived from sapflow rates range within leaf-level estimates determined by porometer (Kostner *et al.*, 1992) and are comparable to model-based estimates of g_c derived from canopy gas exchange (Kostner *et al.*, 1998a).

Since all the water transpired by a tree must pass through the stem (tree trunk), this is a convenient site for measurement. There is no disruption to either the root or crown, and relatively minor perturbation to the stem. Heat is a convenient marker, being non-destructive at the levels used, completely removed by the transpiration stream, has none of the environmental disadvantages of radio-isotopes, and is easily monitored.

Superficially a simple technique, quantification of heat pulse velocity to sap velocity, and in turn to total flow rates has required a fuller understanding of the physics involved in flow, and this has developed slowly in the literature.

As early as 1932, the German physiologist B. Huber used a heat pulse from a resistance wire, sensed by a single thermocouple downstream in the stem of a transpiring plant. Uncertainty in interpretation of the resulting rise and fall in temperature at the thermocouple led to development of the so-called `compensation method' (Huber and Schmidt, 1937), using thermocouples above and below the heat source. If the downstream distance to the thermocouple was larger than the upstream distance, this effectively separated the movement of the heat pulse into its component mechanisms of conduction and mass movement or convection.

Conduction caused the closer, upstream thermocouple to warm first. As the heat pulse was carried up the tree, however, a position midway between the thermocouple to thermocouples was obtained and then passed; at that point the temperature of the thermocouples was the same. Thus if the thermocouples were joined in series with a measurement device, the output became first of one sign, then passed through the balance point to the other sign. The time taken from initiating the pulse till the signal returned through the balance point, together with the distance travelled by the pulse from the point of initiation to the point midway between the sensors, gave the heat pulse velocity.

Difficulties in interpretation remained, since the apparent heat velocity was clearly less than the actual sap velocity in the vessels.

Marshall (1958) provided a better physical basis, by pointing out that the heat pulse moved as if the sap and woody matrix were a single medium, heat interchanging freely between sap and wood. An analogous situation exists with chromatography - the dye front moves more slowly than the solvent. Heat pulse velocity was shown to be a function not only of sap velocity, but also the ratios of
(i) lumen conducting area to total sapwood area
(ii) density of sap to that of wet wood
(iii) specific heat of sap to that of wet wood.
Subsequent work showed that sap velocity derived using Marshall's theory was still less than actual sap velocity, and most workers simply relied on direct calibration.

R L Swanson finally identified the probe implantation wound as a primary source of error. The wound caused a violation of Marshall's assumption of homogeneity within the stem, effectively adding more 'inert' or non-moving material to slow the heat pulse. Swanson and Whitfield (1981) conducted an elegant two-dimensions numerical solution to the problem, and provides tables for wound corrections based on particular probe spacings and construction.

Materials and Methods

Three experimental plots with four different species combinations were chosen for the sap flow measurements in the MDF location described in Chapter 2. They are shown in

Table 6. The exact age of the individual trees was not known because they occurred in the natural forests. However, taking girth as a strong criterion, the entire tree samples except *W. tinctoria* and *D. pentagyna* were more than 30 years old.

The sap flow system used in the present study (Heat Pulser, Edwards Industries, New Zealand) is based on all three of the major advances in this field: i.e., the compensation system of Huber to produce heat pulse velocities, Marshall's analysis to convert to sap velocities, and Swanson's analysis of the effect of wounding. Verification of this system has involved direct comparisons with excised stem sections using forced flow, the cut-off tree technique of J Roberts (1977), weighing lysimetry in both single tree and forest situations, and comparisons with micrometeorological estimates of transpiration using the Penman-Monteith equation.

Heat pulse velocities are measured using the compensation technique of Huber and Schmidt (1937) and Swanson (1974). Two thermistors, accurately placed 10 mm above and 5 mm below a 2 mm diameter tube heater are connected in a Wheatstone bridge configuration. To make a measurement, a short (typically 0.5 to 1 s) electrical pulse is applied to the heater. The heat pulse so produced is conducted onwards from the tube heater in all directions, reaching the lower (closer) thermistor first and throwing the bridge out of balance. As the sap flow carries the heat pulse upwards however, the bridge returns through the balance point at a time when the heat pulse is midway between the thermistors.

Table. 6. Tree trunk dimensions of the species subjected to sapflow measurements in three different plots.

The heat pulse velocity is calculated from the time taken for the pulse to travel the distance of 2.5mm, i.e., the distance between the heater and a point midway between the thermistors.

Implantation of the probes

Four trees of different species in the MDF were selected at a time for measurement of the sap flow velocity. The stem should be regular and not flawed because of damage, also avoiding trees with prominent fluting. The rough outer bark was smoothened with a rasp so that a good over-bark measurement of circumference could be made. If the bark was very thick - say more than 5 mm - then consideration was given to reducing this thickness at the sites of implantation. This is because accurate assessment of probe/heater separations are essential, and implantation through massive bark layers make this difficult to attain. A ring of masking tape was applied around the smoothened portion of the bark for conveniently marking the implantation sites. First mark was made due north. Carefully measured the circumference, recording it on the form - decided the number of probes to be used, typically this will approximate one per 100 -150 mm of circumference, however, we invariably used four probe sets per tree. Each probe site was numbered consecutively. The depth of the probe was decided based on the depth of the sapwood, which was ascertained by core sampling. The shallowest was about 5mm below the cambium. The deepest probe was up to 50 mm. Most trees sampled had sap wood depth not more than 50 mm. Intermediate depths were chosen based on the depth of the sapwood. However, in most of the species the depth chosen were 5, 15, 25 and 40 mm.

A jig was strapped firmly to the tree at the first site, ensuring it is oriented tangentially to the tree so the drills will enter radially. Using a 1.80 mm long-series drill and portable electric drill three holes were drilled to a depth approximately 15 mm below the nominal probe depth. Thus the total drill depth below the surface of the jig will include the jig thickness (20mm) plus bark thickness plus nominal probe depth plus 15 mm. The drill bit was cleaned frequently to ensure that the drill could move freely in and out of the hole and no debris was allowed to get trapped in the hole. Three sets of holes were made for each probe set. The distance between the holes in a set was measured accurately using three stainless steel tubes of the same diameter as the hole. They were inserted gently into the set of holes. A card was gently placed against the tubes starting closest to the tree and rolling the card slightly so the tape makes contact without changing the orientation of the blank probes. Using a scalpel and fresh blade as a marker, both sides of each blank probe was traced so that the blade point is held gently against the probe. Six very thin lines will be formed, easily distinguished under the scaled magnifier using back-lighting. The scaled magnifier was used to make measurements between the three holes using a standard procedure.

The heater elements were now implanted. The heater and the sensors were greased for easy insertion into the hole. In extreme cases of difficulty in insertion the hole was broached using a 1.85 drill. The temperature probes were temporarily marked to the required depth below the cambium plus the bark thickness. All leads were finally strapped to the trunk to avoid strain on the probes. The probes were now connected to it's corresponding channel on the logger. Protection from direct solar radiation was given by wrapping the tree trunk gently with aluminium foil to form a large bulge, constrained top and bottom with tape. The entire set up was left in the field for 2-3 weeks depending on the field conditions. At the end of the specified period, the data from the data logger was downloaded in the field using a laptop computer and the raw data was subjected to analysis using the standard software provided by the manufacturer.

Results

Sapflow measurements taken at four depths in the different species at different seasons are given in the following pages. The measurements were done during the dry period (premonsoon period), the monsoon period and the post monsoon period. The same trees were repeatedly used for measurements irrespective of the seasons. As may be seen from phenological measurements and leaf area measurements, there are wide variations in the leaf area index during the above seasons, at the same time, the soil moisture also differs widely due to the monsoonal activities. The hourly rate of sap flow shows that leaf area is the most important determinant regulating the water loss due to transpiration (Fig. 21 – 24). During the dry period, it may be noted that the species that are totally leafless, *Bauhinia malabarica, Dillenia pentagyna* and *Sterculia guttata* show negligible water flux through the tree trunk. Whereas, species such as *Gmelina arborea* and *Terminalia paniculata*, which retained most of the leaves during this period transpires at relatively high rates of 30-45 litres h^{-1} during this season. The VPD measurements done simultaneously with the sap flow measurements show that all the species have a marked decrease in sapflow during midday when the VPD reaches values greater than 1.5 kPa. This is a very important water conserving mechanism, which prevent excessive water loss from the forest. This decrease was most apparent in *Gmelina arborea,* which transpired at very fast rate and is one of the fast growing species in the MDF (Fig. 23). However, during the beginning of the monsoon season, when the VPD is rather low, this decrease in sap flow did not occur in *Tectona grandis* and *Sterculia guttata,* which transpired at relatively high rates (Fig. 24). Since the soil moisture will be high during this season, the atmospheric control on transpiration was less.

Fig. 25 shows the relation between daily sap flow plotted against daily average VPD in all the species and all the plots put together. It shows a highly scattered relationship although there is a trend towards reduction in sap flow rates after the VPD reaches approximately 1.0 kPa. The scatter in the relation is mainly because of the insignificance of plant characteristics on transpiration when the soil moisture is relatively high. Surface conductance, which describes the potential of leaf and soil surfaces to lose water, is surprisingly insensitive to vegetation properties under moist conditions (Kelliher *et al.*, 1995; Chapin *et al.,* 2002). As soil moisture declines, stomatal conductance and associated changes in surface conductance become increasingly important controls over evapotranspiration. Evapotranspiration tends to be greatest in productive ecosystems.

Fig. 26 shows the daily variations in hourly sap flow rates at Plot 1 for different seasons. It is noteworthy that *Gmelina arborea* is the only species transpiring at maximum rates during the dry period. This is because of the retention of the leaves on this tree during this season, the leaf fall occurring more in the post monsoon period. This is indicated by a reduced sap flow rate in this species during the post monsoon period. It may be also noted that *Wrightia tinctoria*, which is an understorey species, transpires at a very reduced rate throughout the different seasons. In Plot 2, all the four species have a very negligible transpiration during the dry period because all of them are leafless during this season. However, in the early monsoon period, *Tectona grandis* and *Sterculia guttata*, both of which are fairly fast growing species show relatively high rates of sap flow (Fig. 27). The other two species, *Dalbergia latifolia* and *Cleistanthus* show much reduced transpiration in all the different seasons. They are slow growing species. In Plot 3, the early summer measurements of 2006 showed that *Terminalia paniculata* transpired much higher when all the other trees were showing negligible transpiration (Fig. 28). Hence this measurement was repeated in late summer of 2007 when the above species was almost leafless. The water use at this time was very low in *T. paniculata*. The postmonsoon transpiration in this species was comparatively lower. *Dillenia pentagyna* showed a rather idiosyncratic behaviour in transpiration during the different seasons, except in summer of 2006. The wood of this species is very soft; hence there could be some problem with wound injury caused by drilling for insertion of the sensors.

The cumulated daily water use by different species in the three plots during the three seasons is shown in Fig. 29- 38. The temperature and VPD (averages for the day) are also shown along with the sap flux data. *Terminalia paniculata, Tectona grandis* and *Gmelina* *arborea* were the species that consumed the maximum amount of water on a daily basis. Although some of the values may look incredible, still it shows the ability of some of the tropical species to take up relatively high amounts of water from the soil and therefore their ability to give out latent heat. Much of the water that is coming as rainfall is actually lost through evapotranspiration.

The sap flux per unit cross sectional area of the sapwood is also shown in Fig. 29-38. It is worth noting that there is no uniformity between species with regard to the flow. This makes any simple model to work out the stand transpiration a difficult proposition. The variability in flow in different species could be due to the quantity of leaves supported on the tree or the rooting depth of the tree making it variable with regard to exploring for water resources in the soil and also due to shading of the canopy by other dominant species.

Fig. 21. Hourly sapflow (integrated over four depths) in the tree species in Plot 3 of the MDF at Pattakarimbu showing the diurnal variations. VPD, which has been measured simultaneously, is also shown. A midday closure in *Terminalia paniculata* with the increasing VDP is apparent. All the other three species are showing very low sapflow rates because they were in the leafless state.

Fig. 22. Hourly sapflow (integrated over four depths) in the tree species in Plot 2 of the MDF at Pattakarimbu showing the diurnal variations. VPD, which has been measured simultaneously is also shown. A midday closure in all the three species with the increasing VDP is apparent.

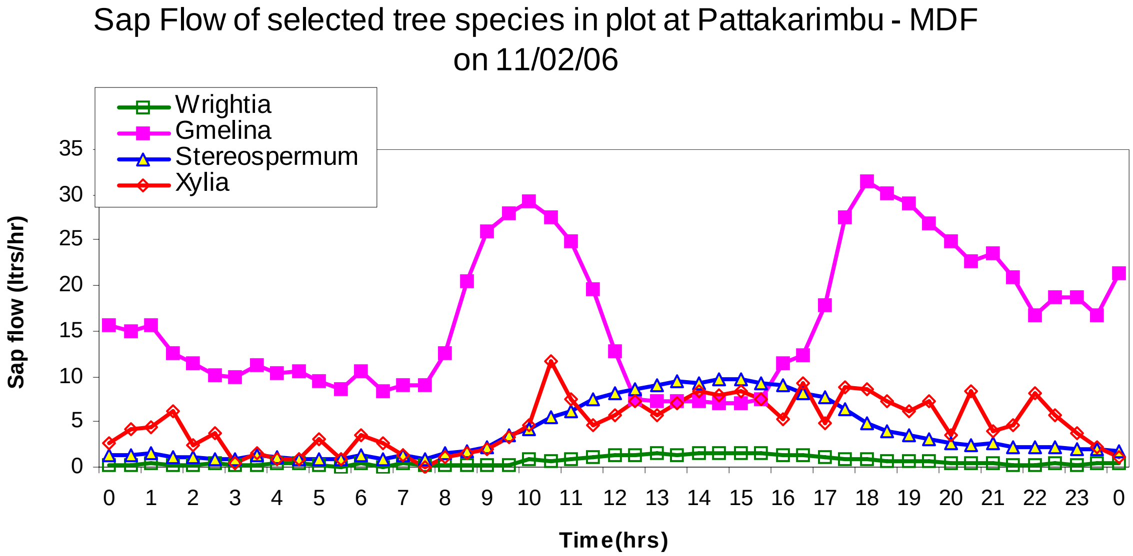

Fig. 23. Hourly sapflow (integrated over four depths) in the tree species in Plot #1 of the MDF at Pattakarimbu showing the diurnal variations. A midday closure in only *Gmelina arborea* is apparent in response to increasing VDP. The other three species seem to be transpiring at lower rates because of the reduced number of leaves on them during this season.

Fig. 24. Hourly sapflow (integrated over four depths) in the tree species in Plot #2 of the MDF at Pattakarimbu showing the diurnal variations. No midday depression in transpiration is apparent in any of the four species because the VPD is very low during this season as the monsoon begins. The plant responses are less when the soil moisture is high.

Fig. 25. Daily sapflow from the different species in the MDF plotted against the daily average VPD. It may be noted that there is a general increase in sapflow rates till the VPD reaches approximately 1.00 kPa beyond which there is a sharp decline in the sapflow rates.

Fig. 26. Sapflow (integrated over four depths) through the trunk at half-hourly intervals..

Fig. 27. Sap flow (integrated over four depths) through the trunk of different tree species in Plot 2 recorded at half-hourly intervals during different seasons of the year.

Fig. 28. Sapflow (integrated over four depths) through the trunk of different species measured in Plot #3 during summer season of 2006 and 2007.

Fig. 29. Daily water flux at Plot #1 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 30. Daily water flux at Plot #1 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 31. Daily water flux at Plot #1 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree.

Fig. 32. Daily water flux at Plot #2 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 33. Daily water flux at Plot #2 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 34. Daily water flux at Plot #2 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 35. Daily water flux at Plot #2 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 36. Daily water flux at Plot #3 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 37. Daily water flux at Plot #3 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

Fig. 38. Daily water flux at Plot #3 of MDF at Pattakarimbu. (a) Daily water flux for a unit sap wood conducting area, (b) Total daily water flux for the tree, and (c) Atmospheric temperature (line graph) and the VPD (histogram) measured simultaneously with the sapflow measurements.

7 WATER RELATIONS AND STOMATAL CONDUCTANCE

Most living plant material is hydrated with a water content ranging from 70 to 90 per cent of the fresh weight. This water is not stationary, it is constantly on the move. As water evaporates into the atmosphere, usually through transpiration, more water is drawn into the plant from the soil. Plant materials can lose many times its total water content per hour in the form of water vapour. This evaporating water is subjected to negative pressure in the xylem conduits and cell walls. The sap tensions increase or decrease in response to environ mental changes. These fluctuations can take place even within minutes or seconds. This is usually measured as water potential (Ψ). The water potential of pure water is considered as zero at normal temperature and pressure. When negative pressure is applied, as it usually happens in xylem conduits through transpiration pull, the water potential becomes negative. Mostly the xylem conduits of plants are under negative pressure, hence the water potential of plants in general is negative. The leaf Ψ values depend very much upon the water availability in the soil, especially during the predawn time (Crombie *et al.*, 1988). Hence it is a good indicator of the water availability in the soil, as well as water stress in plants.

In this study, we have measured the water potential of the trees during the dry season to examine the magnitude of water stress for trees in a MDF. The seedlings were measured for stomatal conductance to know the stomatal functioning in the seedling stage, which will indicate the adaptation of the plants in the seedling phase to water stress conditions.

Fig. 39. Stomatal conductance measurements dominant or subdominant trees in the using a Steady State Porometer in seedlings in MDF.

Materials and Methods

Seven tree species, namely, *Wrightia tinctoria, Mitragyna parviflora, Xylia xylocarpa, Grewia tiliifolia, Terminalia crenulata, Terminalia crenulata, Tectona grandis* were chosen for water potential measurements. Except for *Wrightia tinctoria*, all the other species were MDF. Predawn leaf water potentials were measured using a Scholander type pressure chamber (Soil Moisture Equipment Corporation, Ohio, USA). The leaves were collected in the early morning in plastic bags and immediately subjected to pressure chamber measurements using all precautions mentioned elsewhere (Kallarackal and Somen, 1997). The measurements were done monthly during three months starting from February to April when the soil dryness was maximum.

Stomatal conductance in seedlings of several species were measured using a Steady State Porometer (LI-1600, Li-COR, Nebraska, USA). The measurements were done in the dry season twice daily, first one in the morning and second one at midday or early afternoon.

Results and discussion

Predawn water potentials measured in seven tree species in the MDF is given in Table 7.

Fig. 40. Stomatal conductance values in the seedlings of various species in the MDF at Pattakaribu. 2-3 measurements were made in a day. Note the lower midday values in most specie indicate stomatal closure.

The values for February are in the range of –0.45 to –0.60 MPa (Megapascals). However, the water potential goes up (less minus value) in March after a couple of summer showers in the study site as may be noted in the table. With more frequent showers in April, it can be seen that Ψ values go further up. Compared to the predawn water potentials of exotic species such as eucalypts, acacia, etc., the predawn values shown by the MDF species are much higher than them (Kallarackal and Somen, 2008). In the above exotic species, the Ψ values in the rang of –1.5 to 2.0 MPa have been recorded during the dry period in

Table 7. Predawn water potential (Ψ) (MPa) of MDF tree Species at Pattakarimbu

Species Name	**Febuary**	**March**	**April**
Wrightia tinctoria	-0.45	-0.32	-0.2
Mitragyna parviflora	-0.6	-0.2	-0.115
Xylia xylocarpa	-0.5	-0.19	-0.11
Grewia tiliifolia	-0.58	-0.155	-0.155
Terminalia crenulata	-0.56	-0.4	*
Terminalia paniculata	-0.43	-0.24	-0.105
Tectona grandis	-0.5	-0.12	-0.115

*leaves not available for measurement

Kerala. This shows that the soil of the MDF was retaining reasonably good amount of water in the soil or else their rooting depth was sufficiently deep to exploit the water. From some previous studies (Davies and Becker, 1996), it appears that the MDF trees are relatively shallow rooted. Therefore, it seems that the fallen litter in the MDF could be acting as a good mulch to prevent much evaporation of water from the soil.

Stomatal Conductance

Stomatal conductance (g_s) measured in seedlings of various species in two plots at MDF Pattakarimba is given in Fig. 40. In general, the conductance values do not cross more than 300 mmol m^{-2} s^{-1}. In almost all the species, there is partial closure of the stomata from midday. The maximum g_s values are shown before noon. This is an adaptation for most of the native species to prevent water loss from the plant during the warm sunny days in the tropics.

8

LIGHT AVAILABILITY AND PHOTOSYNTHETIC EFFICIENCY

Solar radiation is a directional resource that governs the energy input into ecosystems. The albedo (shortwave reflectance) of the vegetation-soil surface determines the proportion of incoming radiation that is absorbed, which in turn influences the quantity of heat that enters the soil and the energy available to drive water loss from the ecosystem through transpiration and soil evaporation. The energy that reaches the land surface is partitioned between sensible and latent heat fluxes. Sensible heat directly warms the air in the ecosystem, whereas latent heat flux transfers heat and water vapour to the atmosphere. When water vapour condenses, it gives rise to precipitation. Rough canopies, as in MDFs, efficiently carries water vapour and heat from the ecosystem to the atmosphere, minimizing surface build-up of heat and water vapour. Thus the forests have an important control on the microclimate of the landscape.

Apart from the above, light plays a very important role in determining the photosynthetic productivity of the ecosystem. The visible wave lengths, which are important in photosynthesis, has to penetrate through the canopy cover as transmitted light and also as direct light in the form of sun flecks. What percentage of the light reaches the ground level will depend on how deep is the canopy cover. The seedlings that are regenerating at the ground level will need to harvest this light for their growth. In this study we have made an attempt to understand the light availability at the ground level in the MDF under study.

Chlorophyll (Chl) *a* fluorescence, though corresponding to a very small fraction of the dissipated energy from the photosynthetic apparatus, is widely accepted to provide an access to the understanding of its structure and function. There is a general agreement that at room temperature Chl *a* fluorescence of plants, in the 680-740 nm spectral region, is emitted mainly by Photosystem (PS) II and therefore, it can serve as an intrinsic probe of the fate of its excitation energy (*see review by* Govindjee, 1995). Both the spectra and the kinetics of Chl *a* fluorescence have proven to be powerful, non-invasive tools for such investigations. The derivation of the links between the biophysics of the photosynthetic apparatus and the fluorescence signals and their analytical formulation is based on the Theory of Energy fluxes in Biomembranes (Strasser 1978, 1981) and on the basic concept that the fluorescence yield of PS II is determined by the state – open or closed – of the reaction centre (RC). The great advantage of this method is that the analysis of strong actinic light induced fluorescence rise kinetics O-J-I-P, the so called JIP-test can be applied at any physiological state and for the study of any state transition. Several parameters are derived from this analysis, which are based on kinetic equations. The result analysis is also made simple by the introduction of a derived parameter named 'Performance index' which will give an overall idea on the entire analysis.

The polyphasic Chl *a* fluorescence rise is widely accepted to reflect the accumulation of reduced Q_A (i.e. the RCs' closure), which is the net result of Q_A reduction by PS II and Q_A reoxidation by PS I. It is assumed that under normal conditions Q_A is completely oxidized in the dark, i.e. all RCs are open, and the fluorescence signal at the onset of illumination is F_0. The maximum fluorescence intensity F_p' depends on the achieved oxidation-reduction balance and acquires its maximum possible value, F_M, if the illumination is strong enough to ensure the closure of all RCs. A lot of information has been obtained during the last seventy years from the fluorescence transient (see chapters in Govindjee *et al.*, 1986; Krause and Weis, 1991; Govindjee, 1995). Transients recorded with high time-resolution fluorimeters, e.g. with the PEA-instrument (or its recent version, the Handy-PEA), have provided additional and/or more accurate information (Strasser and Govindjee, 1992a, 1992b; Strasser et ai., 1995), namely a precise detection of the initial fluorescence F_0 even in the presence of DCMU, of the initial slope - which offers a link to the maximum rate of primary photochemistry per RC-and of the amplitude and appearance time of the intermediate steps. Moreover, the fully digitized fluorescence kinetics allows further detailed analysis, e.g. different normalizations, calculation of kinetics differences as well as of time-derivatives.

All oxygenic photosynthetic materials investigated so far using this method show the polyphasic rise with the basic steps O-J-I-P, with minor differences among different phenotypes. The shape of the O-J-I-P transient has been found to be very sensitive to stress caused by changes in different environmental conditions, e.g. light intensity, temperature, drought, atmospheric C02 or ozone elevation and chemical influences (Srivastava and Strasser, 1995, 1996, 1997; Tsirnilli-Michael *et al.*, 1995, 1996, 1999, 2000; Van Rensburg *et al.*, 1996; Kruger *et al.*, 1997; Ouzounidou *et al.*, 1997; Clark *et al.*, 1998, 2000; Force *et al.*, 2003), as well as by senescence (Prakash *et al.*, 2003).

A quantitative analysis of the O-J-I-P transient has been introduced (Strasser and Strasser, 1995) and further developed (for reviews, see Strasser *et al.*, 1999, 2000), called as the 'JIP-test' after the basic steps of the transient, by which several selected phenomenological and biophysical- structural and functional - parameters quantifying the PS II behavior are calculated. The JIP-test, which we used in this study, has proven a very useful tool for the *in vivo* investigation of the adaptive behaviour of the photosynthetic apparatus and, especially, of PS II to a wide variety and combination of stressors. Hence, the JIP-test can provide an access to the ‘vitality' of a photosynthetic sample.

Material and Methods

A line quantum sensor (LI-COR, Nebraska, USA) connected to a Campbell Datalogger (21X, Campbell Scientific, Ohio, USA) was used for collecting light availability at the ground level in the MDF. A similar set up with a point quantum sensor was kept in an open area adjacent to the MDF to collect the open radiation. Both the dataloggers were programmed to collect data at hourly intervals, logging data every 30 seconds. The position of the line quantum sensor was changed every day to account for the variability within the canopy.

Chl *a* fluorescence of the various seedlings growing at the ground level of the MDF was measured in the field itself. Three plots were chosen for the measurements to get most of the representative species. A portable fluorometer (PEA-Plant Efficiency Analyser, Hansatech Instruments, King's Lynn, Norfolk, UK) was used for measurements. Sample leaves from each species were dark adapted for 10-15 min before the measurements and then illuminated with actinic light (2000 µmol m^{-2} s^{-1}, 650 nm peak wave length) for 2 seconds provided by an array of six light emitting diodes focused on a circle of 5 mm diameter of the sample surface. This was repeated 2-3 times in a day. For evaluating the fluorescence induction transients, the Biolyzer v.3.0.6 software (developed by Ronald Rodriguez in the laboratory of Bioenergetics, University of Geneva) was used.

Results and Discussion

Fig. 41. Measurement of PPFD in the open (♦) and underneath (■) the canopy of the MDF using a line quantum sensor. Note the variability with the measurements made in the dry period.

During the dry period, when the light measurements were done for several days, the photosynthetic photon flux density (PPFD) in the open reached more than 1500 µmol m^{-2} s^{-1}, at the same time, at the ground level the PPFD was more than 1000 µmol m^{-2} s^{-1} (Fig. 42). During this season many trees were leafless in the canopy. In contrast to this, when the measurements were made in the post monsoon season, the open values were in the range of 1000 to 1100 µmol m^{-2} s^{-1} mainly due to cloud cover. At this time, the PPFD at the ground level were in the range of 300 to 400 µmol m^{-2} s^{-1} (Fig. 41). Thus much more light is available in the ground level during the dry period. This can heat up the soil surface and water loss from the upper layers can be considerable. However, to a great extent water loss due to evaporation from the soil surface is prevented by a mulch of fallen litter in the MDF during this season. Measurements made elsewhere in the Western Ghats showed that only 10 per cent of the light reached the forest floor during November, when the canopy cover was 94 per cent. Similar measurements in March showed that 54 per cent of the light fell on the forest floor when the canopy opening was increased to 59

Fig. 42. Measurement of PPFD in the open (●) and underneath (■) the canopy of the MDF using a line quantum sensor. Note the variability between the different days and at different positions in the forest, when the open measurements show very similar readings.

per cent (Lee, 1989). It was also noticed by the above author that there were wide differences in the spectral quality of sunlight – the November values had R:FR ratio of 0.30, whereas the March values were identical to that of sunlight in the open, namely, at 1.10. This means that most of photosynthesis could be occurring in the dry period, although there is possibility for photoinhibition also in the seedlings of certain species.

Fig. 43. Typical OJIP curves resulting from the Chlorophyll fluorescence measurements on the leaves of the plants.

Table 9. PLOT-2: Fv/Fm values during morning and afternoon are shown. PI (Avg.) values given in parenthesis.

Species	9.25A.M.	11A.M.	2.10P.M.
Strychnos nux-vomica	0.80 (65)	0.80 (73)	0.80 (48)
Dillenia pentagyna	**0.75 (8)**	**0.75 (17)**	**0.73 (11)**
Pterospermum reticulata	0.73 (37)	0.75 (49)	0.57 (16)
Bauhinia	0.80 (114)	0.80 (114)	0.76 (57)
Cleistanthus collinus	**0.75 (29)**	**0.77 (37)**	**0.77 (32)**
Bambusa bambos	0.78 (43)	0.79 (50)	0.76 (26)
Schlechera oleosa	0.80 (81)	0.78 (56)	0.73 (27)
Naringi crenulata	**0.79 (50)**	**0.79 (50)**	**0.79 (51)**
Xylia xylocarpa	**0.75 (27)**	**0.75 (31)**	**0.76 (20)**
Terminalia paniculata	0.81 (94)	0.79 (69)	0.79 (66)
Mallotus philippensis	**0.76 (34)**	**0.75 (30)**	**0.77 (46)**
Holarrhena pubescens	0.74 (19)	0.71 (17)	0.70 (17)
Macaranga peltata	0.75 (24)	0.79 (44)	0.73 (12)

Table 8. PLOT-1: Fv/Fm values during morning and afternoon are shown. PI (Avg.) values given in parenthesis.

Species	11A.M.	3P.M.
Holarrhena pubescens	0.77 (46)	0.72 (22)
Naringi crenulata	0.80 (44)	0.76 (29)
Cleistanthus collinus	0.77 (41)	0.76 (40)
Bauhinia purpurea	0.81 (68)	0.78 (70)
Bambusa bambos	0.79 (44)	0.76 (28)
Sterculia guttata	0.79 (37)	0.74 (27)
Macaranga peltata	0.77 (27)	0.72 (12)
Schleichiera oleosa	**0.74 (34)**	**0.78 (45)**
Pterospermum reticulatum	**0.77 (41)**	**0.78 (49)**
Dillenia pentagyna	**0.75 (18)**	**0.76 (16)**
Steriospermum colais	0.80 (64)	0.78 (52)
Xylia xylocarpa	0.73 (26)	0.68 (13)
Mallotus philippensis	0.73 (15)	0.66 (13)
Terminalia paniculata	0.81 (111)	0.75 (50)
Gmelina arborea	0.76 (31)	0.74 (24)

The Fv/Fm values derived from Chlorophyll fluorescence measurements (Fig. 43) on seedlings in the forest floor measured at three plots in Pattakarimba MDF is given in the three tables. The values are average of three consecutive measurements taken at three time intervals. The performance index (PI) values are also given in parenthesis in Tables 8 to 10. The measurements taken in the morning may be compared with the afternoon measurements.

The Fv/Fm values give a very good indication of the stress to which the seedlings are subjected to. The optimum value in plants is found to b 0.83, that is, a plant without any stress. By comparing the measured values in the tables with the above optimum, it is possible to judge the magnitude of stress to which the plants are subjected. However, a higher value in the morning compared to the afternoon value indicates the recovery of the plants from stress overnight. The PI values given in parenthesis are actually a derived parameter from several measurements of the chlorophyll fluorescence kinetics.

The PI values are therefore indicative of the stress. It may be noted that in most plants under stress (marked by bold letters for the values in the tables), the PI values also coincide with the Fv/Fm values. However, in some plants, the higher PI values in the morning compared to the afternoon values indicate that the PS II metabolism is going on without much threat of stress to the plants. This way it is possible to screen the species that are under stress in the field. For example, *Dillenia pentagyna*, which occurred in all the three plots measured, showed lower values for Fv/Fm and also the PI values. It can be concluded that the above species is under serious threat because of the environmental stress, probably water.

Table 10. PLOT-2: Fv/Fm values during morning and afternoon are shown. PI (Avg.) values given in parenthesis.

Species	8.30A.M.	11A.M.	2P.M.
Sterculia guttata	0.81 (57)	0.79 (55)	0.77 (22)
Macaranga peltata	**0.75 (10)**	**0.77 (62)**	**0.77 (43)**
Cleistanthus collinus	0.81 (53)	0.74 (13)	0.65 (3)
Strychnos nux-vomica	**0.78 (55)**	**0.79 (41)**	**0.79 (56)**
Schlechera oleosa	0.79 (82)	0.79 (66)	0.77 (37)
Bambusa bambus	0.77 (57)	0.81 (87)	0.78 (38)
Naringi crenulata	**0.80 (43)**	**0.80 (50)**	**0.80 (76)**
Holarrhena pubescens	0.79 (43)	0.79 (52)	0.79 (36)
Mallotus philippensis	0.79 (51)	0.78 (34)	0.77 (39)
Dillenia pentagyna	**0.70 (5)**	**0.71 (9)**	**0.70 (5)**
Bauhinia	0.79 (74)	0.79 (62)	0.79 (52)
Xylia xylocarpa	**0.80 (60)**	**0.81 (70)**	**0.79 (71)**
Terminalia crenulata	0.82 (67)	0.79 (41)	0.74 (17)

9

GENERAL DISCUSSION

Species differ substantially in their effects on ecosystem processes. These species effects are often as strong as, or stronger than the direct effects of environment on ecosystems (Flanagan and Van Cleve, 1983). Organisms seldom affect single processes in isolation. Instead, effects often cascade through a broad range of ecosystem processes, due to the tight linkages among carbon, nutrient and water cycles of ecosystems (Tateno and Chapin, 1997). Species also influence landscape processes through their effects on the spread of materials, organisms, or disturbances among patches on the landscape. An understanding of the effects of organisms on ecosystem, landscape and regional process is therefore essential to the development of policies that mitigate undesirable future changes on the Earth. Species traits are the attributes that most directly affect ecosystem processes (Chapin, 2003). When we examine the evidence for the importance of these traits, it is almost impossible to separate the effects of an individual trait from the effects of the species that has these traits. This is because it is the abundance of individual organisms, rather than an individual trait, that changes with altered biodiversity. Most of the evidence for impact of species traits on ecosystem processes comes from studies in which species composition differs among communities.

It is the interactive controls such as resources, modulators, disturbance regime, human activities and biotic communities that directly regulate ecosystem processes; species that alter these controls generally have strong effects on ecosystems (Chapin, 2003).

The supply of resources required for plant growth is one of the interactive controls to which ecosystem processes are most sensitive. Litter quality, which influences the turnover rate of nutrients in litter and soil organic matter is one of the best documented mechanism by which species alter resource supply rate (Melillo *et al.*, 1982; Hobbie, 1992). In the present study, the litter fall in the MDF has been recorded on a monthly basis. The maximum litter fall occurs during February-March which is the dry season in the study site. The temperatures are relatively high during this part of the year (approx. maximum of 37°C), which is followed by rain during April to August. The high temperature combined with wetness give an ideal situation for decomposition of the litter by climatic factors and microorganisms. Previous studies on the leaf litter decomposition in MDF in Kerala has shown that 90 percent of the decomposition occurs in 3 to 10 months (Kumar and Deepu, 1992; Swarupanandan *et al.*, 2001). Out of all the species, *Xylia xylocarpa* showed the slowest decomposition rate, probably because of the high lignin content in the leaf litter of this species. The leaf litter production analysed in the different plots in the present study reveal that there are variations with regard to the month in which maximum production is recorded. This is probably due to the different tree associations met within a MDF. The litter production in a very similar MDF in Kerala has been reported as 8.5 t ha^{-1}(Swarupanandan *et al.*, 2001). From the weight loss of litter reported in Swarupanandan *et al.*(2001), it may be noted that most of the weight loss of the litter (except in *Xylia xylocarpa*) occurs during the monsoon months which follow soon after the heavy fall of litter. This probably means that trees are able to absorb the minerals released by the litter within a short time. The slow release of minerals from slow decomposing species such as *X. xylocarpa* shows that such species have a different function in the nutrient cycling in a MDF. The C/N ratio of the leaf litter in an MDF needs further analysis to understand more on the nutrient cycling.

The thick deposition of leaf litter in the summer months act also as a good mulch for the forest floor during the summer months when the canopy is very much open and the temperatures are relatively high. This will considerably reduce the albedo (shortwave reflectance) from the forest floor, thereby reducing the sensible heat in the atmosphere. All these findings indicate that the leaf litter from the MDF should not be removed for use in agriculture as done at present in several locations in Kerala.

Traits of dominant species strongly affect the microclimate of the ecosystems because plants are located at the land-atmosphere interface, where water and energy exchange occur. Solar radiation is the major resource that governs the energy input into an ecosystem. The albedo of the vegetation-soil surface determines the proportion of incoming radiation that is absorbed , which in turn influences the quantity of heat that enters the soil and the energy available to drive water loss from the ecosystem through evapotranspiration. Broad-leaved forests such as MDF have higher albedo compared to conifers (Baldocchi *et al.* 2000). However, the height differences and the density in the dominant trees in a MDF result in a very rough top canopy for this forest. Rough canopies generate mechanical turbulence, allowing eddies of air from the bulk atmosphere to penetrate deep within the plant canopy. This will help to carry water vapour and heat efficiently from the forest to the atmosphere, minimizing surface build-up of heat and water vapour. This way the structural attributes of an MDF strongly influence surface temperature, humidity and water loss from this ecosystem (Chapin, 2003).

The net primary productivity (NPP) of a forest is strongly correlated with climate and leaf area available. The length of the growing season and the capacity of the vegetation to produce and maintain leaf area are the major constraints for NPP. On average, plants in most mature stands produce 1-3 g biomass per square meter of leaf area per day during the growing season. This is consistent with the generalization that light use efficiency, that is, the efficiency of converting absorbed radiation to plant biomass is relatively constant (within a factor of two) among plants (Chapin *et al.*, 2002). It is generally agreed that plants differ in leaf area in response to spatial variation in climate more strongly than they differ in photosynthesis per unit leaf area during the time that leaves are photosynthetically active. Therefore, leaf area development is an important factor governing the productive potential of an ecosystem. As observed from LAI measurements, the value in the MDF studied goes to 3.6 during June. The global figures, for MDF ranges between 0.6 and 8.9 with a mean value of 3.9 (Scurlock *et al.*, 2001).

In MDF the leaf area duration in the mature phase is 187 to 256, as observed in the present study. This means that the leaf remain on the tree in a photosynthetically active state only for 8 months of the year. This is much shorter than in evergreen or forests of the colder regions.

SLA is another important trait to explain relative growth rate (RGR) and ecological behaviour in plants (Poorter and de Jong, 1999). It is also an indicator trait for resource use strategies. It has been shown that species with high SLA values show high productivity, because SLA reflects previously captured resources (Chapin, 2003). SLA directly affects both leaf nitrogen levels and net photosynthetic rate. Species with high SLA do better in resource rich environments while species with low SLA do better in resource-poor environments (Chapin, 2003). In the present study, much variations between species have been observed in the SLA of trees in the MDF. Of the seven species studied, the SLA values ranged between 9.6 m^2 kg^{-1} and 20 m^2 kg^{-1}. *T. paniculata, E. officinalis* and *D. latifolia* showed relatively lower values compared to the other species examined in this study. The slow growth rate of the three species, especially that of *D. latifolia* may probably be attributed to the low SLA shown by this species. The variations in SLA in MDF species growing in different habitats will need to be examined before reaching definite conclusions. Probably this could form a good character for choosing plus trees of certain species for genetic improvement.

Water and energy exchanges by an ecosystem not only affect the local microclimate of an ecosystem, but also the input of heat and moisture to the atmosphere, which can affect temperature and precipitation in downwind ecosystems. Although no model for water use by the entire catchment of MDF could be derived in the present study, it has brought out the water use pattern in at least 12 different species, many of them dominant trees in the MDF. The water loss by transpiration in MDF is minimal during the dry months when the leaves are either fallen or in senescent stages. Trees such as *Tectona grandis, Terminalia paniculata* and *Gmelina arborea* exhibit very high rates of transpiration, which is indicative of its high stomatal conductance reported already (Kallarackal and Somen, 2008). Besides, they are fast growing trees in the MDF and hence grown as plantation species. *Wrightia tinctoria,* which is an understorey species, shows reduced rates of transpiration throughout the different seasons.

The effects of species traits on ecosystem and ecosystem functions need more studies in the tropics in general and in MDF in particular. These factors are important in developing regional and global models that link changes in vegetation with changes in ecosystem processes. The traits of dominant species that determine the ecosystem properties, such as leaf area, SLA, phenology, litter dynamics, water use characteristics, stress factors that cause failure in regeneration, etc. can be critically studied using modern technology. They can provide the basis for incorporating species effects into large scale ecosystem and climate models to provide information for developing policies that will help us to adapt or mitigate the undesirable effects of anthropogenic climate change and other global change phenomena.

10

RECOMMENDATIONS

The following recommendations are given based on the studies conducted in this project:

1. The major litter fall in a moist deciduous forest happens during a short period, during a span of three to four months. This is during the dry season. The litter is very important in maintaining nutrient cycle of the forest which regulates the growth of the trees. Besides, the litter serves as a mulch preventing water loss by evaporation from the soil. This is important for the survival of the seedlings on the forest floor. Hence litter should not be allowed to be removed from the forest for agricultural purpose. Also, maximum protection should be given to the forest during this period from fire which can totally burn away the litter as well as the trees.
2. The moist deciduous species can be freely used for raising plantations because they have very good stomatal regulation for water use. Moreover, during the dry period, they shed their leaves totally, thus conserving the soil water resources.
3. From the vegetation analysis, it appears that there is much degeneration in the forest in the study location, especially as shown by the number of tree species. This will need to be taken care of by discouraging grazing, fire wood collection and pole collection from the natural forests.
4. There is need to make studies on the hydrology of the moist deciduous forests as they form catchments for many of the reservoirs in the country.

The above recommendations could be implemented through the State Forest Departments.

11

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