s^{-1}, respectively. The "apparent" light compensation points for ACP and NCP declined as the canopy grew because photosynthetic capacity became larger relative to the CO_2 efflux from plant and soil. In any case, light compensation points for ACP and NCP failed to approach values typical for individual leaves and casts doubt on the use of ACP or NCP as an estimate of photosynthetic uptake of CO_2.

3.3 Impact of soil water deficit on CO_2 flux components.

Tables 1 and 2 give photosynthetic parameters for an irrigated crop and a water-stressed crop at 57 days of age. The droughted soybeans first began to wilt visibly on day 52. Water stress clearly reduced ACP and TCP responsiveness to PPFD. Respective PGMAX values were 24 and 71 micromoles m^{-2} s^{-1} for stressed and irrigated canopies. The two treatments had similar light compensation points for ACP, but the CO_2 efflux from plant and soil was reduced. Crop respiration was reduced 2.6 micromoles m^{-2} s^{-1}, but soil CO_2 efflux was reduced 4.3 micromoles m^{-2} s^{-1} by the drought. The reduction in ACP (67%) was greater than the relative reduction in TCP (56%).

3.4 Impact of diurnally varying temperature on ACP and CO_2 flux components.

While the DARKFLUX component measured at midday was fairly stable from day to day, it varied about twofold throughout the day (AM, midday, and PM values shown in Table 2). From 16 measurements taken throughout the day, DARKFLUX showed a strong linear response to diurnally varying air temperature in the range of 24 to 38 C {DARKFLUX (neg) = 14.42 - 0.898 * TEMP}. The correlation coefficient was 0.943. SOILFLUX varied only moderately during the day, and showed that PLANTRESP was the major component of DARKFLUX which was responding to temperature.

The result of this diurnal temperature effect on respiratory CO_2 flux was to alter the ACP and NCP-light response parameters from morning to afternoon. Light response equations were computed for AM, midday, and PM using CER's measured from 0800 to 1400 hours, midday only, and from 1400 to 2000 hours, respectively. The parameters in Table 2 show that the DARKFLUX and PLANTRESP intercepts became more negative and the "apparent" light compensation point for ACP and NCP increased from morning to afternoon, primarily in response to changing temperature. The effect was that ACP and NCP appeared to undergo a mid-afternoon depression when temperature was warmest. However, if carbon exchange is expressed as TCP, photosynthetic uptake in mid-afternoon scarcely showed any depression.

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CANOPY PHOTOSYNTHESIS IN RUBBER (HEVEA BRASILIENSIS): CHARACTERISTICS OF LEAVES IN RELATION TO LIGHT INTERCEPTION

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INTRODUCTION

The productivity of any crop, including that of Hevea, is influenced by its photosynthetic assimilatory capacity. Photosynthesis of a tree stand, such as rubber plantation, is regulated by additional factors viz. interception of photosynthetically active radiation (PAR), level of leaf insertion, microclimate etc. (Helms 1976). The objectives of present study are to examine the PAR distribution pattern in relation to canopy architecture and to estimate canopy photosynthesis. The information from these experiments can be used to model and predict the productivity of Hevea canopy. Such studies with Hevea are important also because of limited publications available on canopy photosynthesis of broad leaved tree crops (Porpiglia, Barden 1980; Tenhunen et al. 1980).

MATERIALS AND METHODS

The observations were made on a 22 year old (height 14.5 m) rubber tree (Hevea brasiliensis Muell. Arg.) located on eastern border of the plantation in Institute's campus.

The pattern of PAR distribution was examined at three levels inside the canopy at a height of 9.9, 6.7 and 2.7 m, respectively, from the ground. The incoming PAR was studied at 1 m above the canopy. Photosynthetic photo flux density (PPFD) was measured with quantum sensors (LI-190SB, Li-Cor, USA) and one min integrated values (through a LI-550B Printing integrator, Li-Cor, USA) were recorded at 15 min intervals during the day. The reflection was estimated by directing the quantum sensors towards the canopy. The diffusive resistance, transpiration, relative humidity (RH) and leaf/air temperature were monitored with a LI-1600 steady state porometer (Li-Cor, USA). The response to PPFD of carbon assimilation by leaves was investigated in the laboratory using labelled CO_2.

RESULTS

On a clear day (average sunshine h 10.6), the incident PPFD increased steadily from 8 h until 12 h and decreased afterwards (Fig. 1a). Until 10 h, more light quanta were available at the bottom than at the top two layers, while after 10 h the pattern was vice-versa. On a cloudy day (average sunshine h 4.9), PPFD fluctuated widely because of cloud cover (Fig. 1b). The available PPFD at bottom part of canopy was always less than that at the top, all the day. The typical PAR budgets of three canopy levels are given in Table 1. The extent of transmission as well as reflection by the top two layers was more on a cloudy than that on a clear day. As a result, the interception by these two layers was maximum on clear days.
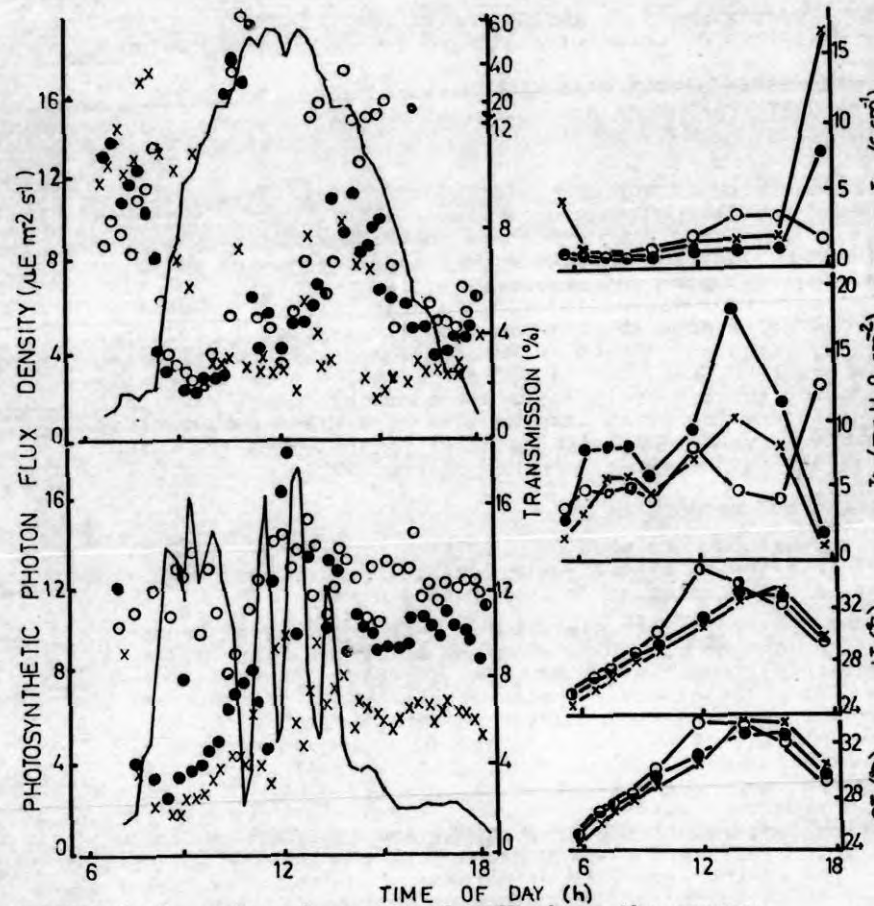
FIGURE la-b. Diurnal course of PPFD above the canopy
(continuous line) and transmission of PAR at three levels
inside the crown of Hevea brasiliensis on a clear day (a) or
a cloudy day (b). c-f: Pattern of stomatal resistance (c),
transpiration (d), leaf temperature (e) and air temperature
(f) at different times of day at three levels in canopy:
Top (o), middle (●) and bottom (x) layers.

Although the stomata of top layer offered the least
resistance, maximum transpiration was from middle layer of
the canopy (Fig. lc-f). Maximum RH was detected at the top
of the canopy in early morning and late afternoon hours while
between 10 and 14 h the bottom layer was the most humid. The
leaves at the top had less chlorophyll, smaller area, shorter
internodes, greater specific leaf weight than those at the
bottom (data not shown). The carbon assimilation capacity

of upper leaves was ·at least 40 per cent more than that of leaves from lower canopy. The photosynthetic rate of leaves from top layer was saturated at light intensities greater than 1000 μE s^{-1} m^{-2} while those from lower layers required 100 μE s^{-1} m^{-2} for saturation.

TABLE 1. PAR budget of three strata in Hevea canopy.

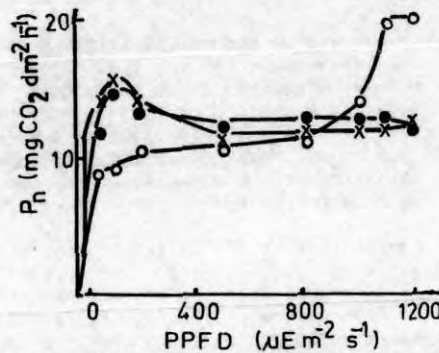| Observation	Clear day			Cloudy day		
Average PPFD (μE m^{-2} s^{-1})	1083			689		
Day's integration (E m^{-2})	49			31		
Canopy strata	Top	Middle	Bottom	Top	Middle	Bottom
% of incoming PPFD						
Reflection	2.3	0.5	0.4	2.8	0.6	0.4
Transmission	10.3	7.2	6.2	12.4	9.2	5.6
Interception	87.4	92.3	93.4	84.8	90.2	94.0

FIGURE 2. Photosynthetic carbon assimilation by leaves from three layers of Hevea canopy in response to PPFD. Symbols as in Fig. 1.

DISCUSSION

The pattern of PAR distribution within Hevea canopy reveals that maximum interception of PPFD is effected by upper layer, within 4.6 m from the top of canopy. Only a slight increase in cumulative interception at lower levels of canopy suggests that the relationship between light penetration and leaf density may be non-linear, as observed in apple (Heinicke 1963) and citrus (Jahn 1979). The incidence of greater PAR at the base of canopy than at the top in early hours of clear days was noticed also in coconut (K.V. Satheesan, unpublished). Such pattern may be a feature of trees with trunks bare upto certain height away from the ground. The increase in transmission and reflection by upper layers of Hevea crown on a cloudy day, compared to a clear day, is similar to the findings of earlier workers (Anderson 1964).

Heavy transpiration from middle layer despite restricted stomatal conductance may be due to a steeper gradient of temperature and RH between leaf and air (Kaufmann 1981). The subtle changes in leaf/air temperature or RH, in addition to the light and CO_2 profiles, at different levels in the canopy, should therefore be incorporated in the components of any model for photosynthesis of Hevea canopies.

The reduction in PAR at lower levels of canopy is compensated by the adaptation of leaves, which required only 1/10th of light intensity required by leaves at upper region for maximal photosynthesis. Leaves at the top with maximum availability of PAR, larger leaf area and less chlorophyll resemble closely sun adapted or 'sun' leaves (Boardman 1977). Leaves at lower layers represent the 'shade' leaves.

Further observations on light interception would be useful in selection and manipulation of Hevea canopies for optimal utilisation of solar energy. The data on diffusive resistance, light- and temperature effects on leaves at different strata would help in estimating and modelling canopy photosynthesis in rubber tree, Hevea brasiliensis.

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PHOTOSYNTHETIC PERFORMANCE OF POPLAR LEAVES AT DIFFERENT LEVELS IN THE CANOPY

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1. INTRODUCTION

To model the photosynthetic behaviour of poplar stands, data on the net CO_2-exchange of the leaves are needed. This is measured in the field as a function of photosynthetic photon flux density at different levels in the canopy. This would ensure information on the photosynthetic behaviour of leaves in their natural environment and on possible adaptive mechanisms. Other leaf characterstics measured, which are important for CO_2-exchange and light harvesting capacity are leaf conductance, chlorophyll content, specific leaf area, leaf reflectivity and transmitivity for photosynthetically active radiation and leaf inclination.

2. MATERIALS AND METHODS

In the summer of 1980, measurements on the above said were made in an experimental poplar (Populus trichocarpa X P. deltoides cv. Unal) stand at Wachtebeke, Belgium (Impens et al.,1976). A mast was built so that different levels in the tree could be reached. All measurements were made on fully grown mature leaves.
Net CO_2- exchange (nCER) was measured with a small (20 cm^2), self-constructed, ventilated clamp-on-leaf cuvette, used in an open measuring system with a portable, differentially measuring infrared CO_2 analyzer (BINOS 1.2,Leybold-Heraeus) and Brooks Sho-Rate flowmeters. A LICOR quantum sensor (LI 190S) on the cuvette measured photosynthetic photon flux density (PPFD). Average leaf temperature, as measured with a thermocouple in the cuvette was 25°C. Stomatal conductances for CO_2 (k_s') were calculated from measurements of the conductances for water vapour (k_s) with a Delta-T automatic porometer MkII, as: $k_s'=k_s/1.54$.

Leaf samples of known area taken in the field were frozen in liquid nitrogen and later chlorophyll was extracted in aceton+buffer. Other pigments were removed with silicagel. The absorbance of the solution at 645 and 663 nm was measured with a Coleman-295 spectrophotometer and Chl a and b content was calculated (McKinney, 1941). Dry weights of similar leaf samples were also measured.
Transmission for PAR (τ) was measured in full sunlight by holding leaves over a LICOR quantum sensor in a small black holder. Reflection (ρ) was measured by holding the sensor upside down at 10 cm above a closed leaf layer (0.4 m^2) placed on a black surface. Absortion (α) was calculated as: $\alpha=1-(\tau+\rho)$
Leaf inclination, i.e., the angle between leaf lamina and the horizontal plane, was measured with a protractor.

3. RESULTS AND DISCUSSION

Table 1 shows the results of the nCER measurements of the adaxial and abaxial leaf side at three levels, indicated by the height from the ground level and the mean PPFD. The parameters and the confidence limits are obtained by fitting a rectangular hyperbola to the data points (Acock et al.,1976). The nCER of the whole leaf (adaxtial+abaxial side) is also described by a hyperbola (FIG. 1A, TABLE 1). Despite considerable variability following