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Canopy dynamics and light climates in a tropical moist deciduous forest in India

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ABSTRACT. The canopy dynamics and light climates within a 20 by 60 m quadrat were studied in a disturbed moist deciduous forest near Bombay, India. A map was drawn of individual trees within the quadrat, the taxa were identified, and their phenology was followed from November 1984 to July 1985. The quadrat contained 14 species, the most common being *Tectona grandis, Terminalia tomentosa, Butea monosperma, Mitragyne parviflora* and *Albizia procera.* Some individuals were in leaf at all times, more so at the moister east end of the quadrat. In November at the end of the rainy season, light measurements documented percentages of total daily photosynthetic photon fluence (PPF) at 10.0% of full sunlight; 44% of this flux was due to sunflecks whose duration was approximately 17% of the daytime hours. Values for six sites were similar to mid-day measurements along a 40 m transect, and consistent with the 94% canopy cover of the sites, photographed with a fish-eye lens. The March dry season measurements revealed a more intense radiation environment (54% of solar PPF), and 59% of the photosynthetic photon flux density at mid-day along the transect. Canopy openings were increased to a mean of 59.4%. Light in the understorey in November was spectrally altered, with typical R:FR ratios of 0.30, compared to March values identical to those of sunlight, at 1.10.

KEY WORDS: India, monsoon, phenology, photosynthetic photon flux density, spectral quality, tropical deciduous forest.

INTRODUCTION

Despite their great area, economic importance and threatened status, little research has been conducted on the ecology of tropical deciduous forests (Murphy & Lugo 1986). In India remnants of tropical deciduous forests represent the country's greatest forest resource. Although some ecological research has been conducted in them (Desh 1970, Misra 1972, Seth & Kaul 1978, Singh 1975, Vyas *et al.* 1977), most of the studies have been floristic and geographical in nature (Champion & Seth 1968, Puri *et al.* 1983).

Indian tropical deciduous forests vary considerably in structure and species composition, depending on climate and geology. Forests in the region of the Konkan, which is on the west coast north and south of Bombay in Maharasthra State, are strongly influenced by two factors: (1) high seasonal rainfall, and (2) the soils produced on the basaltic substrate. Ecological research has been principally floristic (Billore 1972, Santapau & Randeria 1955, Satyanarayan 1955) and geographical (Gaussen *et al.* 1966, Legris & Meher-Homji 1978). Only Das

(1954) has described successional changes of very disturbed forest in the Sanjay Gandhi National Park near Bombay. The purpose of this study was to analyse the canopy characteristics (species composition, distribution and individual tree phenology) and light climates within a tropical moist deciduous forest near Bombay before and after the monsoon season.

It is important to know the patterns of light availability if we are to understand the ecology of plants living in the understorey (Brokaw 1985, Horn 1971). Because of the complexity and dynamic nature of a forest canopy the light climate of a forest floor is not easily characterized (Reifsnyder *et al.* 1970). Considerable research has been conducted on the light climates of humid tropical forests in Malaysia (Yoda 1974), Australia (Bjorkman & Ludlow 1972), Costa Rica (Chazdon & Fetcher 1984) Hawaii (Pearcy 1983) and India (Lee & Paliwal 1988). This research has revealed the low levels of irradiance on the forest floor, typically 1-2% of that above the canopy, and the large contribution of brief light flecks to the daily irradiance total. Light in the rain forest understorey is also different in spectral quality from full sunlight (Lee 1987), and such changes may affect the developmental ecology of plants (Lee 1988, Smith 1982). There is simply no published research on the light climates of tropical deciduous forests. The strong seasonal changes in the degree of canopy cover obviously result in seasonal shifts in the light climates of these forests, as in the case of temperate deciduous forests (Ross *et al.* 1986, Tasker & Smith 1977). How large are the shifts, and how do they correlate with the development of plants in the forest?

SITE DESCRIPTION AND METHODS

The forest is in Thana District, Maharashtra State, about 80 km north-east of Bombay. It is 4 km due north of the village of Ganeshpuri, at the base of the west-facing slope of Mondagni Mountain, 19° 31′ N, 73° 4′ E. It is adjacent to the small tribal village of Digota and is within an area of protected forest (Figure 1). The soil is high in clay content and moderately alkaline, known locally as black cotton soil. The closest meteorological records are the detailed ones for Bombay and less complete records at the Aspee Foundation Experimental Farm at Met, approximately 9 km east. The 72-year average for rainfall in Bombay (to 1963, Meher-Homji 1979) is 1924 mm, with a standard deviation of 517 mm. At the Aspee station the total was 2296 mm in 1982 and 3175 mm in 1983 (Anonymous 1984, 1985). Since the forest site is at the base of the mountain's west-facing slope, it receives somewhat more rainfall than the other sites. It thus falls within the climatic zone for moist deciduous forest of Puri *et al.* (1983) as a '*Tectona-Terminalia-Adina-Anogeissus* series of intermediate teak deciduous forest', or the type C1b moist teak forest of Champion & Seth (1968). The rainy season begins in early June. Precipitation is heaviest in July, and decreases in August. By mid-October the rains cease. There is little or no precipitation until the following June. In 1984-85 there was absolutely

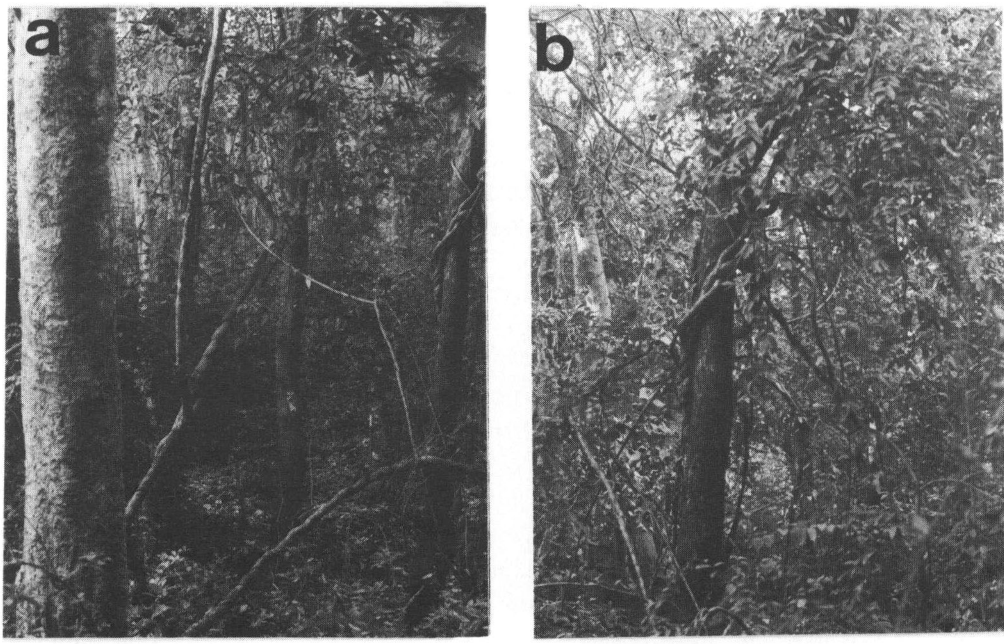

Figure 1. Photographs of forest research site, both taken from the south-east corner of the quadrat. (a) Taken on March 21. The large trunk is of *Albizia procera.* (b) Taken on November 21. Note the thick growth in the understorey and the woody vine, *Calycopteris floribunda*, growing on a *Terminalia tomentosa* individual.

no precipitation at the site from 8 October until 7 June. From December to May there is an increase in maximum daily temperature from 32°C to 43°C (Anonymous 1984, 1985). The maximum temperature of approximately 32°C from June to September is apparently the result of the cloud cover and heavy rainfall.

Although the forest site is covered by a relatively dense canopy (Figure 1b), and many of the trees are large in stature, the forest has been influenced by a long history of human intervention. It was harvested for mature teak trees by the British, and has more recently become a source of firewood for the villagers of Digota as well as other tribal people in the area. The presence of individuals of *Wrightia tinctora* and *Holarrhena antidysenterica*, as well as the high frequency of *Terminalia tomentosa* and *Tectona grandis* are evidence for a history of disturbance (Champion & Seth 1968, Das 1954, see Table 1). The frequency of *Carissa congesta* in the understorey, a thorny evergreen shrub, suggests a recent history of grazing. More mesophilic species, such as *Mitragyne parviflora* and *Albizia procera*, suggest a species component that would be present in undisturbed conditions (Brandis 1921, Talbot 1909). Many of the individual trees in the forest were estimated to be at least 60 years old (Mr D. V. Patari, Forest Officer).

A site was selected, and a 20 m by 60 m east-west quadrat was surveyed and staked. In this quadrat a 40 m transect was established, as were individual sites

Table 1. A list of species identified in and adjacent to the quadrat. These are subdivided into categories as trees, shrubs and lianes, and perennials. An abbreviation is provided for each species identified in Figures 3, 4 and 5. For canopy species the observed times of flowering, fruiting, and foliage are given.

Scientific name	Family	Code	No. observed	Flowers	Fruits	Foliage
		Trees				
Albizia procera (Roxb.) Benth.	Fabaceae	AP	10	May	Jan-Feb	May-Mar
Bauhinia racemosa Lamk.	Fabaceae	BR	1	Mar-Apr	Nov-Jan	Jun-Mar
Bombax ceiba L.	Bombacaceae	BC	1	Jan-Feb	Apr-May	Jun-Jan
Butea monosperma Lamk. Taub.	Fabaceae	BM	11	Feb-Mar	Jun-Jul	Jun-Apr
Crataeva nurvula Buch.	Capparidaceae	CN	1	Apr	Jul	Apr-Jan
Ficus glomerata Roxb.	Moraceae	FG	1	None	None	All year
Holarrhena antidysenterica (L.) Wall. ex DC.	Apocynaceae	HA	1	Mar-Apr	Mar	Apr-Feb
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	LC	1	Feb-Mar	Jun-Jul	Jun-Dec
Madhuca indica J. F. Gmel.	Sapotaceae	MI	1	Feb-Mar	Apr-May	May-Mar
Meyna laxiflora Robyns	Rubiaceae	ML	2	Apr-May	None	May-Feb
Mitragyne parviflora Roxb. Korth.	Rubiaceae	MP	5	Jun	Dec-Jan	All year
Pterocarpus marsupium Roxb.	Fabaceae	PM	1	May-Jun	Dec-Mar	May-Mar
Saccopetalum tomentosum Hook. f. & Thoms.	Annonaceae	ST	1	Jun-Mar	Apr	Jun
Schleichera oleosa (Lour.) Oken.	Anacardiaceae	SO	3	Mar-Apr	Jun-Aug	Apr-Feb
Tectona grandis L.	Verbenaceae	TG	19	Jun-Aug	Dec-Feb	Jun-Feb
Terminalia belerica (Gaertn.) Roxb.	Combretaceae	TB	7	May	Jan-Mar	May-Mar
Terminalia tomentosa W. & A.	Combretaceae	TT	23	Apr-May	Feb-Apr	Jun-Feb
Wrightia tinctoria R. Br.	Sapotaceae	WT	1	Mar-Apr	Jan-Feb	May-Jan
Zizyphus xylopora Willd.	Rhamnaceae	ZX	1	May	Aug-Sep	All year
		Shrubs and vines				
Abrus precatorius L.	Fabaceae					
Acacia concinna DC.	Fabaceae					
Calycopteris floribunda Roxb. Lamk.	Combretaceae	CF		Feb-Mar	May-Jun	All year
Carissa congesta Wt.	Apocynaceae	CC		Feb-Mar	May-Jun	All year
Combretum ovalifolium Roxb.	Combretaceae					
Mucuna prurita Hook.	Fabaceae					
Vitis adnata Roxb.	Vitaceae					
Zizyphus oenoplia (L.) Mill	Rhamnaceae					
		Herbs				
Amorphophallus commutatus Engl.	Araceae					
Arisaema tortuosum (Wall.) Schott.	Araceae					
Iphigemia indica (L.) A. Gray	Liliaceae					
Zingiber macrostachyum Dalz	Zingiberaceae					

on the north sides of six large trees, two each of *Tectona grandis* (TG), *Terminalia tomentosa* (TT) and *Albizia procera* (AP). The transect and the six sites were used for light measurements at the end of the monsoon, in November of 1984, and before the beginning of the monsoon, in March of 1985. All trees with trunk diameters greater than 6 cm were located in the quadrat, and their canopy spreads were estimated by sighting against subdivisions within the quadrat. Trunk diameters were measured and heights of the largest trees were estimated by sight, using a 2 m scale lined up on each trunk. All trees were identified in the quadrat and 10 m beyond each boundary. All species (Table 1) are common forest taxa in the area (Talbot 1909); the small number of taxa suggests the partially degraded condition of the forest.

The phenology of the trees and associated vines was observed at biweekly intervals from November to July, as was the appearance of herbaceous understorey plants during the monsoon. The percentage of full canopy for each tree within the quadrat was estimated at biweekly intervals from November 1984 until July 1985 during the study period, as 67%-full cover, 33-66%, and 0-33%. The site was protected from the cutting activity of local villagers by the Forest Guard, as well as a local villager hired during this research.

Quantum irradiance, as photosynthetic photon flux density (PPFD), was measured inside and outside of the forest using a Li-Cor 190SB quantum sensor (Li-Cor Instruments, Lincoln, NB 68504, USA). All measurements were made on typically cloudless days 12-20 November and 21-24 March. For individual measurements the sensor was attached to a Li-Cor 185B radiometer. For continuous measurements at the six sites within the quadrat the sensor was attached to a Linear Model 142 millivolt chart recorder (Linear Instruments, Reno, NV 89502, USA), powered by a 12 V car battery. All PPFD measurements were made 1 m above the forest floor with the sensor facing vertically. Total daily photosynthetic photon fluence (PPF) of sunlight above the canopies was estimated by measurements in an adjacent field. The radiometer was used to measure light at different times of the day in March, and a Li-1800 spectroradiometer automatically scanned sunlight at fixed intervals during the November measurements. Flux densities at the six sites were measured for one full day each with the chart recorder. Total daily PPF's were estimated by integrating the area under the curve with a planimeter. Total daily duration and intensity of sunflecks was estimated by taking the areas of intensities greater than 80 μmol m^{-2} s^{-1}. PPFD's were measured at 1 m intervals in the transect within 1 hr of solar zenith both in November and March. The six sites were also measured in this way. For the March measurements, the chart recorder no longer functioned. Total PPF's for the six sites were estimated by measurements at each of the sites every 15 minutes. Curves of these measurements were constructed and integrated, and the individual observations were examined to determine the frequency of sunflecks.

Spectral distribution of radiation at the six sites within the quadrat was measured with a Li-Cor Li-1800 spectroradiometer at a range of 300-100 nm. The instrument has a 2 nm accuracy and a half-peak bandwidth of 6 nm. Light of different intensities was measured at the six sites. Thus the effect of the canopies of each species on spectral quality of light in the shade could be compared. Software in the spectroradiometer integrated regions of scans for PPFD, in μmol m^{-2} s^{-1} at 400-700 nm, irradiance at 300-1100 nm as W m^{-2}, and the

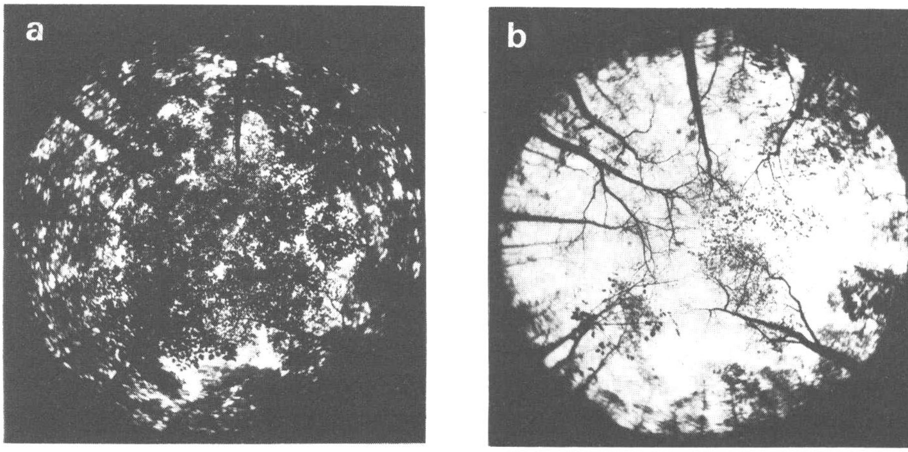

Figure 2. Fish-eye lens photographs at site 1TG. The right margin of each photograph is due east. (a) Taken 21 November 1984. (b) Taken 24 March 1985.

ratio of quanta at 658-662 nm to 728-732 nm, or the R:FR ratio of Smith (1982).

A Spiratone fish-eye lens (Spiratone, Flushing, NY 11354, USA) attached to a 35 mm single lens reflex camera was employed to photograph the canopy of each of the six sites before and after the monsoon (Figures 2a and b). The negatives were printed on transparent lithographic film, and the canopy areas estimated by integration with a Li-Cor Li-3100 leaf area meter.

RESULTS

Forest structure and phenology

The species composition (Table 1) and size of individuals suggest a history of disturbance in this forest. The largest individuals were of *Tectona grandis* (17 m high with dbh's of 40 cm); *Terminalia tomentosa* (21 m with dbh's of 58 cm); *Mitragyne parviflora* (22 m with dbh's of 34 cm); and *Albizia procera* (26-30 m and dbh's of up to 95 cm). The cover is discontinuous with some open areas and varying canopy height (Figures 1b, 2, 3).

Four large woody vines (*Acacia concinna, Calycopteris floribunda, Combretum ovalifolium* and *Zizyphus oenoplia*) were important components in the forest canopy. Other vines, including *Abrus precatorius, Mucuna prurita* and *Vitis adnata*, were common in the understorey.

The degree of canopy cover varied during the year (Figure 2). During and immediately after the rainy season the canopy was thick and the forest floor was covered with a lush growth of rhizomatous perennials, such as *Arisaema tortuosom, Iphigemia indica, Amorphophallus commutatus* and *Zingiber macrostachym* Figure 1b). After the rains stopped, the soil within the forest remained moist until January, long after streams in the adjacent open countryside had dried. During this time the understorey perennials steadily died back.

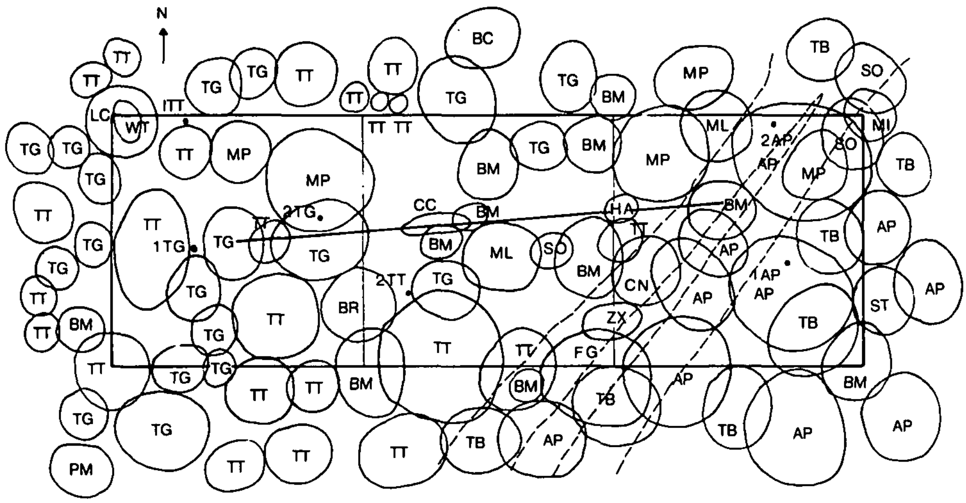

Figure 3. Map of the quadrat, with the positions of canopies and distributions of individual species. Each square is 20 m on a side. Symbols for species are given in Table 1. The six light-sampling locations are indicated on the map (1TT, 2TT, 1TG, 2TG, 1AP and 2AP). The line across the quadrat shows the location of the 40 m transect.

After December the foliage steadily dropped from individual trees. Some lost their leaves early, and others, such as *T. grandis* and *T. tomentosa*, maintained some foliage until March. In March and April the forest was most open (Figures 1a, 2a, 4), but the forest canopy was never at any time totally bare. Individuals of *A. procera* were never quite leafless, nor were those of *Ficus glomerata, M. parviflora,* or *Zizyphus xylopora.* Other species (*Crataeva nurvula, Schleichera oleosa* and *Terminalia belerica*) lost their leaves early or briefly, and then came into foliage well before the onset of monsoon, April to May. This pattern of leaf production (and flowering and fruiting, Table 1) is typical of tropical deciduous forests in general (Frankie *et al.* 1974, Lieberman 1982, Zapata & Aroyo 1978). The two most common species, *T. grandis* and *T. tomentosa*, lost their foliage late in the dry season, but did not begin to regain their canopies until the beginning of the monsoon. Because of the different behaviour of the component species of this forest, the degree of canopy cover during the year will much depend on the species composition. The eastern section of the quadrat was more damp and had more canopy cover during the dry season (Figure 4). The seasonal differences in phenology of the six sites is consistent with the differences in percentage of canopy cover revealed by fish-eye lens photography, of 94.0 ± 3.1% during November compared to 40.6 ± 18.8% during March (Table 1, Figure 2).

Understorey light climates

Both quantum irradiance and spectral quality in the forest understorey was strongly affected by seasonal changes in the canopy cover (Table 2). In November the mean daily PPF for the six sites was 3.6 mol m^{-2} ± SD 1.3, which was

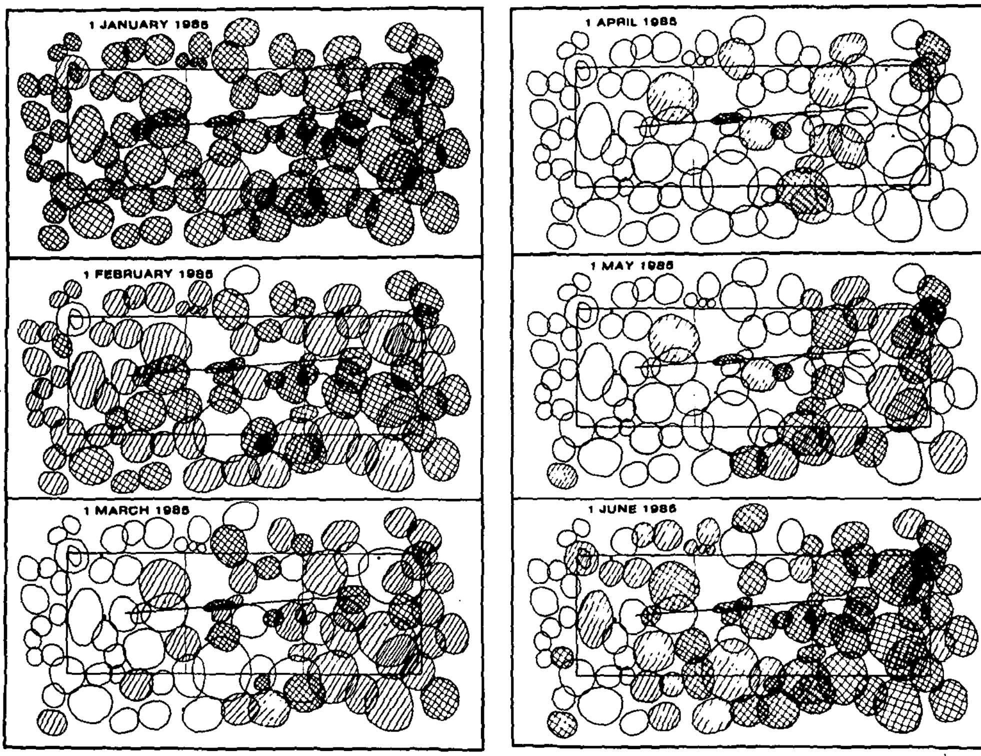

Figure 4. The variation in canopy cover in the quadrat from 1 January until 1 June of 1985. The canopy was completely foliated by 1 July. The degree of canopy cover is indicated for each tree by: (XXXX) full-2/3 cover, (//////) 2/3-1/3 cover, ( ) 1/3 cover-leafless. Individual species can be identified by referring to Figure 2 and Table 1.

a mean of 10% of the daily PPF of sunlight (35.3 ± 0.1, Table 2). In March the same sites received 25.3 mol m^{-2} ± 6.6, a mean of 54% of PPF as sunlight, of 46.8 ± 0.6 mol m^{-2}. In November 44 ± 17% of total PPF was due to sunflecks, which occurred during 17 ± 8% of the daylight, but there was considerable variation between sites. In March all irradiance, with the exception of very early and late hours was greater than 80 μmol m^{-2} s^{-1}. In November, individual measurements of mid-day PPFD were a mean of 195 ± 133 μmol m^{-2} s^{-1}, compared to direct sunlight of 1694 ± 71 μmol m^{-2} s^{-1}, but typical values (medians) were lower at 89 ± 91 μmol m^{-2} s^{-1}. Under more open canopy conditions in March the mid-day mean for the six sites was 1058 ± 263 μmol m^{-2} s^{-1}, compared to 1718 ± 105 μmol m^{-2} s^{-1} of sunlight, and median values were similar.

Differences in light climate from post-monsoon to pre-monsoon seasons are also documented by the mid-day readings along the 40 m transect (Figure 5). There was considerable variation at each site, and from site to site, in these readings but the seasonal differences are clear. The mean PPFD for November was 175 ± 171 μmol m^{-2} s^{-1}, and for March was 1068 ± 249 μmol m^{-2} s^{-1}. These values are very similar to those for the six sites, suggesting that they are representative of the forest quadrat as a whole.

Table 2. Data for the light climates analysed in the quadrat. Locations in the quadrat (Figure 3) are given in the left-most column. The columns are, in order, (1) daily PPF, or photosynthetic photon fluence, in mol m^{-2}; (2) percentage of daily sunlight, as PPF; (3) duration of PPFD greater than 80 $\mu mol\ m^{-2}\ s^{-1}$; (4) percent daily duration of PPFD greater than 80 $\mu mol\ m^{-2}\ s^{-1}$; (5) Mid-day measurements of PPFD as mean, median and range; and (6) percentage of canopy cover revealed by analysis of fish-eye lens photographs.

					Mid-day PPFD			
Location	Daily PPF	% sunlight PPFD	% sunfleck duration	Sunfleck % daily PPF	Mean	Median	Range	% canopy cover
				November				
1AP	3.7	10.4	22	66	401 (N = 30)	275	27-1400	96.2
2AP	2.7	7.5	16	34	134	50	31-620	92.2
1TG	5.3	15.0	24	54	313	56	14-1430	89.7
2TG	2.2	6.0	7	15	60	45	26-239	93.8
1TH	5.0	14.0	26	56	100	59	27-460	98.5
2TH	2.6	7.0	10	48	162	51	29-790	93.7
Mean values	3.6 ± 1.3	10.0 ± 3.8	17 ± 8	44 ± 17	195 ± 133	89 ± 91	14-1430	94.0 ± 3.1
Sunlight (N = 3)	35.3 ± 0.1	–	–	–	1694 ± 71 (N = 11)	1676	1605-1850	
				March				
1AP	21.8	47	95	94+	925 (N = 15)	960	300-1560	72.1
2AP	16.5	35	96	99	739	465	150-1650	55.2
1TG	30.3	65	94	99+	1184	1320	123-1740	25.9
2TG	29.5	63	95	99+	1132	1230	300-1600	31.7
1TH	33.1	71	95	99+	1480	1560	600-1740	27.0
2TH	20.4	44	95	99+	890	1020	240-1560	31.6
Mean values	25.3 ± 6.6	54 ± 14	95 ± 0.6	99+	1058 ± 263	1092 ± 376	123-1740	40.6 ± 18.8
Sunlight (N = 3)	46.8 ± 0.6	–	–	–	1718 ± 105 (N = 6)	1680	1560-1830	–

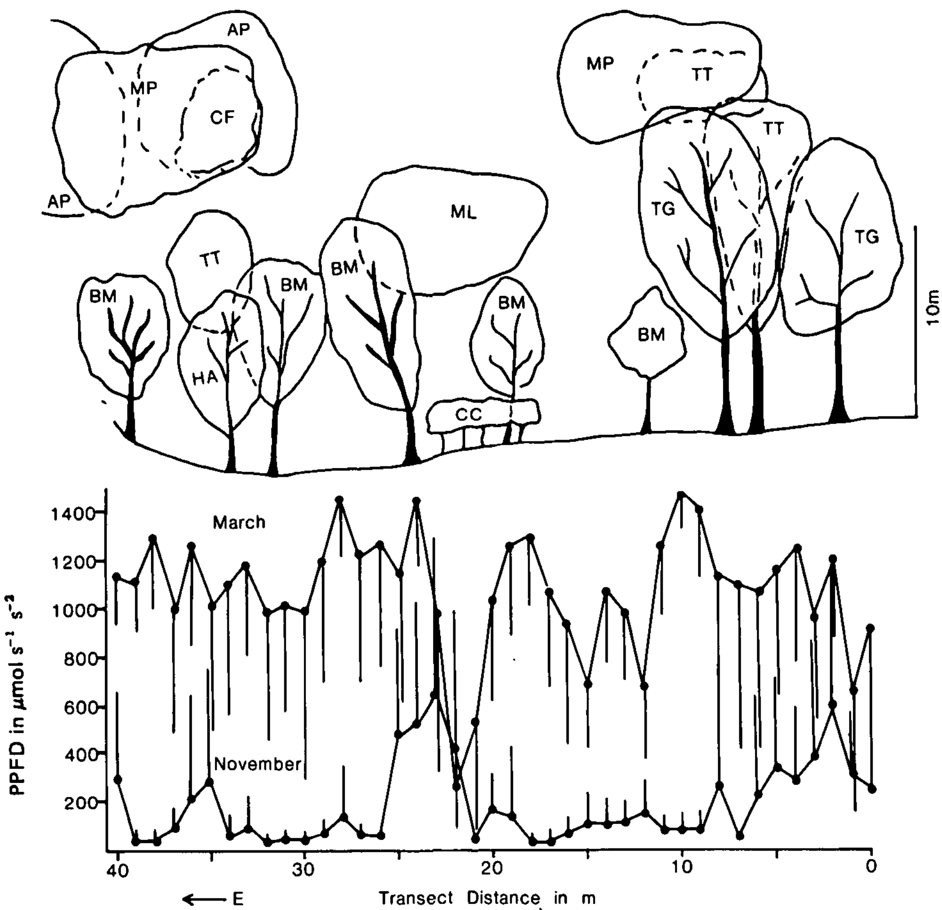

Figure 5. Description of the transect within the quadrat, viewed from the north side. Both horizontal and vertical distances are to the same scale. The distribution of mean ± SD of mid-day PPFD values at one metre intervals are given for March and November. The least difference between the two seasons is seen under the thicket of *Carissa carandas*, an evergreen shrub. Symbols for species are given in Table 1.

Forest canopy cover also had an important effect on the spectral distribution of radiation in the understorey. Typical measurements for site 1TG compared to full sunlight are shown in Figure 6. In full sunlight the R:FR was 1.13. In shade underneath the canopy of *T. grandis* the PPFD was reduced to 35 μmol m^{-2} s^{-1}, or 2.0% of full sun PPFD. The percentage of irradiance 300-1100 nm was less reduced, 39 W m^{-2} or 5.7%, because the canopy absorbs much less radiant energy at wavelengths above 750 nm. Thus the R:FR ratio of the site was reduced to 0.22. The relationship of percentage of full solar PPFD to R:FR for the six sites (two per species) is shown in Figure 7. For typical shade conditions of 5% the R:FR ratio is reduced to 0.33. During the March observation period there was no spectral alteration beneath the open canopy (R:FR=1.10).

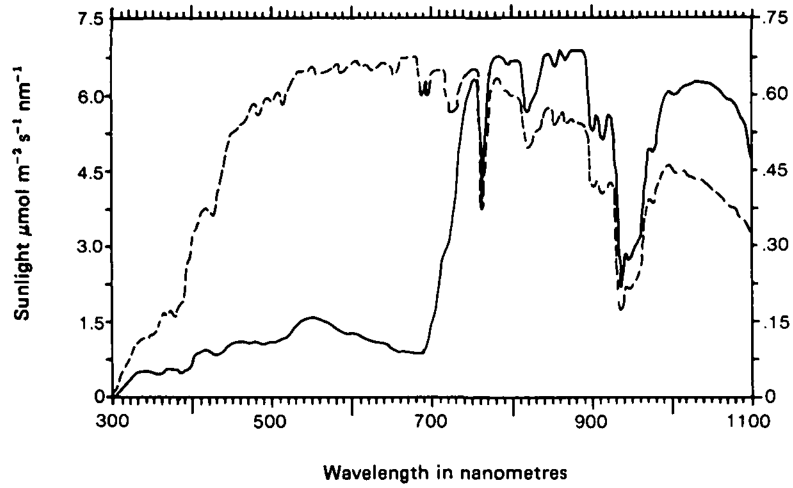

Figure 6. Comparison of spectral distribution of radiation at site 1TG and full sunlight in field adjacent to forest quadrat. (— — —) is of full sunlight, irradiance 300-1100 is 684 W m^{-2}, PPFD is 1763 $\mu mol\ m^{-2}\ s^{-1}$, and R:FR is 1.13. (———) is of shade underneath the canopy, irradiance 300-1100 nm is 39 W m^{-2}, PPFD is 35 $\mu mol\ m^{-2}\ s^{-1}$, and R:FR is 0.22. Note the ten-fold difference in scale between sunlight and shadelight readings.

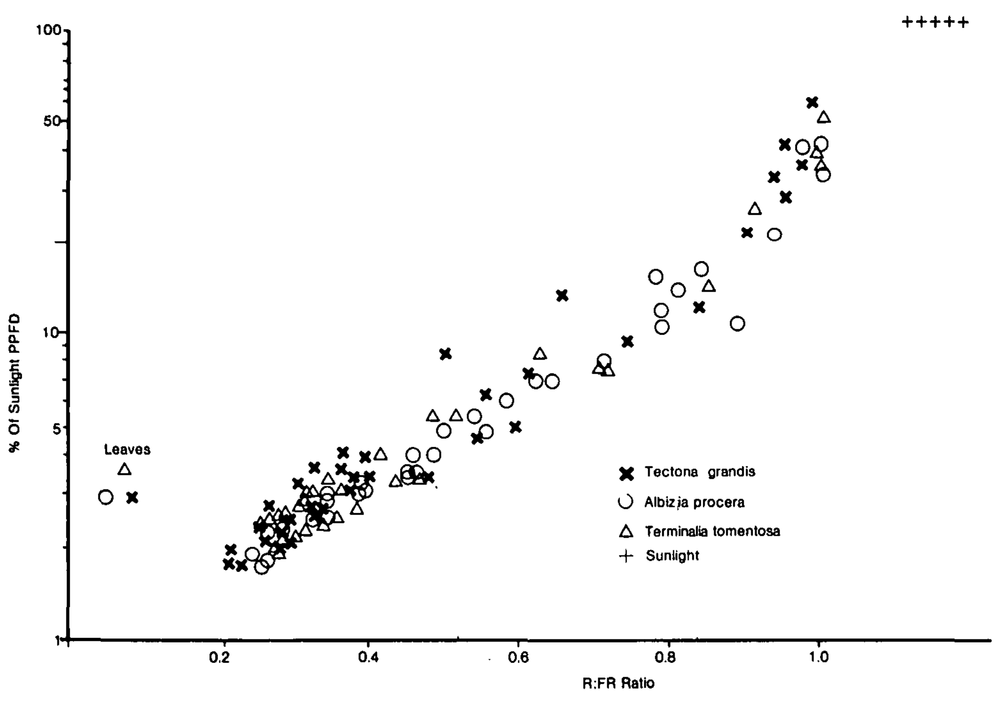

Figure 7. Relationship of decrease in PPFD, as the log percentage of full sunlight, to alteration of the R:FR ratio. Legend describes values for the three species, each measured at two sites (seen on Figure 3).

DISCUSSION

Although the light climate analysed in this research can be considered representative of the forest site, variation in species composition of forests in the area would be expected to contribute to substantially different light climates. Forests even more dominated by *Tectona grandis* and *Terminalia tomentosa*, on drier or more disrupted sites, would show a greater difference between post and pre-monsoon light climates. More mesic and less disturbed sites would have a greater species richness, with more canopies in foliage during the hot and dry months of March, April and May. The forest site analysed in this research can be considered as moderately disturbed and on a moist site.

The results for this research must also be understood in the context of a long history of disturbance at this forest site. There were few seedlings and saplings of the larger tree species, probably because of cutting for firewood and grazing by goats and cattle. Two trees (dbh of 12 cm) had been cut down within the past five years. Lopping branches for firewood as well as grazing within the site have undoubtedly opened up the understorey more than forest untouched by human intervention. Since such intervention is the rule in India, it seemed preferable to study a partially disrupted site.

Changes in the degree of canopy cover largely determined the amount of light available in the forest understorey (Table 2, Figures 4 and 5). The canopy of this forest site during and after the monsoon is more open than a typical humid tropical forest. Thus, the light environment in it is brighter and less spectrally altered than in typical forest. Typical PPFD values and percentage of daily totals were 5-10 times higher than those reported by Pearcy (1983), Chazdon & Fetcher (1984) and Björkman & Ludlow (1971). The spectral alteration is also significantly less than that reported for forests in Panama and Costa Rica (Lee 1987). In a comparable but less detailed study in evergreen forest in the south of India, Lee & Paliwal (1988) measured percentages of daily totals, typical PPFD values, and reductions in R:FR similar to the other humid forest sites.

The light data are more similar to measurements of temperate deciduous forests; their mid-summer values are less than the post-monsoon measurements reported here (Hutchison & Matt 1977), and the winter and early spring values are similar to those of the pre-monsoon measurements.

The irradiance and spectral quality measurements also indicate the importance of the canopy during the dry season. The mean daily PPF for the six sites was approximately 54% that of full sunlight, and percentage of mid-day PPFD along the transect was 61% that of sunlight (Table 2). These percentages are corroborated by the estimates of canopy cover of 40.6% (or 59.4% of the area open to the sky; Table 2, Figure 2a). Although the fish-eye lens employed for these photographs distorts certain sectors of the sphere (Herbert 1987), these distortions are not significant for estimates of percentage of canopy (T. Herbert, personal communication). There is considerable variation in the March measurements because of the greater canopy cover in the more moist easterly 20 metres, with a shallow seasonal creek bed running across it. This degree of canopy cover and reduction of irradiance should have a profound effect on soil temperatures and evaporation during the dry season (Pinker 1980), and differences between forest and adjacent scrubland were greater than I had anticipated. Individuals of *T. grandis* and *T. tomentosa* observed in scrubland away from the site lost their leaves one month earlier than individuals in the forest.

Light passing through foliage is attenuated and drastically altered in spectral quality. For instance, leaves of *T. grandis* allow only 3.0% of PPFD to be transmitted, and the R:FR of that transmitted radiation drops to 0.09, much lower than that in the forest (Lee *et al.* 1986). Canopy phenology strongly affected the spectral distribution of radiation in the understorey. March R:FR ratios were identical to those under sunlight. November R:FR ratios were as low as 0.20 at PPFD levels of 2% of solar irradiance, and there was little variation among the canopy effects of the three species studied in detail (Figure 7). These results also allow an estimation of the contribution of diffuse sky radiation to the spectral quality of shadelight under the canopy after the wet season. The reduction in transmission compared to the reduction of R:FR is similar in the three species whose canopies were analysed (Figure 7). The canopies of the three species are not different in their lowering of R:FR with reduced PPFD; their correlation coefficients were very similar. Knowing the R:FR of a canopy at a given reduction in PPFD, and comparing it to those of individual leaves, one can determine the contribution of sky radiation and solar penumbral radiation to the final light climate. For these canopies the contribution of diffuse skylight was approximately 30%. A similar technique could be employed to learn the contribution of skylight to the light environments of other forest types.

Reductions in PPFD and R:FR during the monsoon could affect the development of plants in the understorey (Smith 1982). However, most of the changes in the forest are more likely due to the availability of water, changes in photoperiod, or endogenous rhythms anticipating the monsoon. The gradual loss of foliage of emergent trees and die-back of perennial herbs in the understorey after the monsoon season is correlated with the drying out of soil and the increase in PPFD and R:FR. The reappearance of foliage in most tree species occurred very rapidly after the beginning of the monsoon (Figure 4). Some taxa, as *Schleichera oleosa*, and some perennial understorey herbs, including *Amorphophallus commutatus* and *Iphigemia indica*, developed in anticipation of the rainy season. From March to May there was a gradual increase in canopy cover, but the understorey was clear save the scattered evergreen shrubs of *Carissa congesta*. In May and early June scattered plants of a small lilly, *Iphigemia indica*, emerged and flowered, as did an aroid, *Amorphophallus commutatus*, (whose foliage appeared only after the monsoon had commenced).

Once the forest canopy is re-established the reduction in PPFD and R:FR ratios must strongly affect the growth of understorey shrubs and tree saplings, especially the herbaceous perennials that develop rapidly in the wet and shady conditions. With the coming of the monsoon in early June the balance of radiation changed sharply and the canopy rapidly completed its coverage (Figure 1b, 2b, 4). From individual measurements of PPFD (of 100-200 μmol m^{-2} s^{-1}) under those extremely cloudy conditions, I estimate a 5-10 fold reduction in radiation under monsoon conditions. During the 1985 monsoon, the sun did not appear for many days at a time, and its appearance was brief when the rapidly moving clouds parted. The monthly totals of sunshine for Bombay for the years 1933-1942 show a high of 87% daily direct sunlight for February and as little as 17% for July (Santapau & Randeria 1955). Thus, despite the lower attenuance of this canopy compared to temperate and tropical forests the light levels within the canopy probably approach those of the understorey of a humid tropical forest. Despite the greater light penetration under diffuse sky conditions (Chazdon & Fetcher 1984), the little irradiance penetrating the cloud cover would mean that the plants growing in the understorey must photosynthesize at very low light levels. At the end of the monsoon the amount of sunshine increased and the understorey perennials gradually died back. Total direct solar PPF for November was 35.3 mol m^{-2}, compared to 3.6 mol m^{-2} underneath the canopy. The canopy cover changed very little until January.

In summary, the environment of this tropical moist deciduous forest is characterized by extremes in light climates in the understorey. At specific locations these are dependent upon: (1) the season; (2) species composition; (3) local habitat differences; and (4) patterns of human disturbance. Shifts in the spectral quality of radiation should influence the developmental ecology of understorey species, just as they do in temperate forests.

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