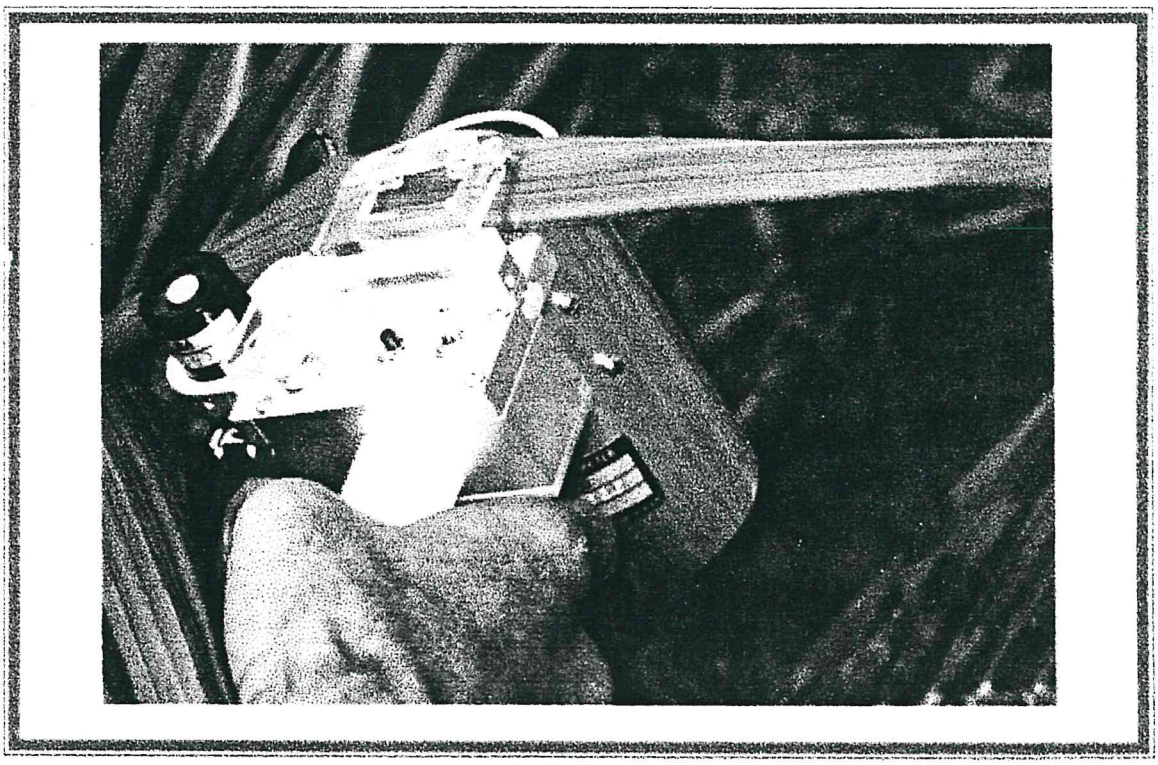
Physiological components of oil palm yield elaboration



Progress Report 3

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March-October 1996

CIRAD-CP 1996/11

Progress Report 3

IOPRI*-CIRAD** Joint Project

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March-October 96

Introduction

Since the end of 1993 a joint research programm within IOPRI and CIRAD have been undertaken on the study of the physiological components of oil palm yield elaboration in North Sumatra, more precisely in the Marihat Research Station. The general aim of this physiological work is already well-described in several previous internal reports (Lamade : Planned Operations 94, 95 and 96; Progress Report 1 and 2). It has been focused on the test of a carbon balance model, derived by Dufrêne (1989) in Ivory Coast conditions on the control family L2T x D10D, with measured physiological parameters in North Sumatra conditions as the maximal photosynthetic rate, the quantum yield efficiency, the extinction coefficient of the studied canopy and the standing biomass of each involved family, the LAI and so one (at least around 14 parameters have been collected directly from field study). This test have been undertaken on both seeds and clonal material at different age : sexual material are dealing with two families presenting constrating yield and morphological caracteristics ("La Mé" origin : DA18D self x LM7T; " Local" origin : BJ13D self x BJ21P) of 10 years old, clonal material are dealing with 3 different clones of 6 years old, respectively MK10 (parent : BJ169 D x RS4 P), MK04 (DS29D x LM2T) and MK22 (RS4T x TI221D).

Simultaneously from this test, news experimental developments concerning the identification of some constraint factors to leaf gas exchange as the VPD (Vapour Pressure Deficit), the leaf nitrogen content, the air temperature, the soil water content (both excess as waterlogging and possible surface temporary "drought") have been emphasized during this third data campaign. These experimental points are exploded with essentially keeping in mind further development in modelling as to reach respectively the second (including a water balance model) and third level (including a nutrient model) in sense of De Wit (De Wit & Goudriaan, 1978) in the next years. From all these physiological investigations, two possible applied field are pointed out : the first one is plant breeding because differences between the respective pattern of the studied material (both sexual and clonal) are significantly obvious and the second one may be in cropping husbandry practices (density planting, prunning and interaction between waterlogging and fertilizer apply for example).

This actual progress report is done with the general goal to, of course, described what was done during the period from March to October 96 in the field, in Marihat, but also to give tools for the data processes and some guideline fo next publications. At the end, proposals will be done for purchase new equipment to raise respectable facilities required in further important physiological investigations in IOPRI- Marihat.

Chap. 1. Realisations

Gas exchange

1. Calibration

In the "planned operation report", several calibrations are proposed : they concerned especially PAR sensors , one , a Il-Cor 190 from meteo park which needs to be re-calibrated nearly every year and those for both analysers LCA4 and LCA2. Also temperature thermistor and the output of the IRGA Cells for CO2 concentration and Relative Humidity were compared to the results (sometimes a direct calibration is not possible) to single sensors as the thermohygrometer Vaisala (see ANNEXE 1 for more specifications).

Results and comments :

Both LCA2 and LCA4 have performed well for CO2, RH and temperature by given similar results. Sometimes the LCA4 system, for unknown reason, presents a quite low output as far as the CO2 concentration is concerned : in that case, zero and span calibration are required (chemical have to be refresh before). Span calibration can be obtained by pumping the air at 10 m height and assuming that the concentration is equal to 350 ppm (total procedure for Span calibration is well exxplained in the notice).

About chemicals : all along this data campaign, the "drierite" was exhausted due to very poor recovering by drying again and other chemical , the Magnesium Perchlorate mixed with glass balls have been used. The silicagel cannot be used refered to its strong interaction with the carbon dioxide.

Meteo

What was done before in during 93-95 :

A first calibration have been done with a JYP 1000 (see ANNEXE 1 for more details on specification) in April 94 :

From 278 points following regression was found :

$Y = 0.0071\ X - 0.00197$ (1) ($R2 = 0.999$, $df = 278$) where Y = amount of radiation measured by IL-190SA in mV and X = amount of radiation measured by the JYP sensor (as a reference) in µmol.m-2.s-1. From that calibration, a new value for the multiplier (MULT) can be obtained with

Logger). We get following regression :

Il-Cor = 0.2205 * S94 BL (r2=0.99, dl=153)
Il-Cor =0.2439 * S92 BL (r2=0.99, dl= 153)

With the reference sensor of the begining (Fig. 1)

Pont = 0.97 * S92 Bl - 0.0025
Pont = 1.08 * S 94 BL - 0.0229

It's possible to determine a mean value for the new calibration of the Il-Cor

* S 94 BL 1 mV Il-Cor = 444.44 µmol.m-2. s-1
1 mV Il-Cor = 400.445 µmol.m-2 s-1 (401.80 and 399.09)

The total mean value for 1994 is **15.9 MJ. m-2.day-1.** Comparing this value with Forster 's work concerning the evaluation of the global radiation from the % percentage of insolation in Marihat, it can be observed that this one is relatively low (from Forster's work the scale between 1983 and 1989 is 15 to 18)

Table 1. Element of first calibration for the meteo sensor Il-Cor 190SA. File CAL196.WQ1.

	A	B	C	D	E	F
1	"DELTA-T LOGGER					
2	untitled					
3	29/03 08:31:36					
4	29/03 11:37:46					
5	TIMED					
6	Channel number	4	6	13	29	
7	Sensor code	4	VLT	VLT	VLT	
8	Label	4	pont1	pontE	licpor	licpor
9	Unit	4	mV	mV	mV	umol
10	Minimum value	4	0,017	0,066	-0,001	
11	Maximum value	4	21,688	23,752	6,984	
12	29/03 08:33:38	4	9,224	8,432	3,006	935,49
13	29/03 08:34:38	4	9,400	10,224	3,055	950,74
14	29/03 08:35:38	4	9,512	10,328	3,085	960,08
15	29/03 08:36:38	4	9,544	10,360	3,097	963,81
16	29/03 08:37:38	4	9,648	10,480	3,127	973,15
17	29/03 08:38:38	4	9,744	10,592	3,161	983,73
18	29/03 08:39:38	4	9,792	10,640	3,169	986,22
19	29/03 08:40:38	4	9,904	10,744	3,208	998,36
20	29/03 08:41:38	4	10,016	10,864	3,241	1008,63
21	29/03 08:42:38	4	10,104	10,968	3,271	1017,96
22	29/03 08:43:38	4	10,200	11,072	3,305	1028,54
23	29/03 08:44:38	4	10,272	11,144	3,327	1035,39
24	29/03 08:45:38	4	10,320	11,192	3,344	1040,68
25	29/03 08:46:38	4	10,384	11,264	3,361	1045,97
26	29/03 08:47:38	4	10,440	11,304	3,376	1050,64
27	29/03 08:48:38	4	10,536	11,408	3,407	1060,29
28	29/03 08:49:38	4	10,632	11,504	3,433	1068,38
29	29/03 08:50:38	4	10,712	11,600	3,463	1077,71
30	29/03 08:51:38	4	10,840	11,736	3,504	1090,47
31	29/03 08:52:38	4	11,000	11,912	3,558	1107,28
32	29/03 08:53:38	4	11,152	12,080	3,608	1122,84
33	29/03 08:54:38	4	11,240	12,176	3,635	1131,24

the following calculation :

$$\frac{2.708\ \text{mV}}{1000\ \mu\text{mol.m-2 s-1}} \times \frac{1\ \text{volt}}{103\ \text{mV}} \times \frac{1}{604\ \text{ohm}} = \frac{4.483 \times 10\text{-}6\ \text{Amp}}{1000\ \mu\text{mol.m-2.s-1}}$$

$$\text{calconstant} = \frac{4.483\ \mu\text{Amp}}{1000\ \mu\text{mol.m-2 s-1}}$$

we have Multiplier = (-1)/calconstant *(K)

with "K" as a conversion factor with typical K values for Il-Cor quantum sensor = 1

We have MULT = (-1)/(4.483 µA /1000 µmol.m-2 s-1

What is interesting to know is the correspondance between the output signal of the sensor and the value in µmol.m-2 s-1.
In the notice of Il-Cor, for the IL-190SA Quantum sensor they give 8µA = 1000 µmol.m-2.s-1. To obtain from that sensor an output signal in mV we need a specific adaptor with a resistance of 604 ohms.

We get :

1 mV = 206.95 µmol.m-2 s-1

After first calibration in April 94, the signal is more "weak" :

We have **1 mV = 369.30 µmol.m-2.s-1**

There are two way to join this result :
1. 1/(4.483 µA/1000 µmol) = 223.06

1 µA = 223.06 µmol and with an adaptor equal to 604 ohm we get last results.
2. Another way is to use the calibration with the "Pontailler sensor ". The specific value of the "Pontaillier" sensor is

1mV = 95 µmol.m-2 s-1

We get from equation (1) 1000 µmol = 2.70 mV

1 mV = 1000/ 2.70 = 370.37 µmol.m-2.s-1

In December 94, It have been done a new calibration with 2 other "Pontailler" sensor , the S94 BL and the S92 BL. All sensors were connected to a Delta-T Devices data logger (AT Delta-T

HME 32 HUMIDITY CHECKER

Humidity checker HME 32 is used to check the accuracy of the calibration of Vaisala humidity measurement instruments. The operation of the calibration checker is based on the humidity equilibrium of the air surrounding a saturated salt solution. The value of the relative humidity in the air depends on the salt solution used. The humidity checker consists of a body which has two plugs for different probe diameters and a capsule which contains the salt solution.

CHECKING PERIOD AND TEMPERATURE

When a new humidity capsule is mounted on the body, the checker must not be used for one hour; during this time the body reaches the same humidity with the capsule. After this the checker is ready to be used. The minimum checking time is 10 minutes.

CARTRIDGES FOR DIFFERENT HUMIDITY RANGES SHOULD NOT BE USED IN THE SAME BODY AS THE HUMIDITY STABILIZATION PERIOD MAY BE UNREASONABLY LONG. SHAKING THE HUMIDITY CHECKER SPEEDS UP THE HUMIDITY STABILIZATION.

The best results are achieved by performing the checking in a temperature of +10...+30 °C (LiCl above +18 °C).

STORAGE

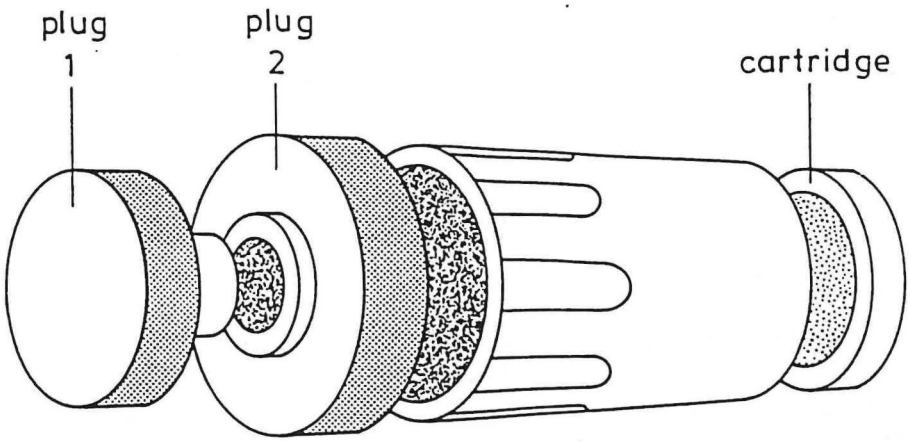
The humidity capsules are delivered in foil bags in which they can be stored for approximately two years. When opening a NaCl or K_2SO_4 bag you may find some dampness in it, but this is quite natural and does not mean the capsules are leaking. Simply wipe the capsules clean. If the foil bag has been opened but the aluminium foil has not been removed, the capsule will be good for six months. With the aluminium foil removed and mounted on the body closed with plugs, the capsule is usable for two months. Removed from the body with no aluminium foil on it, the capsule remains usable from a few days to a few weeks depending on ambient conditions. The storage temperature should be 0 ... +60 °C, and for LiCl capsules +18 ... +60 °C.

USAGE

The humidity checker HME 32 can be used to check probes of 12 mm and 18.5 mm diameter. When a probe of 12 mm diameter is checked, plug 1 is removed and when a probe of 18.5 mm diameter is checked, both plugs 1 and 2 are taken out. During the checking the sensor protection must be removed.

Do not hold the humidity checker in your hand when checking a sensor, as this will raise the temperature of the checker and distort the reading.

Note. LiCl is harmful if swallowed. If it comes into contact with your skin, rinse with water.



CALIBRATION

If the probe after the humidity stabilization period does not give a correct reading within ±5 %RH, we recommend that it is recalibrated with HMK 11 calibrator or it is sent to Vaisala representative for calibration.

TEMPERATURE EQUILIBRIUM

The HME 32 and the probe to be checked must be at the same temperature before checking.

A temperature difference between the probe and HME 32 checker causes an error which has an effect on the interpretation of measuring results. For example, a temperature difference of 1 °C at the humidity of 97 %RH causes an error of 6 %. The corresponding error is smaller when the reference value of relative humidity is smaller.

A cold probe can even reach a dewpoint in the checker; water may condense on the sensor and distort the reading. Within the checker the sensor dries very slowly.

GUARANTEE

Vaisala issues a guarantee for the material and workmanship of this product for one (1) year from the date of delivery. Exceptional operating conditions, damage due to careless handling or misapplication will void the guarantee. See the Warranty and the Standard Conditions of Sale of Vaisala Oy.

TECHNICAL DATA

Checking accuracy +20 °C	±5 %RH
Operating temperature	+10 ... +30 °C
Diameter	33 mm
Length	76 mm

Compatible with all Vaisala humidity probes with Ø 12 or Ø 18.5 mm diameter.

Available humidities

11 %RH	lithium chloride LiCl
33 %RH	magnesium chloride $MgCl_2$
54 %RH	magnesium nitrate $Mg(NO_3)_2$
75 %RH	sodium chloride NaCl
97 %RH	potassium sulphate K_2SO_4

In 1996 a new calibration have been done with the newly calibrated PAR sensor of the porometer Il-Cor. Two files can permit to raize a good calibration : CAL196.DAT and CAL296. DAT. A same work and calculation as it is described behind has to be done again for 1996.

2. The new LCA4 software.

On the basis of Dufrêne work, some mistakes have been identified especially on the energy balance equation. Correct formulation can be found in the "Planned Operation". From LCA4 system all data must be entered again throught these calculations before processes. After it can be valuable to compare the both output of the internal LCA4 system and the new one actually proposed.

3. Few comments about the checker of the thermohygrometer Vaisala.

Two chemical humidity checkers have been used to re-calibrate the probe of the Thermohygrometer Vaisala at two different levels of relative humidity :

- 75 % : with a Na Cl cartridge
- 33 % : with Mg Cl2 cartridge

These cartridges and the kit of calibration may be obtained in Vaisala (Helsinki, Finland). For the use of this simple and cheap method, only one constraint has to be taken into account : to wait carefully around 10 minutes to make the reading.

Experiments

1. Variation of the maximal photosynthetic rate with the leaf rank, the leaflet position and the leaf nitrogen content

Investigations have been started in the clonal trial BJ 26 on following trees and leaf rank (see Table 2). At the same time leaf nitrogen analysis have been done on a basis of 10 leaflets around

the point B per leaf rank per studied leaves.

Last year on other plot BJ 27 S, on five trees per clones, the resultsfor N (% of dry matter) was (MK10 : 15/7, 15/29, 14/27, 13/28, 16/27
MK04 : 7/22, 5/22, 5/23, 7/21, 8/21
MK22 : 10/22, 10/25, 12/25, 9/22, 12/24)

leaf rank	MK22	MK10	MK04
1	2.82	2.65	2.866
9	3.13	3.03	3.003
17	2.83	2.77	2.847
25	2.67	2.65	2.668
33	2.5	2.47	2.16
41	2.3	2.2	2.008
49	1.95	2.03	2.05

Table 3 . Results of nitrogen leaf analysis on studied trees

Clone	tree	leaf rank	N (%)
MK04	11/4	3	2.77
MK04	11/4	9	2.60
MK04	11/4	17	2.71
MK04	11/4	30	2.18
MK04	11/4	38	2.08
MK04	12/4	9	3.47
MK04	12/4	17	2.73
MK04	12/4	25	2.20
MK04	12/4	33	2.07
MK04	12/4	41	1.59
MK10	6/5	9	3.13
MK10	6/5	17	2.73
MK10	6/5	25	2.21
MK10	6/5	33	2.03
MK22	14/10	3	3.09
MK22	14/10	9	3.09
MK22	14/10	17	2.79
MK22	14/10	27	2.39
MK22	14/10	33	2.37
MK22	14/7	9	3.02
MK22	14/7	17	2.78
MK22	14/7	25	2.35
MK22	14/7	33	2.19
MK22	14/7	41	1.95
MK22	14/7	49	1.67

Initially it has been proposed to use the method of the additionnal filter to get more quickly a total PAR response curve to the light. But due to a quite important inertia in the response of the LCA4, just direct photosynthetic measurements have been realized. This experiment required at least to work on a minimum of 5 trees per clone from a range of leaf rank coming from 1 to 49. Until now only these following trees have investigated :
MK10 : 6.5, 5/3, 5/2
MK22 : 14/40, 14/7, 14/10, 14/20
MK04 : 11/4, 12/4

Few more repetitions are needed : can be done during the next campaign !

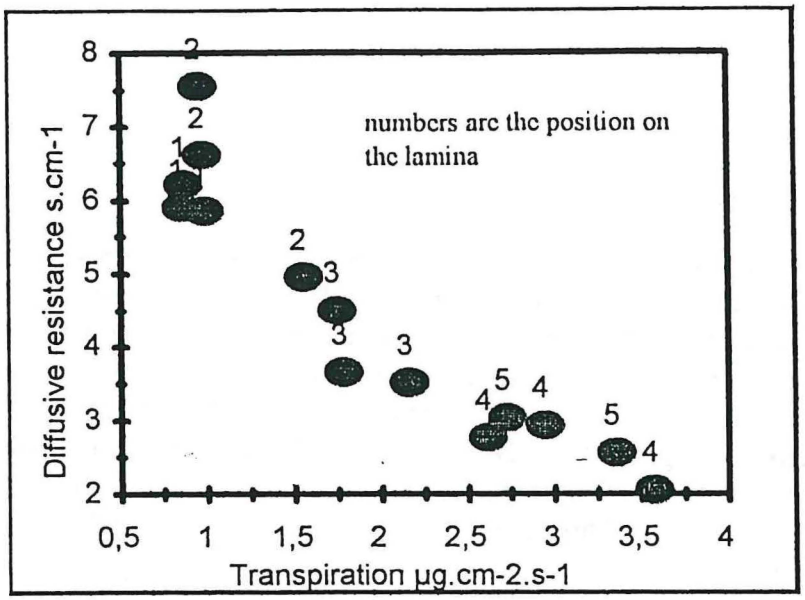
A test of lamina variability and on measurements repetition effect on a same lamina have been done on palm n° 14/40 (clone MK22), on leaf rank n° 3 . A quik ANOVA have shown that the response of porometer is quite stable from one repetition to another, on a non cut leaflet of course. There is also a signficant gradient along the lamina with an increase of observed stomatal resistance towards extremities : this is a new result compared with what has been observed by Dufrêne (1989) but with another equipment from Delta T Device (Mark II and Mark III) that he didn' t pointed out difference along the leaflet.This result may have influence on the way to measure stomatal conductance by only "clipping" the central-upper part of the leaflet where the resistance seems to be minimal.

ANOVA on limb position for

the diffusive resistance (s.cm-1):

	Df	MS	F test	Proba
Total variance	24	1.29		
Variance "Pos"	4	4.17	5.84	0.0029
Residual	20	0.71		

The figure 1 gives a good illustration of the effect of the position on the lamina for the diffusive resistance and the transpiration rate.



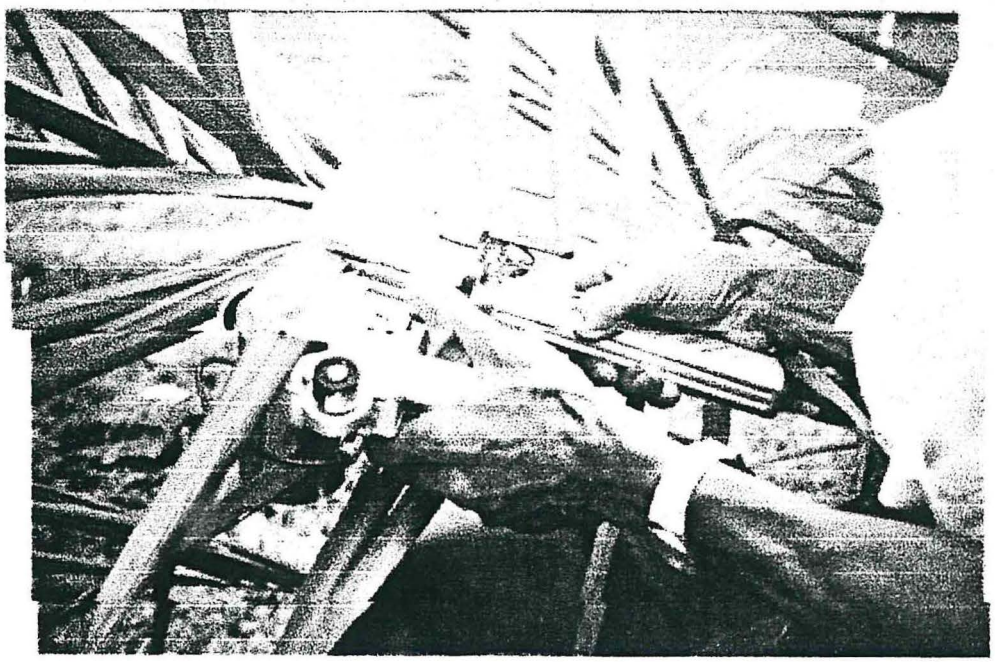
All observations have been done with the respect to minimize the difference between both temperatures between the cuvette and the leaf. Due to hight radiation and occasionnal wind, this difference can rize sometimes more than 1° C. These points have to be neglected in the data process.

The main constraint of this experiment is to get old leaves in good sanitary conditions : that was not the case several times because severe problems (essentially fungus) appears from already the rank number 25.

Concerning the main orientation of the data process, the main work will consist, first by comparing results from LCA4 and the Il-Cor porometer and after to identify the main factor of variation (environmental factors as the VPD, the PAR and the air/leaf temperature and the leaf rank effect) on stomatal conductance. After collecting again more measurements it will be possible to see, if eventually, the stomatal conductance, per se, may become an indicator of the level of plant nutrition in Nord Sumatra where there is no water constraint.

In all calculations the stomatal conductance has to be in mmol.m-2.s-1.

Example of the data file obtained from the measurements with the Il-Cor 1600 on the clone MK04



Waterlogging Experiment . Top : with the same level of water supply : effect of fertilizer application on two years old commercial seedlings (left : N0; right : N1). Down : gas exchange measurements with the PLCN4 chamber (ADC) and the li-Cor steady state porometer 1600 on the same leaflet.

2. *Effect of the waterlogging on leaf gas exchange, on growth and on biomass allocation, interaction with fertilizer application*

Following the planned operation, seedlings have been submitted for around 4 months to temporary waterlogging. Different water supply were apply following treatment "L", "M" and "H":

L : control, standard water supply
M : partially flooded
H : completely flooded.

The control of the water table was control every day by checking the water level in an external plastic tube.

In each water treatment, 3 levels of NPK fertilizer were apply :

NO : no fertilizer
N1 : 35 g of 12/12/17/2 + TE NPK per tree and twice a months during 2 months
N2 : 3 x 35 of 12/12/17/2 + TE NPK per tree and twice a months during 2 months

In addition , before starting experiment 1 liter of a solution of a 2% of Dithane M45 have been put in each pot to avoid pest infestation.

Following measurements have been realized :

Leaf gas exchange :

* Photosynthesis : with the LCA4. At the end of the total treatment, on the leaf n° 4 and on 10 leaflets with 2 repetitions.
- A total of 20 x 45 measurements.
* Stomatal conductance : with the steady state porometer 1600 of Il-Cor, with the same design than for photosynthesis.
- A total of 20 x 45 measurements.

Leaf Area :

- with the Tailliez et al. (1992) method : for each tree, 3 leaves were sampled (see list below) and measured, and after dried.

HN11 : 2; 9; 11	HN25 : 1; 9; 11	MN05 : 2; 9; 12	LN01 : 2; 10; 14
HN12 : 2; 9; 12	HN01 : 3; 9; 10	MN11 : 2; 9; 11	LN02 : 3; 9; 12
HN13 : 2; 9; 11	HN02 : 2; 9; 12	MN12 : 2; 9; 12	LN03 : 2; 9; 12
HN14 : 2; 9; 11	HN03 : 2; 9; 12	MN13 : 2; 9; 12	LN04 : 2; 8; 13
HN15 : 2; 9; 12	HN04 : 2; 9; 11	MN14 : 2; 9; 12	LN05 : 2; 8; 13

HN21 : 2; 9; 11 MN01 : 2; 9; 12 MN15 : 2; 9; 12 LN11: 2; 8; 13
HN22 : 2; 8; 12 MN02 : 2; 9; 11 MN21 : 2; 9; 12 LN12 : 2; 9; 12
HN23 : 2; 6; 8 MN03 : 2; 9; 12 MN22 : 2; 9; 11 LN13 : 2; 9; 12
HN24 : 2; 9; 12 MN04 : 2; 9; 11 MN23 : 2;9; 12 LN14 : 1; 9; 14
LN15 : 2; 9; 12 LN21 : 2; 9; 12 LN22 : 2; 8; 12 LN25 : 2; 9; 12

* Leaf nitrogen content

Leaf nitrogen analysis have been done for each trees before starting experiment to control the nutrient status of each tree (they were already 2 years in nursery when there were used for this experiment) on leaf number 4 with 20 leaflets per sample.

	A	B	C	D	E
1	Waterlogging		N(%)		
2		before	after	gain	
3	HN01	2,02	2,56	0,54	
4	HN02	1,77	1,4	-0,37	
5	HN03	2,01	2,37	0,36	
6	HN04	1,96	2,76	0,8	
7	HN05	2,03	1,12	-0,91	0,084
8	HN11	1,78	1,95	0,17	
9	HN12	2,1	2,12	0,02	
10	HN13	1,92	2,15	0,23	
11	HN14	1,91	1,82	-0,09	
12	HN15	2,14	2,48	0,34	0,134
13	HN21	2,2	2,31	0,11	
14	HN22	2,22	2,7	0,48	
15	HN23	1,83	2,13	0,3	
16	HN24	1,74	2,53	0,79	
17	HN25	1,99	2,65	0,66	0,468
18	LN01	2,23	1,51	-0,72	
19	LN02	1,68	1,51	-0,17	
20	LN03	2,23	1,44	-0,79	
21	LN04	2,27	1,78	-0,49	
22	LN05	2,22	1,37	-0,85	-0,604
23	LN11	2,1	2,33	0,23	
24	LN12	2	2,61	0,61	
25	LN13	2,07	2,27	0,2	
26	LN14	1,58	2,09	0,51	
27	LN15	1,91	2,52	0,61	0,432
28	LN21	2,35	3,08	0,73	
29	LN22	2,23	3,21	0,98	
30	LN23	2,26	2,91	0,65	
31	LN24	2,4	3,01	0,61	
32	LN25	2,17	3,03	0,86	0,766
33	MN01	1,88	1,18	-0,7	
34	MN02	2,05	1,45	-0,6	
35	MN03	2,26	1,44	-0,82	
36	MN04	2,08	1,54	-0,54	
37	MN05	1,7	1,25	-0,45	-0,622
38	MN11	2,15	2,07	-0,08	
39	MN12	1,92	2,08	0,16	
40	MN13	2,17	2,39	0,22	
41	MN14	2,07	2,25	0,18	
42	MN15	1,83	2,38	0,55	0,206
43	MN21	1,95	2,53	0,58	
44	MN22	2,13	2,79	0,66	
45	MN23	2,19	2,84	0,65	
46	MN24	2,05	2,64	0,59	
47	MN25	2,29	2,53	0,24	0,544

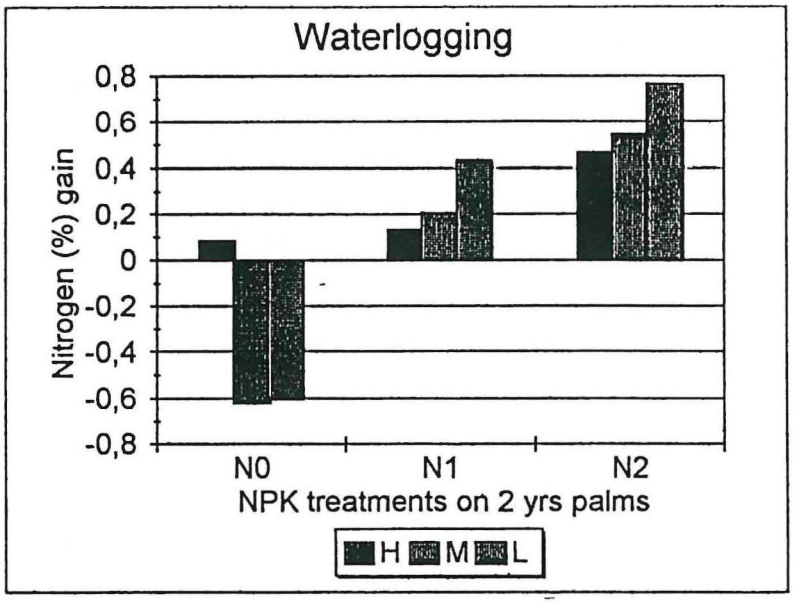


Fig. 2. Effect of the watrlogging on fertilizer efficiency

* Biomass

- Above ground biomass : all leaflets of all leaves , petioles and rachis for all the trees have been collected and dry (leaflets : 12 hours, 85 °C; petioles and rachis : 48 °C, 85 °C). Each collet have been isolated from petioles bases and roots and dry during more than 3 days. Every part have been weighed precisely.

- Below ground biomass : roots have been completed collected by washing the total pot pack upper a sieve, and dry during more than two days at 85 °C and separated into only two categories (the primary roots in one category and the the II, III and IV in another one) due to time constrainst and lack of human ressources.

- Petioles diameter and rachis lenght were measured for all trees and all leaves.

* Individual Foliage Density using the PCA 2000 LAI (Li-Cor)

The evaluation of the LAI of individual tree bring to conceptual problem and the general methodology which was apply for 6 years old planting palms (Lamade & Setiyo, 1996) cannot be used in the same way for discontinued canopy (given by a group of young planting palms for example). For this reason and following the advices of the Li-Cor notebook other methodology was tested :

Only one data logger was used with one A reading and 8 B readings for each tree, with

a view cap of 45 °. All measurements were done with the sensor, for the B readings, oriented from the trunk towards outside. For each tree, the distance vector has been measured (half of the diameter). The LAI, when the distance vector is fixed is becoming the foliage density; At the same time the individual plant canopy volume was also determinate for each tree by using coordinates (6 to 10 for each palm) and the procedure "Canopy Model" of the software C2000.

The best accurency ("calibration") has to be found between an indirect method using the PCA 2000 in a simple way and what can be obtained from the evaluation of the total leaf area of each canopy.

Example of file :

Without option on distance vector :

File	Date	Time	BIBIT	LAI	SEL	DIFN	MTA	SEM	SMP
5	13 Aug	8:23:16	HN04	0.92	0.28	0.000	0	11	8

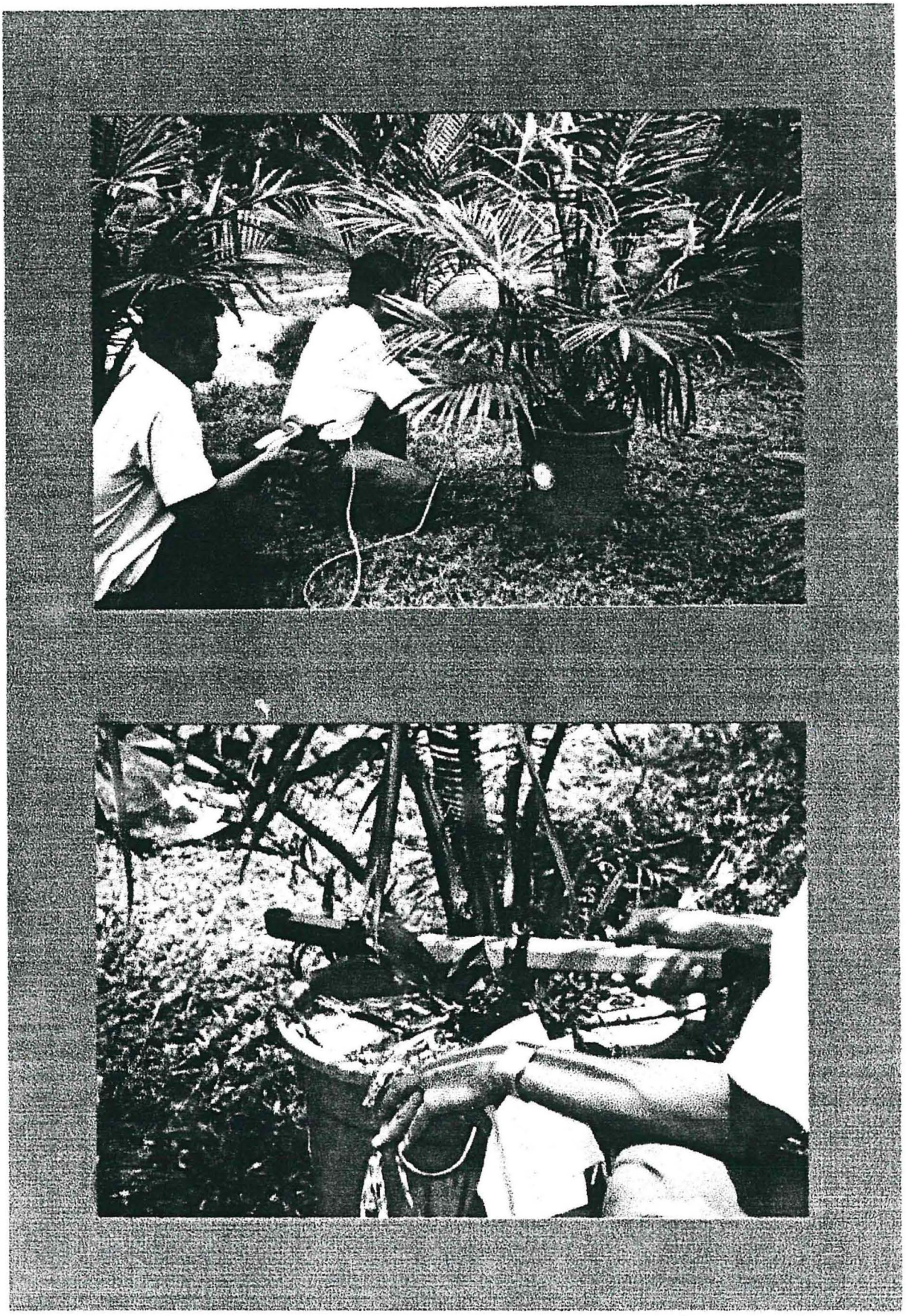
ANGLES :	7.000	23.00	38.00	53.00	68.00
CNTCT :	7.991	7.340	4.044	3.123	2.671
STDDEV :	7.991	7.340	4.044	3.123	2.671
DISTS :	1.008	1.087	1.270	1.662	2.670
GAPS :	0.0	0.0	0.0	0.0	0.0

A	1	08:23:37	2.823	5.502	6.019	6.481	7.849
B	2	08:24:04	0.873	1.646	2.198	1.365	1.044
B	3	08:24:12	0.883	1.288	4.059	6.947	5.423
B	4	08:24:23	2.381	7.762	17.06	20.81	11.10
B	5	08:24:36	2.350	3.831	13.30	24.81	15.85
B	6	08:24:46	1.574	2.751	6.124	13.38	9.584
B	7	08:24:55	0.887	2.495	4.392	5.600	1.881
B	8	08:25:03	0.487	1.458	1.319	1.210	1.037
B	9	08:25:12	0.439	0.648	0.904	1.064	2.161

With option on the distance vector :

FILE	DATE	TIME	BIBIT	BIBIT	LAI	SEL	DIFN	MTA	SEM	SMP
6	13 AUG	08:27:07	HN04	HN04	1.41	0.44	0.428	51	2	8

ANGLES	7.000	23.00	38.00	53.00	68.00
CNTCT	0.852	0.799	0.666	0.700	0.682
STDDEV	0.551	0.598	0.705	0.846	0.623
DISTS	1.192	1.192	1.192	1.192	1.192
GAPS	0.363	0.387	0.453	0.435	0.444



Foliage density evaluation with the PCA LAI 2000, waterlogging experiment

A 1	08:27:25	2.694	5.377	6.533	6.935	7.929
B 2	08:27:49	2.904	7.013	14.45	24.31	10.10
B 3	08:28:03	1.779	3.955	5.472	13.78	14.10
B 4	08:28:11	0.869	2.143	7.018	7.668	2.059
B 5	08:28:21	0.639	1.349	1.549	1.306	1.069
B 6	08: 28:28	0.560	0.767	1.043	1.519	4.209
B 7	08:28 :38	0.370	0.719	0.756	0.395	1.543
B 8	08:28:49	0.742	2.665	3.126	3.759	3.305
B 9	08:29:03	2.019	3.832	8.183	12.59	8.259

From that base what can be done ?

- with the file 5 use the *Canopy Model (Individual)* , enter 6 coordinate (assuming that the palm is like a cylinder), compute with the *Standard Option* which remove the bad B readings automatically and get new distant vector again with a new value of the foliage density to compare with direct measurements. There is no need to remove ring...(personal point of vue);

- Comparison with the option on distant vector on file 6.

3. Identification of stomatal limitation and non-limitation of the photosynthesis in relation with factors as soil moisture, VPD, night temperature and assimilats.

Only two days of fully observations have been done with a complet set of physiological observations as :

- leaf photosynthesis with the LCA4 (ADC, GB)
- Leaf stomatal conductance with the steady state porometer Il-Cor 1600 (Il-Cor, USA)
- Leaf respiration - close system- with the LCA2 (ADC, GB)
- Soil respiration - close system - with the LCA2 (ADC, GB)
- Rachis respiration - close system - with the LCA2 (ADC, GB)
- Soil Water potential with the STM2150 Multiway Mercury Tensiometer (SDEC, Fr)
- Variation of the specific leaf area by sampling small limb discs

Other parameter as the night temperature (in fact we are only interested by the minima) can be collected from Marihat Meteo Station.

The main constraint during that year was to get a fully sunny day or nearby : that was quite impossible during last months. It is the reason why this experiment has to be undertaken during more drier period which can be really sometimes impredictable in North Sumatra.

In a practical way what was important to notice ?

That the system of the STM2150 Multiway Mercury Tensiometer is easy to install quite quickly (around two hours to get equilibrium of the mercury in the plastic tubes) and is quite sensitive to get variation along the day.

Technical aspect

Multiway Tensiometer system with Mercury STM 2150 (SDEC France) [1]

Introduction

This system is functionning on the same base as the mercury manometer and presents avantages to be very precise in the measurement.It is used to measure the soil water potential. The principle is to measure a depression in a air close system from a transfert of the water thorough a porous ceramic. This one is connected to a PVC tube, both full of water and in relation throught a capillary tube to a mercury tank. Several cases may be bring out :

1. The soil is saturated : there is no water flux between the porous ceramic and the soil and as a consequence no depression in the whole system, the mercury is not going up the capillary tube.

2. The soil is under water stress : the soil, in that case, is "pumping" the water from the ceramic and a depression occurs in the system and the mercury will go up in the capillary tube.

More the mercury will go high, more the soil will be under water shortage.

A great precision in the measurement can be obtained from the direct reading in millibar on the rod.

A. Procedure for field installation

a. Preparation of the tensiometric stick

For all experiment, it is preferable to use water released from gas : this one can be obtained from boiling the water during 10 minutes.

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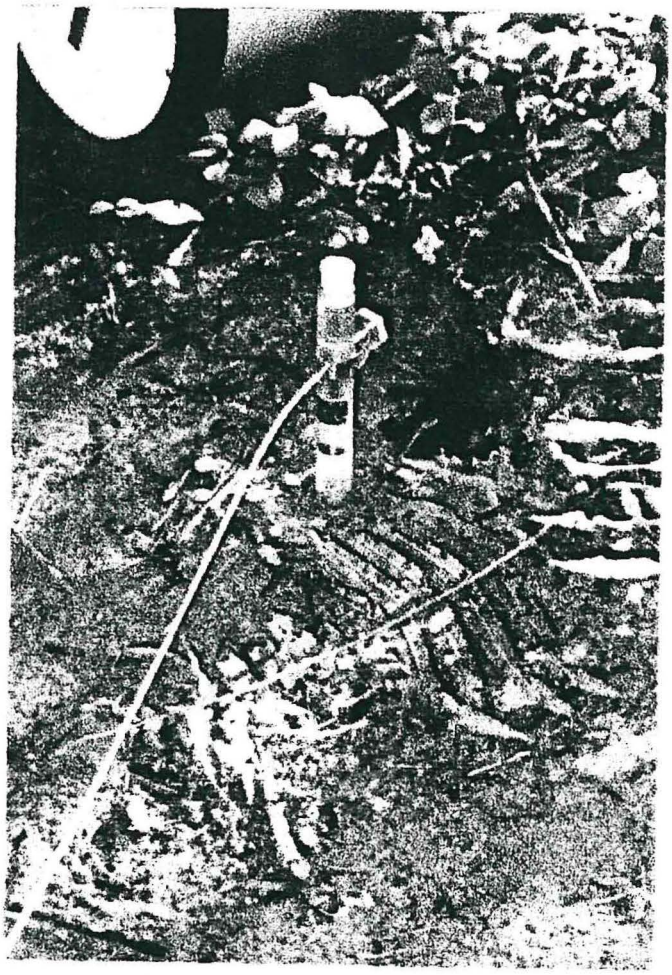
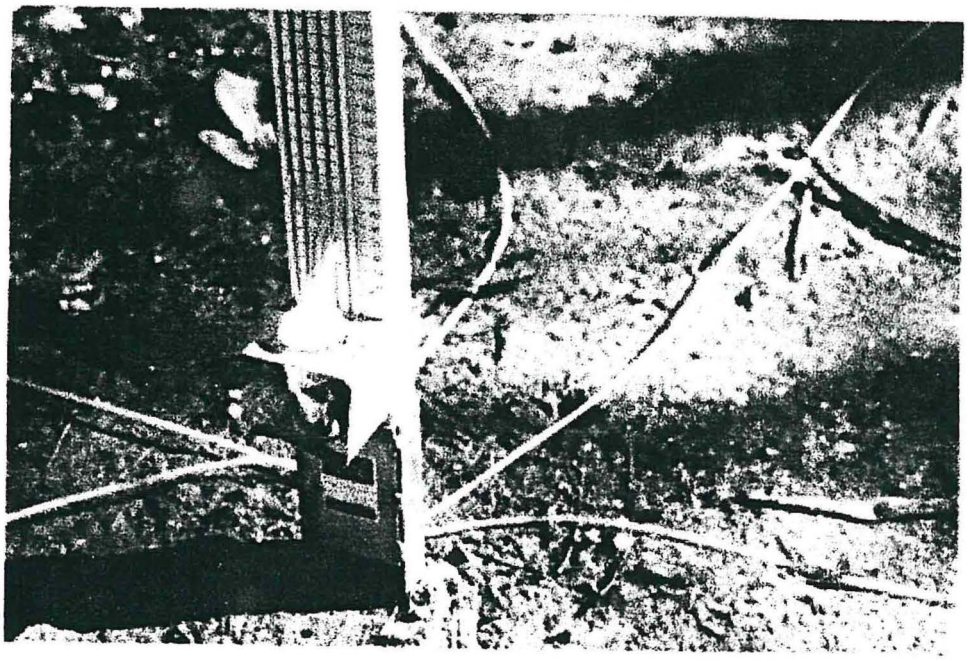
[1]SDEC France 19, rue Edouard Vaillant 37 000 Tours (France) tel : 1 47 92 22 00, Fax 1 47 92 86 16.

MULTIWAY TENSIOMETER WITH MERCURY STM 2150 , SDEC (France)





- A. The porous ceramic has to be put in the water during around 8 hours. Be carrefull that the water level is always over the ceramic.

- B. Take out the porous ceramic from the water, fill completly the PVC tube with water and wait during 30' that a part of the water is coming out.

-C. Fill again completly the PVC tube with water and put the stick in the water again. Then pull the piston, which is before introduced in the top of the stick, to inverse the water flow thorought the ceramic. The water will "boiled" inside the PVC tube.

-D. The tensiometric stick at that time is in stand-by and may stay several months like that in the water before being put in the field.

IMPORTANT :

The porous ceramic presents extremely small pores (3 µm < pores < 6 µm). These one may be cloged up very quickly by the contact with a fat thing (especially fingers) : it that case the performance of the ceramic will be dramatically decreased. It is strongly reccommended to don't old the tensiometer by the porous ceramic side.

b. Drilling for the field installation of the sticks

The holes for the sticks have to done with the maximum of precision to avoid run-off between the ground and the stick. The maximum diameter size for the auger will not exceed 21.5 mm.

c. The size of the capillary tubes and the installation of the tensiometer in the soil

These will not exceed 10 m to avoid gas accumulation in the system. The capillary tube as to go until the bottom of the porous ceramic. It is reccommended to introduce with the PVC sticks in the hole some mud to steady contact between the soil and the sticks.

Before starting, all sticks have to be completly filled with water and the pressure syringe will be used to push the water and the air out of the system. The level of mercury will be ajusted by moving the bottle of mercury along the rod to get Δ (lenght between the level of mercury in the bottle and the zero of the rod equal to :

Y/ 12.6 cm , where Y is the distance between the level of mercury in the bottle and the soil surface (see figure).

After, very precise reading will be done directly looking the scale of the rod in mbar (negative)

Some theoretical points :

ζ is the high of the mercury in the manometer (expressed in cm) and Y, the distance between the level of the mercury of the bottle and the surface of the soil. At the level of the interface mercury/water in the manometer, the pressure PA

is the same in the water and in the mercury. Pressure will be spread hydrostaticaly in all the colonne:

(1) PE = PA + ρω g (ζ + Y + Z) where ρω is the volumic mass of the water.

Between A and B : (2) PB = PA + ρHg g ζ where ρHg is the mercury volumic mass.

We get also : PA = PO (atm) and from (1) and (2) it is possible to get

PE = (PO - ρHg g ζ) + ρω g (ζ + Y + Z) with Pω the pressure of the water in the soil at the level of the porous ceramic.

By convention, this value will be caracterized by h defined as follow :

h = (Pω- PO) / (ρω g)

If we suppose that the water pressure between the interior and the exterior of the porous ceramic is in equilibrium, then ρ = PE and we get :

h .ρω g + PO = PO - g ζ (ρHg - ρω) + ρω g (Y + Z) with :

ρHg = 13.6 g/cm3, ρω = 1 g /cm3

h = 12.6 ζ + Y + Z or H = h - Z

and H = 12.6 ζ + Y

For example if the tensiometer is depth Z = 50 cm, the scale indicates a charge H = - 450 m bar, the effective pressure at the level of the tensiometer will be h = - 400 mbar.

4. *Estimation of the photosynthesis and the canopy conductance in relation with the seasonnal evolution of the soil water balance in North Sumatra.*

In relation with an important work undertaken for the elaboration of a water balance model (thesis), leaf gas exchange measurements have been done on the clone MK60 in way to asses canopy photosynthesis and the all canopy conductance and this all during a season. Following what was done in Ivory Coast by Dufrêne leaf level 7/9/10 , 16/17/18 and 24/25/26 were investigated with the LCA4 and Il-Cor 1600 steady state porometer.

For the stomatal conductance only 10 leaflets have been cutted from in situ leaves at each studied level (it has been noticed that after cutting, the leaflet staying in the shade, there is no significant effect of the cutting during at least 5 minutes) and five points along the limb have been measured in way to get the mean value of all the limb.

Photosynthesis measurements have been done at the top of an aluminium tower (3 m height) more specially (due to the difficulty to work on it) on leaf 17, considering five leaflets per leaf and five points per leaflets. Measurements have been done once monthly. All results will be related with

other parameter as the soil water potential (mbars), the soil volumic humidity (%), the leaf water content, the rainfall and the potential evapotranspiration (mm.day-1).

From these observations, a model of stomatal conductance may be elaborated. Already some good interelation between the stomatal conductance and the leaf photosynthesis have been pointed (fig. 2).

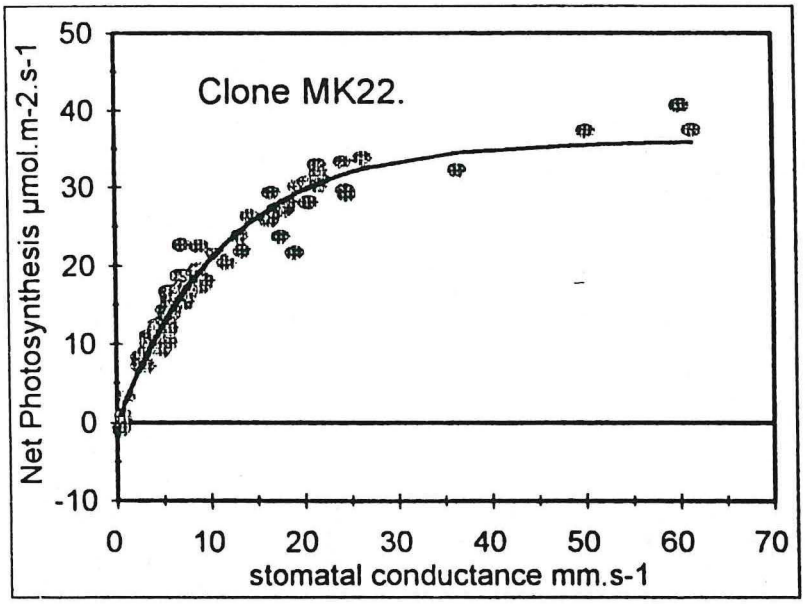


Fig. 2. Relation between Net Photosynthesis and stomatal conductance at saturated light.

This may be represent a first step to derive a link between a carbon balance model and a water balance one at the plant scale.

PHENOLOGY

The observations routines already started in march 94 on both families "La Mé" and "Local BJ" have been maintained all along this year (see below one file sample).

To process data 3 years observations (a minimum) are required. From CIRAD-CP reccomendations (Tailliez, passation de service, CIRAD-CP, 1992) for the set of observations done in Lamé during 6 years , following parameters may be calculated :

No. Palm:155/5 NLEAF	DEMISS	DRANK1	DCUT	LPET	LRAC	SEX	DFLOW	DHARVE	WINFLO
45	26/04/94	13/06/94	01/05/96	139	630	M	23/01/95	//	//
46	05/05/94	30/06/94	25/10/95	130	625	M	13/02/95	//	//
47	05/05/94	21/07/94				M	27/02/95	//	//
48	24/05/94	11/08/94	14/08/96	120	670	M	14/03/95	//	//
49	13/06/94	25/08/94	22/05/96	120	680	M	31/03/95	//	//
50	20/06/94	01/09/94	01/05/96	138	610	F	21/04/95	Rat	
51	30/06/94	12/09/94	12/06/96	135	650	F	05/05/95	25/10/95	25000
52	21/07/94	26/09/94	10/07/96	150	670	M	23/05/95	//	//
53	15/08/94	06/10/94				M	30/05/95	//	//
54	25/08/94	25/10/94				M	20/06/95	//	//
55	//	22/11/94	07/08/96	120	628	M	04/07/95	//	//
56	//	29/11/94	14/08/96	120	630	M	21/07/95	//	//
57	//	08/12/94	22/05/96	125	675	M	18/08/95	//	//
58	//	26/12/94	05/06/96	135	679	M	25/08/95	//	//
59	29/10/94	09/01/95	12/06/96	130	635	M	08/09/95	//	//
60	07/11/94	26/01/95	10/07/96	155	680	M	22/09/95	//	//
61	22/11/94	02/02/95				M	03/10/95	//	//
62	29/11/94	23/02/95				F	14/11/95	22/05/96	20000
63	08/12/94	17/03/95	07/08/96	145	630	F	30/11/95	05/06/96	22000
64	26/12/94	28/03/95	14/08/96	145	650	F	15/12/95	12/06/96	35000
65	09/01/95	18/04/95	10/07/96	157	700	F	05/01/96	10/07/96	28000
66	26/01/95	23/05/95				M	05/01/96	//	//
67	02/02/95	05/06/95				M	23/01/96	//	//
68	23/02/95	16/06/95				F	12/02/96	07/08/96	27000
69	17/03/95	04/07/95				F	08/03/96	14/08/96	38000
70	28/03/95	01/08/95				A	//	//	//
71	18/04/95	18/08/95				M	19/03/96	//	//
72	23/05/95	08/09/95				M	01/04/96	//	//
73	05/06/95	26/09/95				M	18/04/96	//	//
74	16/06/95	03/10/95				F	29/04/96		
75	04/07/95	20/10/95				F	31/05/96		
76	08/09/95	03/11/95				M	04/06/96	//	//
77	12/09/95	17/11/95				F			
78	26/09/95	26/11/95				M	25/07/96	//	//
79	03/10/95	04/12/95				M		//	//
80	20/10/95	19/12/95				M	23/08/96	//	//
81	03/11/95	09/01/96							
82	17/11/95	19/01/96							
83	26/11/95	30/01/96							
84	04/12/95	08/02/96							
85	19/12/95	15/02/96							
86	09/01/96	11/03/96							
87	19/01/96	11/04/96							
88	30/01/96	25/04/96							

* At the level of each leaf :

- variation of the period between the spear leaf and rank n° 1

- variation of the period between Rank 1 and the anthesis of the corresponding inflorescence
- variation of the period between the rank 1 and the harvesting
- variation of the period between the rank 1 and the cutting of the leaf

* At the rank level :

- number of spear leaf when leaf n° N is rank 1
- rank of the leaf n° N during anthesis of the corresponding inflorescence
- rank of the leaf N when harvesting
- rank of the leaf N when cutting

Remarks :

The main constrainst of these observations routines is finally to enter new observations in the computer file which normally is an easy job. Routines to entering data in the computer file have to be done every week , on Friday for example.

CARBON BALANCE MODEL and SIMPALM software

A first test of the Dufrêne model has been derived on two adult families with the meteorological conditions of the Marihat Research Station with an important set of parameters. Results can be seen with what was presented for PIPOC 96 (see below)

Test of the Dufrêne's production model on two contrasting families of oil palm in North Sumatra".

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Abstract

A simulation model of production have been established by Dufrêne (1990) on the control family L2T x D10D in Ivory Coast conditions. The results of the simulation in the african ecological environment shows a high compatibility with the observations in the field when the oil palm are in potential conditions without water or nutrient constraint. It was highlighted that a lack of radiation may be at the origin of the relative low yield observed in Africa. To test the validity of this model in indonesian conditions, a large set of parameters (at least 14 with both physiological parameters such as the maximal photosynthesis, the quantum yield, or biometrical one such as the leaf area, the number of leaves per crown, the specific leaf weight, the trunk height, the root biomass and so one) have been studied on two contrasting families (one belonging genetically to the Lamé origin, the other to a local material). At the same time, a precise recording of daily radiation was undertaken to get an appropriate "meteo input file" for the model. A first comparaison between both situation "Lamé" and "Marihat" taking into account only the difference of radiation (around 2 $MJ.m^{-2}.day^{-1}$ more for indonesian conditions) shows a "theoretical" increase of annual photosynthetic assimilates of 4%, a general decrease of respiration cost of 2% due to lower daily temperatures in Marihat, an increase of 18 % of the annual production of the dry matter at the plantation level and an important increase of FFB (fresh bunches) of around 80 % (from 18 $tFFB.ha^{-1}$ to 30 $tFFB.ha^{-1}$). The test of the model on the two families with an "indonesian meteo file" based on theirs respective biometrical and physiological patterns shows differences in their respective yield, giving an advantage of near 5 t of FFB for the "Lamé" group (theoretical production : 40.1 $tFFB.ha^{-1}$) compared to the local material, "Local BJ" (35.8 $tFFB.ha^{-1}$). This is due essentially to a higher maintenance respiration cost for "Local BJ". The observed yield was around 24 t FFB for the Lamé group and 17 tFFB for the local material. This difference between estimations and the observations in the field may be due to a lack of photosynthetic assimilates consequence of pest damage to foliage and/or negative effect on root system due to frequent temporary flooding.

Introduction

A priliminary carbon balance model has been established by Dufrêne (1989; et al.,1990) on oil palm, especially on the control family of CIRAD " L2T x D10D ". Belonging to the "de Wit" nederland school (de Wit et al., 1978, 1982), it is a determinist one, iterative and runs with an input meteorological file composed by daily recording of radiation and temperature. This model is based on physiological parameters as the maximum photosynthetic rate, the apparent quantum yield or optical properties of leaves as the extinction coefficient, K, and biometrical trends as annual growth rate of organs and standing biomass. All parameters have been measured, in situ, in La Mé (Ivory Coast) and the final results of the simulation fit well with the potential expected yield in this agroecological zone. The model is functionning without nutrient and water constrainst : it is belonging to the first level of production in sense of de Wit at al. (1982). The daily gain of carbon, throught the photosynthesis is used to cover the respiration and the vegetative growth needs. At the end of the year, the remaining carbon, theoretically located in a "reserve pool" is allocated to the bunches (Fig. 1) . To extend the scope of this model in different ecological region, especially in North Sumatra (Indonesia), an important physiological study has been undertaken on two adult families during two years at the Marihat Research Station, contening both biometrical and physiological features of the studied material. A precise daily radiation recording has been realized during all 1994 and used to elaborate an appropriate input meteo file. For each family, a set of 24 trees was selected and their total phenological development (rhythm of leaf emission, sexualisation, anthesis, bunch harvesting) have been following weekly. The intercepted light by the respective canopy of both families has been measured during several days. Finally, the new package of parameters was tested with a C++ computing interacting version "SIMPALM " (Bonnot, 1995) of the Dufrêne 's model. The results of both simulation in Lamé (Ivory Coast) and in Marihat (Indonesia) will be compared in a way to, first, test the hypothesis of a radiation constraint in Africa and second, to identify possible environmental constrainst factors in North Sumatra.

Materiel and methods

* Physical environment

The study was conducted in Marihat Research Station (Balai Penelitian Marihat, 2°55' E, altitude 369 m, North Sumatra, Indonesia) in a genetic trial situated at Andarasi (PTP VII, Afdeling III) near the Station. Meteorological daily recording in Marihat from 1972 allow to characterize local conditions. The total annual sunshine duration is 2087 hours (average 1984-1995), the mean annual rainfall is 2890 mm (average 1972-1994) and the annual mean temperature is 24.7 °C (mean maxima : 29.8 °C; mean minima : 20°C). Over the same period (1972-1994), the mean relative humidity recording three time a day, at 7h, 13h and 18h is respectively 92.9%, 68.3 % and 84%. The global radiation has been estimated (over a period from 1972-1994) from hourly visible radiation recording (with a quantum sensor Li-Cor, type Li-190 SA) is equal to 16.24 $MJ.m^{-2}.day^{-1}$ (Lamade et al. 1996). In 1994, at

Marihat, the global daily radiation varied from 12.1 $MJ.m^{-2}.day^{-1}$ in october to 18.6 $MJ.m^{2}.day^{1}$ in July with an annual mean equal to 15.1 $MJ.m^{-2}.day^{-1}$ .On figure 2, it has been plotted the daily variation of S (global radiation) and the mean daily temperature during one year (1994) : these values will be used for the input meteo file for the model. On the same figure we have plotted also, in way to compare with Ivory Coast, the daily recording with the global radiation and the temperature used as an input file in the model to make running it in African conditions. The global radiation estimated in North Sumatra put this agroecological zone in middle comparing with what was observed in Ivory Coast (Dufrêne et al. 1990) with an annual mean of 14.2 $MJ.m^{-2}.day^{-1}$ and in Malaysia (19.6 $MJ.m^{-2}.day^{-1}$).

* Material

An important phenological and biometrical study was done on two contrasting families ("Lamé" : block MA007S, cross n° 4, DA18D self x LM7T self; "Lamé" : block MA008S , cross n° 8 ,BJ13D self x BJ21P, "Local BJ") with 24 trees per family (composed by two plots of 12 trees for each). The planting density is around 128-130 trees/ha and the year of planting is 1986. On Table 1 it is possible to see theirs vegetative and reproductive characteristics during 94/95.

* Methods

On Dufrêne et al. (1990) a list of 24 variables is given to test the model. This list evolves both physiological parameters and environmental one. This list of variables is given on Annex 1 and we have highlighted those that were effectively measured in Marihat on both studied families.

1. Canopy assimilation and light interception

- Photosynthesis

Daily photosynthesis was measured during sunshine hours from 8.30 h to 18h with an analyser IRGA portable from ADC (LCA2) and a leaf chamber (PLCN) following the methodology already used by the autors on other material (Lamade and Setiyo, 1996a) with the difference that all equipment and observers were put at the top of a 6 m heigh aluminium tower due to the height of the trees (trunk height : more than 4 m). All measurements were conducted on the leaf n° 17 supposed to be representative of the all canopy and more specially on leaflets around the B point.

The photosynthesis response to the light can be ajusted following Dufrêne and Saugier (1993) according to an equilateral hyperbola :

$$A = (a.\ Io\ Ainf) / (a\ Io + Ainf)$$

where a is the apparent quantum yield ($mol.mol^{-1}$), Io the PAR received by the leaf ($\mu mol.m^{-2}.s^{-1}$) and Ainf the photosynthesis for infinite radiation ($\mu mol.m^{-2}.s^{-1}$).

2- Light interception

To get values for the respective extinction coefficient of both families, we have used the simple model of Monsi and Saeki (1953) :

$$dR = K\ I\ dF$$

where a small canopy part with a LAI equal to dF is absorbing an amont of radiation dR, proportionnal to the incident radiation I. " K" is the extinction coefficient mostly related to the optical and the direction of the leaves. A quantum sensor (SLAM) was put at the top of one tree to measure the incident PAR (400-700 nm) at the top of the canopy, and 6 others quantum sensors were placed each one in a triangle, part of the lozenge made by a central tree and its 6 neighbours. Each triangle is sub-divided in 9 small triangles. During one hour, each sensor is moving throught the 9 triangles. All sensors are connected to a data logger (Delta T devices , Delta-T devices LTD, 128 Low Road, Burwell, Cambridge CB5 OEJ, England), recording output sensors ' signal every minute. Measurements were done from 10 h to 15 h (local time).

3- LAI

The leaf area index of each material have been estimated with two different methods. The first one is the "direct method" where the leaf area is measured on representative samples following Tailliez et al. (1992) and the second, the "indirect method" where the Plant Canopy Analyser (LAI-2000 of Li-Cor) is used. Both methods are described in Lamade and Setiyo (1996b) : they give similar results.

The canopy assimilation is calculated from (1) and (2) :

$A = (Ainf / k)\ LN((a\ K\ Io + Ainf) / (A\ K\ Io\ e\text{-}kLAI + Ainf))$ in $\mu mol.m^{-2}.s^{-1}$.

4- Biomass and growth

Leaves

For 16 trees per family, leaves (rank 17 and 33) have been collected and several measurements have been done to get valuable estimation of their total dry weight. Each leaf is divided in 10 equal segments from C to A.These segments are measured (volume), dried and weighed to determine the rachis density. Petioles were dried and weighed so. One leaflet per segment was collected, measured dried and weighed to determine the specific leaf weight.

Roots

The roots sampling has been done among 7 trees per family with two replicates and 6 lines between trees have been exploted with 3 holes per line. In each hole the soil sampling have been done with a ducht auger every 15 cm until 1.05 m. Samples were first washed up a sieve of 1 mm and roots collected after a first soft

drying of the residues. Roots were drying (85°C during 24 h) and separated into 3 categories (primary, secondary and tertiary , quaternary roots toghether).

Trunks

On the same trees already concerned by leaves sampling, trunks diameter have been measured (at 1.30 m height) at two opposite sides after removing the base of the petioles. The trunk height was measured from the base to the leaf n° 33.

5- Phenology

Precise observations (twice a week) have started in 1994 on 24 trees per family concerning the above ground organogenesis and development (in particular the leaf emission rytmth, the date of the rank one, the inflorescence anthesis, the harvest of the bunch) to get information about sexualisation and growth.

Results

The extinction coefficient and the LAI (Table 2)

The respective mean radiation coefficients over two days (including more than 200 recordings) for the "Lamé" family has been calculated equal to 0.46 (+or- 0.065, n = 362 * 6) and 0.39 (+or- 0.049, n = 100 * 6) for the "Local BJ" family for a respective LAI of 4.4 and 7.31 (in june 1994). These values are much higher that those already found by Squire (1984) in Malaysia (0.31) or by Gerritsma (1988) in Papua New Guinea (0.33). They tend to be more similar with Dufrêne et al. (1990) in Ivory Coast (0.4). In our experiment, the mean percentage of transmitted light under the "Lamé" canopy was 14.1 (+or- 0.069) and only 6 (+or- 0.023) under the "Local BJ" canopy. It is possible to notice already a big difference between both studied canopies concerning the light transmition and extinction.

The photosynthesis (Table 2)

Taking into account the big dispertion of the points in the photosynthesis response to the light, Ainf for both families has been determined by estimating the asymptote of the curve "photosynthesis-stomatal conductance " at saturated light in reference at Lamade et al. (1996) (Fig. 3). Ainf for the "Lamé" family has been estimated equal to 30.9 (confidence interval at 5 % : 25.7; 36.) and 26.4 (22.1; 30.7) for the "Marihat". The respective apparent quantum yield was estimated by the calculation of the slope of the equation 1/NP = 1/PAR A + B for the points under low radiation (130 $\mu mol.m^{-2}.s^{-1}$). They were found equal to 0.054 mol.mol-1 for "Lamé" and 0.058 mol.mol-1 for "Local BJ", highter than for L2T x D10D (0.053) in Ivory Coast (Dufêne et al., 1993).

The standing biomass

The vegetative dry matter content (above and belowground parts) of both studied families is given on Table 3 at the same time with what was obtained by Dufrêne (1989) in Ivory Coast.

The above ground biomass of the two families are very different with 46.7 t_{dm} ha^{-1} for "Lamé" and 83.7 t_{dm} ha^{-1} for "Local BJ".This result pointed out the genetic effect on the aerial parts. The above ground biomass of "Local BJ" is higher than Gray (1969) observed in Malaysia. For that case it is possible to notice that the petiole biomass makes the a big part of the difference (21.6 % of the total biomass for "Local BJ" against 12.3 % only in Ivory Coast).Similar results may be found in Henson (1993) who measured a total frond bases biomass of 11.7 t_{dm} ha^{-1} in Malaysia. The leaf emission rate measured during 1994 on both families highlighted again significant difference between "Lamé" and "Local BJ" with respective values of 23.9 leaves per year (+or- 2.97) and 29.5 leaves per year (+or- 1.69). The "Local BJ" present a higher rate than what was already observed in Malaysia (23 leaves/year for Gray ,1969). The area and the biomass of the leaves are higher compared to the observation in Ivory Coast (L2T x D10D : 4.95 t_{dm} ha^{-1}) with 6.25 t_{dm} ha^{-1} for "Lamé" and 10.69 t_{dm} ha^{-1} for "Local BJ".

The specific leaf biomass measured for "Lamé" (136.9 $g\ m^{-2}$, +or-29.7) and for "Local BJ" (140.5 $g\ m^{-2}$, + or- 22.2) are much higher than for L2T x D10D in Ivory Coast (only 106 $g\ m^{-2}$)

The important trunk biomass of "Local BJ" with 39.30 t_{dm} ha^{-1} is the result of both a higher vertical growth rate (0.54 m year-1) and a bigger trunk diameter (70.3 cm +or- 7.44) compared to "Lamé" which presented even a lower vertical growth rate (0.34 m year-1) that L2T x D10D in Ivory Coast (0.48 m year-1).

The study of the roots biomass certainly contributed to a better understanding of the carbon allocation in Indonesian conditions. Very poor roots biomass have been measured for both families ("Lamé" : 14.12 t_{dm} ha^{-1} ; "Local BJ" : 9.7 t_{dm} ha^{-1}) compared with L2T x D10D in Ivory Coast (31.5 t_{dm} ha^{-1}). If, in Ivory Coast, roots are an important sink (43% of the total biomass), the same is not observed in Indonesia with only 23.2 % for "Lamé" and only 10.4 % for "Local BJ".These results may be put in relation with those of Henson (1993) in Malaysia who evaluated the roots system as 20 % of the total biomass.

The simulation

A first test has been done by changing only the meteo input file, keeping all the parameters values of Ivory Cost. It can be seen (Table 4) that an increase of 2 $MJ.m^{-2}.day^{-1}$ may conduct to an increase of bunch yield equal to 80% and an increase of the total dry matter production of 18 %. It can be also observe that, due to a lower daily mean temperature in North Sumatra (24°C), in Marihat, compared to Ivory Coast (27°C), the maintenance respiration rate of all vegetative organs is lower of 16 % in North Sumatra.

A second test has been done on both studied families by entering measured values of input parameters in the conditions of North Sumatra in the Dufrêne's model.

All the values of parameters are given in Table 2 with a comparison with the Dufrêne 'one (Dufrêne et al., 1990). For the simulation , the maintenance and the growth respiration coefficients for each organs are remaining the same than in Ivory Coast, also roots turn-over and the allocation rules to the reproductive and the vegetative parts. The results can be seen on Table 4.The expecting potential yield is different for both studied families. For "Lamé", the theoretical simulated FFB will be 40.1 tFFB.ha^{-1} when only 35.8 tFFB.ha^{-1} for the "Local BJ". The reason of the difference may be found essentially in the maintenance respiration cost of the important above ground standing biomass of "Local BJ" (consumption of 52.1 t_{CH20}.ha^{-1}.year^{-1} for only 36.9 t_{CH20}.ha .year for "Lamé") which is not compensated by the higher photosynthetic assimilate production (131 t_{CH20}.ha^{-1}.year^{-1} against only 113.3 t_{CH20}.ha^{-1}.year^{-1} for "Lamé"). A difference between the expecting simulation yield and what was observed during 1994 in field may be pointed out. The observed yield for "Lamé" in 1994 is 24 tFFB.ha^{-1} whereas "Local BJ" produced only 17 tFFB.ha^{-1} . This difference between the expecting and the observed yield may be due to important pest damage already pointed on these families or temporary flooding frequently coming on this trial, especially on "Local BJ". The temporary flooding in that place may be an explanation of the quite low roots biomass observation : waterlogging induces soil hypoxia and leads to a big decrease in the root biomass (Dreyer, 1994).

Conclusion

The test of the Dufrêne 's model in North Sumatra conditions on two contrasting families pointed out the importance, as far as the test on L2T x D10D in Ivory Cost is taken into account, of the carbon allocation at the plant level and the cost of the maintenance respiration of the aerial part. The measured radiation in North Sumatra (16.2 MJ.m^{-2}.day^{-1}), compared with those, lower observed in Ivory Cost (14.2 MJ.m^{-2}.day^{-1}) is, of course, as it was highlighted by Dufrêne et al. (1990) a main factor to increase yield dramatically (+79 % for L2T x D10D under Marihat radiation).If we compare with the simulation model, L2T x D10D, "Lamé" (LM7T slf x DA128D slf) and "Local BJ" (BJ13D slf x BJ221P) under "north Sumatra conditions" and at the same planting density, we see that "Lamé" give a better yield (40.1 tFFB.ha^{-1}) that both other essentially due to a lower maintenance respiration cost of the vegetative part (36.9 t_{CH20}.ha^{-1}.year^{-1} for Lamé against 40 for L2T x D10D and 52.1 for "Local BJ". In fact the main difference between L2T x D10D and "Lamé" is with the roots standing biomass (31.48 tdm.ha-1 for L2T x D10D and only 14.12 for "Lamé"). The yield of L2T x D10D simulated in North Sumatra, with 130 palm.ha-1 and with the same roots system of "Lamé" will be equal to 53.3 tFFB.ha^{-1}. For "Local BJ", the very important sink of the aerial part maintenance give explanation a lower theoretical yield (35.8 tFFB.ha^{-1}) under North Sumatra conditions.

Still remain to found hypotheses about the difference observed between the simulation results and what was observed in the field. For "Local BJ", it may be obvious that the unusual and unpredictable disparity between the aerial part and the roots system (root /shoot equal to 0.23) may be responsable for some physiological disfunctionning : The rate of male inflorescence apparition in the crown of this family is quite high and may indicated stress conditions. There is also may be a lack of assimilate, in spite of a big LAI value (7.31), due to the important shade upon the leaves in the lower part of the canopy (may be more than 30 leaves : from leaf rank 17 to 49). For that case an appropriate prunning could give visible yield improvment. Root system could be indirectly increasing by the improvment of the water run-off and drainage in the plot and by a severe control in apply nitrogen fertilizer (an access may conduct to increase aerial part towards the below part). For the "Lamé" family, we think that cause may be found in the quite poor sanitary conditions : some years a lot of pest damage can be observed on trees. The "Lamé" family doesn't present an important canopy (less leaves may be counted in the canopies than reccommended one) and in that case a restriction of LAI by pest could be an important constrainst factor.

Nevertheless, this test on Dufrêne 's model in North Sumatra conditions contribute clearly to identify in this simple yield simulation an adequate tool to predict potential yield of different kind of genetic material, taking into account physiological and biometrical pattern of trees, and to highlight possible constrainst factors (cropping practices) on the observed yield. The actual C++ version, "SIMPALM", is simple to use for non-specialist and may be apply in many conditions in Indonesia.

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Table 1. Vegetative and reproductive caracteristics of the studied material. The data are coming from phenological observations during 1994/95. The year of planting is 1986, density : 130 palm.ha-1 with 24 studied trees per family. The "Local BJ" is the cross "BJ13D self x BJ21P" and "Lamé" is "LM7T self x DA18D self". Standard errors are in [ ].

Block	Cross	Abrev.	Yield kg.tree^{-1}.yr^{-1}	Mean reproductive composition of the crows: Mean nb of bunch per tree	Female per tree Mean nb	Male per tree Mean nb	Abortion per tree Mean nb
MA008S	8	Local BJ	131.8 [43.3]	5.4 [1.8]	9.3 [3.4]	24 [5.7]	5.5 [3.5]
MA007S	4	Lamé	187.7 [49.5]	9.9 [3.3]	17.1 [6.9]	9.9 [7.7]	5 [4.4]

	LAI	Trunk height (m)
Local BJ	7.31	4.28 [0.49]
Lamé	4.4	2.76 [0.44]

Table 2. Standing biomass (Leaves, Trunk, Roots) of the two studied families "Lamé" (LM7T slf x DA128D slf) and "Local BJ" (BJ13D slf x BJ221P).Comparisons with L2T x D10D in Ivory Cost (Dufrêne, 1989).

LEAVES

organs	Leaflets			Petioles			Rachis		
	L2T	LM	BJ	L2T	LM	BJ	L2T	LM	BJ
$t_{dm}.ha^{-1}$	4.95	6.25	10.69	8.97	10.93	20.14	6.05	8.31	13.60
% dm total	6.8	10.3	11.4	12.3	17.9	21.6	8.3	13.6	14.6

	TRUNK			TOTAL ABOVE GROUND		
	L2T	LM	BJ	L2T	LM	BJ
$t_{dm}.ha^{-1}$	21.75	21.23	39.30	41.72	46.72	83.73
% dm total	29.6	34.9	42.1	57	76.8	89.6

ROOTS

	I			II			III+IV		
	L2T	LM	BJ	L2T	LM	BJ	L2T	LM	BJ
$t_{dm}.ha^{-1}$	8.33	5.71	4.11	11.36	3.88	3.73	11.79	4.53	1.84
% dm total	11.4	9.4	4.4	15.5	6.4	4	16.1	7.44	2

	TOTAL BELOW GROUND			TOTAL BIOMASS		
	L2T	LM	BJ	L2T	LM	BJ
$t_{dm}.ha^{-1}$	31.48	14.12	9.69	73.2	60.84	93.42
% dm total	43	23.2	10.4	100	100	100

with L2T as "L2T x D10D"; LM as "LM7T self x DA128D self"; BJ : BJ13D self x BJ221P.

Table 2. List and values of the measured parameters used to test the simulation model of Dufrêne (1989) in Indonesian conditions, for both studied families "Lamé" and "Local BJ". Comparison with L2T x D10D (Ivory Coast) : the values of the parameters are from Dufrêne et al. (1990) .

Parameters	L2T xD10D	" Lamé"	" Local BJ"
Ainf ($\mu mol.m^{-2}.s^{-1}$) (1)	30.7	30.9 [25.7;36.2]	26.4 [22.1; 30.7]
α (mol.mol^{-1}) (2)	0.053	0.055	0.058
K extinction coefficient	0.401	0.46 [0.065]	0.39 [0.049]
LN (leaf number)	35	32 [5.6]	49 [5.23]
LS (mean leaf area) m^2	9	10.6 [1.79]	11.48 [0.99]
SLB (specific leaf biom.) $g.m^{-2}$	106	136.9 [29.7]	140.5 [22.2]
LT (leaf turn over) nb $l.yr^{-1}$	22	23.9 [2.97]	29.3 [1.69]
TRR (trunk radius) m	0.2	0.32 [0.4]	0.35 [0.7]
TRH (trunk height) m	4.44	2.76 [0.44]	4.28 [0.49]
TRDS (trunk density) $kgDM.m^{-3}$	184	Not measured	Not measured
PROOTS tdm.ha^{-1} (3)	8.3	5.7	4.1
SROOTS tdm.ha^{-1} (4)	11.4	3.9	3.7
ABSROOTS tdm.ha^{-1} (5)	11.7	4.5	1.8
Density palm.ha^{-1}	143	130	130

(1) : Photosynthesis when the radiation is infinite
(2) : apparent quantum yield efficiency
(3) : primary roots biomass
(4) : secondary roots biomass
(5) : absortive root biomass
[] : standard error

Table 4. Results of the simulation on L2T x D10D (at two different planting densities : 143 and 130 palms.ha^{-1}), "Lamé" and "Local BJ" under two meteorological conditions : Lamé (Ivory Coast) and Marihat (Indonesia).

	North Sumatra conditions				Ivory Coast conditions			
	L2T XD10D		"Lamé"	"Local BJ"	L2T x D10D		"Lamé"	"Local BJ"
density	143	130	130	130	143	130	130	130
photosynthesis ($t_{CH2O}.ha^{-1}.yr^{-1}$)	110.6	106.3	113.3	131.1	105.9	101.9	108	125.5
Total respiration ($t_{CH2O}.ha^{-1}.yr^{-1}$)	71.2	67.9	68.8	83.5	72.5	69	69.3	85
Maintenance respiration ($t_{CH2O}.ha^{-1}.yr^{-1}$)	43.9	40	36.9	52.1	52.6	47.8	43.5	62.3
Growth respiration ($t_{CH2O}.ha^{-1}.yr^{-1}$)	10.6	9.6	10.7	12.4	10.6	9.6	10.5	12.5
Inflorescence Respiration ($t_{CH2O}.ha^{-1}.yr^{-1}$)	16.6	18.3	21.3	19	9.2	11.5	15.3	10.2
Dry matter production ($t_{dm}.ha^{-1}.yr^{-1}$)	39.4	38.5	44.5	47.7	33.4	32.9	39.2	40.5
Vegetative growth ($t_{dm}.ha^{-1}.yr^{-1}$)	25.7	23.4	26.9	32	25.7	23.4	26.5	32.1
DW inflorescences tot ($t_{dm}.ha^{-1}.yr^{-1}$)	13.7	15.1	17.9	15.7	7.6	9.5	12.7	8.5

DW Bunches ($t_{dm}.ha^{-1}.yr^{-1}$)	12.5	13.8	16	14.3	7	8.7	11.6	7.7
FFB $t.ha^{-1}.yr^{-1}$	31.3	34.5	40.1	35.8	17.4	21.6	28.9	19.3

Annexe 1

List of variable used in the model of Dufrêne (1989) and variables effectively measured in Marihat (*).

A : Assimilation rate
Ainf : Assimilation rate for an infinite PAR (*)
K : Canopy extinction coefficient (*)
LAI : Leaf Area Index (*)
a : Apparent quantum yield (*)
T°C : Temperature (*)
Rg : Global radiation (*)
PAR : Photosynthetically Active Radiation (*)
GR : Growth respiration
MR : Maintenance respiration
LG : Leaf growth (*)
TG : Trunk growth (*)
RG : Root growth (*)
LLB : Leaflet biomass (*)
PETB : Petiole biomass (*)
RCHB : Rachis biomass (*)
Bunches : Bunches Biomass (*)
LD : Leaf death
RD : Root death
MFD : male flower death
HARV : bunch harvest

What is interesting to do is to test the model on clones (MK10, MK22, M04) performances. For this reason, that year, some parameters acquisition have been completed as the extinction coefficient and the roots biomass on clonal material, following methodologies already described in lastest progress report.

RESPIRATION

- SOIL -

With the general aim to get an estimation of the carbon allocation to the roots from soil respiration measurements, a set of measurements have been completed for clonal material during the night. From these measurements and the previous one it is possible to get roots respiration, annual turn over and root biomass. The method of calculation following the principle of Raich and Nadelhoffer (1989) is well explained is the paper "Estimation of carbon allocation to the roots from soil respiration measurements of oil palm" by Lamade et al. (1996) (Annexe).

MBT

PENAWARAN
Quotation

Tanggal : 15 Oktober 1996
Date

Nomor : 1589/AGS/MBT/JKT/X/96
Our Ref

Kepada Yth.
Ms. Emmanuelle Lamade (CIRAD)
Pusat Penelitian Marihat
J a k a r t a

Memenuhi permintaan, dengan ini kami tawarkan
For response to your inquiry, we quote the following

1. **Proyek** Project	:	**PUSAT PENELITIAN MARIHAT**
2. **Nama Alat** Equipment	:	Peralatan Laboratorium CIMEL
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4. **Jumlah Item** Total items	:	T e r l a m p i r
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Rekomendasi dan dukungan teknis, atas barang yang kami tawarkan, akan kami susulkan bila diperlukan.

Demikianlah penawaran ini, kami tunggu kabar lebih lanjut, atas kerja sama ini disampaikan terima kasih.

Recomendation and technical support of the g quoted will be sent later, if required.

Waiting your further news, we thank you for cooperation.

Your sincerelly

M. Arief Y. R. Pawennei

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Chap . 2 Purchase of equipement

General justification

Physiological investigations on oil palm have been since the end of 1993 developped in Marihat Research Station and now, several improvements must be acheived to keep on progress. The first very important equipment to purchase is a complete meteorological station; For modelling several parameters as the global radiation, the VPD, the temperature are absolultly needed. It is the reason why Marihat must be equiped with adequate automatic meteo Station and also a Physiology Laboratory.

METEO

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27 May 1996

Ref. No. 303/MSPE/SPII/R/V/96

Dr. Emmanuelle Lamade
MARIHAT RESEARCH STATION
P.O. Box 37
Pematang Siantar
Sumatera Utara
Fax. 622 21 197

Dear Sir,

Your letter has been received by us from our Singapore office. In accordance with your inquiry for Minolta's product i.e. Chlorophyll meter SPAD-502, so herewith we submit quotation as follows :

NO.	DESCRIPTION	UNIT PRICE
1.	**CHLOROPHYLL METER** Type : **SPAD-502** Brand : MINOLTA	Rp 4.000.000,-

*** **Remarks :**
- The above price is FOB Jakarta and excluding PPN 10%.
- Terms of payment : 20% Down Payment at placing order and balance 80% payable on time of delivery..
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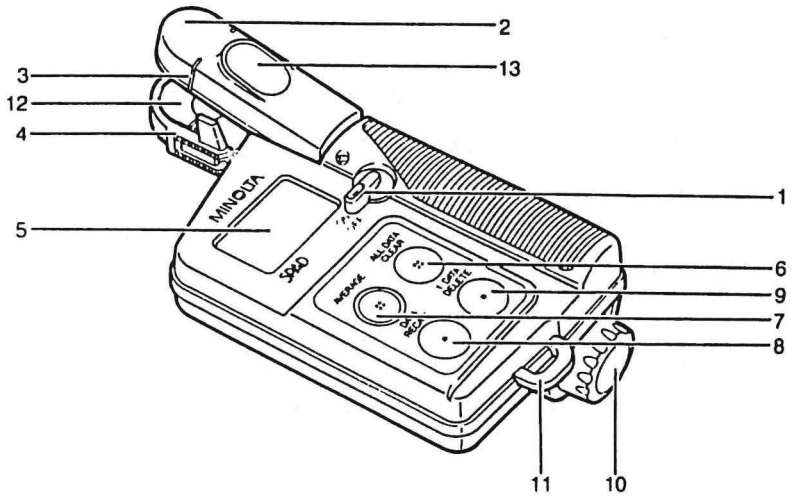

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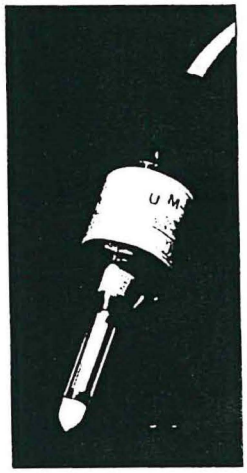

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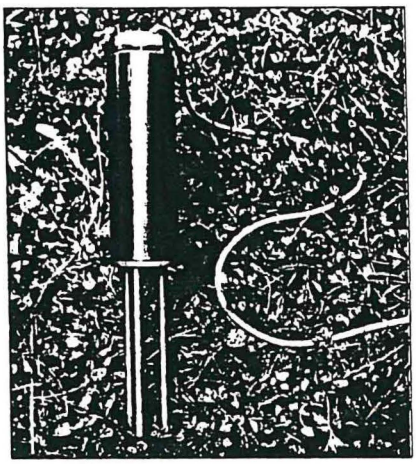

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CONCLUSION

The last three years have seen, in Marihat-IOPRI Research Station the development of an important physiological programm dealing with the investigations of physiological parameters related to the yield for oil palm. It is already possible to test the carbon balance model derived by Dufrêne (1989) on the control family L2T x D10D in Ivory Coast, in North Sumatra conditions . The photosynthetic potential (31 µmol.m-2.s-1) of clonal material have been also fully assessed and environmental constrainst factors as the VPD and the temperature pointed out as major constrainst in North Sumatra. Important linkage between the stomatal conductance and the photosynthesis when the radiation is over 1000 µmol.m-2.s-1 have been highlighted and may be a base for furher modelling. Differential sensitivity of the planting material to the VPD leads to further investigations for plant breeding.

For the futur, many subjects could be undertaken as the interaction between planting material (genetic point of view) and density, the research of new selection criteria as the chlorophyll content for example, for the moment strongly related to growth and total dry matter production and also the development of new models integrating architecture, taken into account the water balance and nutrient status of studied palms. More specific points, for Sumatra for example, may be developped as the regional effect on yield (phyiological study from the North to the South of Sumatra). Last point is regarding the forescasting of sexual cycles still not solved in spite of many works and thinking : may be the best subject !!!

ANNEXES

Plant and Soil **181:** 329–339, 1996.

Estimation of carbon allocation to the roots from soil respiration measurements of oil palm

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Key words: oil palm, root carbon allocation, root respiration, soil respiration, soil temperature, soil moisture

Abstract

CO_2 flux from the soil was measured in situ under oil palms in southern Benin. The experimental design took into account the spatial variability of the root density, the organic matter in the soil-palm agrosystem and the effect of factors such as the soil temperature and moisture.

Measurements of CO_2 release in situ, and a comparison with the results obtained in the laboratory from the same soil free of roots, provided an estimation of the roots contribution to the total CO_2 flux. The instantaneous values for total release in situ were between 3.2 and 10.0 μmol CO_2 m^{-2} s^{-1}. For frond pile zones rich in organic matter, and around oil palm trunks, root respiration accounted for 30% of the efflux when the soil was at field capacity and 80% when the soil was dry with a pF close to 4.2. This proportion remained constant in interrow zones at around 75%, irrespective of soil moisture.

Subsequently carbon allocation to the roots was determined. Total CO_2 release over a year was 57 Mg of CO_2 ha^{-1} yr^{-1} (around 1610 g of C per m^2 per year), and carbon allocation to the roots was approximately 53 Mg of CO_2 ha^{-1} yr^{-1} of which approximately 13 Mg CO_2 ha^{-1} yr^{-1} (25%) was devoted to turn-over and 40 Mg CO_2 ha^{-1} yr^{-1} (75%) to respiration.

Introduction

Total CO_2 release from soil, commonly referred as soil respiration (Singh and Gupta, 1977) is an excellent indicator of both root system activities and soil microorganisms activities especially those involved in the organic matter mineralization. Consequently, soil CO_2 is often used as an index of biological activity in soil. Recently, the soil respiration is taking into account in calculations of carbon budgets. Despite methodological difficulties to distinguish autotrophic respiration (CO_2 flux from the roots) from heterotrophic respiration (same flux from decomposition of litter and organic matter in soil), soil respiration gives precise information about the dynamics of the root system. Concerning the below ground compartment, many studies have already pointed out the difficulties to get precise measurements on root biomass, highly labor intensive, respiration and annual turnover. For oil palm, first estimations were made through a simulation model of production (Dufrêne et al., 1990). However, the extent of the root sink, estimated by Dufrêne et al. (1990) at 40% of total carbon, needs to be checked. This value is much higher than what is usually reported in the literature for forest ecosystems with values more often closed to 20%. For example, Santonio et al. (1977) showed that the proportion of the root biomass to total biomass for forest ecosystem varied between 15% and 25%. Vogt et al. (1987) highlighted the relation between this proportion and the closure of the canopy : before closure, the leaf biomass dominates (the proportion of the root biomass to total biomass varies from 13% to 27%) whereas after closure this ratio may increase to 40% to 65%.

Faced with all the methodological difficulties involved in the direct field study of in situ oil palm root compartment, we proceeded indirectly by mea-

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suring the bulk CO_2 flux passing through the soil surface, and then developed a procedure in laboratory in order to distinguish between these two sources of CO_2. We then deduced the amount of carbon allotted to the roots from the measured CO_2 flux, by applying the relations developed by Raich and Nadelhoffer (1989). These relations are mainly based on the assumption of an equilibrium of the carbon content in soil over a year as well as of both carbon fluxes entering and leaving the soil system. Concerning the interaction of the CO_2 release with some environmental factors, many authors have pointed out the strong dependence of the heterotrophic respiration with both temperature and moisture in relation with the amount of organic matter in soil. In this present study, general aims are first to contribute to the general knowledge of the soil CO_2 release in tropical conditions in relation with climatic factors as temperature and moisture and to describe the influence of cropping husbandry practices on the spatial heterogeneity of the soil respiration in an agrosystem like an oil palm plantation. Secondly, by comparison with measurements on free-root soil, a simple method is given to estimate the root respiration from the total release. The last point of this work is to apply the knowledge accumulated on the carbon balance of an oil palm plantation and our contribution on below ground compartment to estimate the total annual carbon allocation to the roots. For the two last points, assumptions and clear limitations in the methods will be underlined.

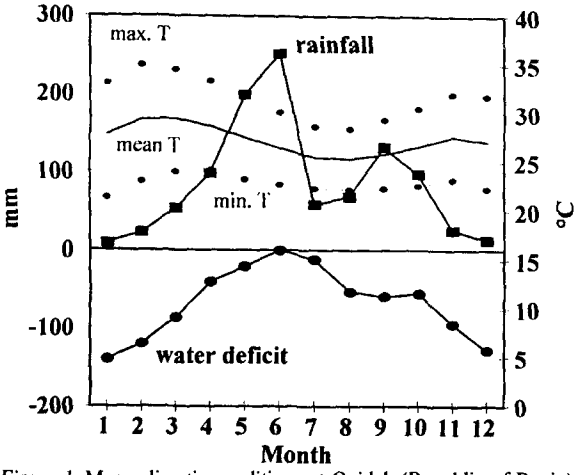

Figure 1. Mean climatic conditions at Ouidah (Republic of Benin) according to CIRAD (1992) and Chaillard et al. (1983). The monthly water deficit was estimated using the IGM 12 method from CIRAD (W.D = R + AW - ETP with ETP (potential evapotranspiration) equal to 150 mm per month when there is less than 10 days with rainfall, otherwise ETP is equal to 120 mm, R as rainfall and AW as available water for plant in soil).

Material and methods

Study site and material

The study was carried out in a 20 year-old plot at the SONICOG commercial plantation at Ouidah in southern Benin (6.23° N, 2.08° E). Figure 1 gives the main climatic characteristics of the Ouidah station. Annual rainfall is 950 mm distributed into two rainy seasons: March to July and September to November. There is a long dry season from December to March. The annual water deficit, based on the IGM 12 method from CIRAD (CIRAD, 1992), can reach 1000 mm and is 800 mm on average. The water deficit is low from May to July and high for the other 9 months. The mean temperature is 27 °C, with no major variations, and mean annual sunshine is 1747 hours.

The soil is a ferralsol, according to the FAO's classification (FAO-UNESCO, 1989), called locally 'terres de barre'. It has been studied in detail by Djegui et al. (1992). It is a ferrallitic soil, poor in clay, slightly leached, with a pH between 5.4 and 5. 8 (from 0 to 35 cm depth). Bulk density is 1.5, total porosity is 41 to 42% (from 0 to 35 cm depth). The sum of exchangeable bases is low (1.9 cmol (+) kg^{-1}). The organic matter content varies from 2.13% for the soil of the frond pile where fallen leaves are gathered to 1.71% for the bare soil.

Field measurements were carried out in January and February 1993, in the middle of the dry season.

The oil palm plantation comprises *Elaeis guineensis dura* × *Elaeis guineensis pisifera* crosses of Déli × La Mé or Déli × Yangambi origin. The palm trees are planted in a staggered design, at a density of 143 palms ha^{-1}, each tree being located at the tip of a 9 m equilateral triangle (Fig. 2).

Measuring techniques

We used a method of direct in situ measurement of CO_2 release from the soil using an infrared analyzer and a closed chamber.

CO_2 release from the soil was measured in situ, with a semi-closed system (During the measurement, the air pumped by the analyzer is not re-introduced in the circuit) comprising a removable metal cylinder (40 cm in diameter and 50 cm long), fitting hermetically onto a support pushed 15 cm into the soil and connected to an

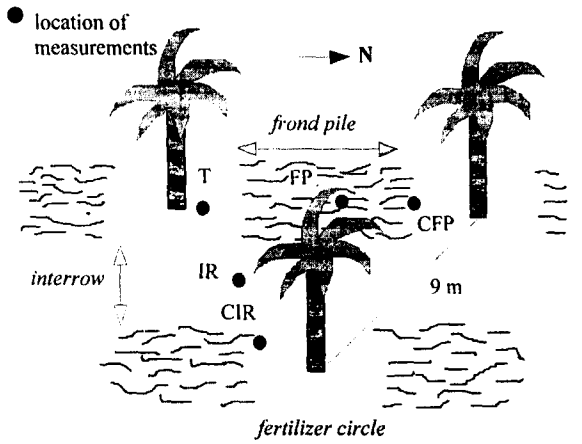

Figure 2. Location of the 5 measurements zones : T (*Trunk*), 1 m from the trunk in the fertilizer circle on frond pile side; CIR (*Circle Inter Row*), at the edge of the circle on interrow side; IR (*InterRow*) on the diagonal line between 2 palms in the interrow); FP (*Frond Pile*) in the middle of the frond pile and CFP (*Circle Frond Pile*) at the edge of the circle on frond pile side. The palms are planted in a staggered design, 9 m apart at a density of 143 palms ha^{-1}.

Table 1. Carbon content and root densities in each measurement zone : *Inter Row, Trunk, Circle Frond Pile, Frond Pile and Circle InterRow.* The C content for three different zones are from Djegui et al. (1992). In the same column, the numbers followed by the same letter are not significantly different at 5% (Newman and Keuls test)

Measurement point	C content from 0 to 15 cm (%)	Root density (0 to 15 cm) (g DM cm^{-3})
Trunk (T)		0.008 (ab)
1 × m from trunk to frond pile (CFP)	0.55 (b)	0.012 (a)
1 × m from trunk to interrow (CIR)		0.006 (b)
Interrow (IR)	0.46 (c)	0.005 (b)
Frond pile (FP)	0.82 (a)	0.011 (a)

ADC LCA2 type portable analyzer (Analytical Development Company, Hoddesdon, Herts, UK), Four fans (Micronel, 80 mm, 12 V) ensured effective air homogenization inside the cylinder and a thermistor (Sagimeca, 10K3 A1), connected to a multimeter (Fluke 70 II), series, measured the air temperature in the chamber. Two standard thermometers pushed into the ground measured the soil temperature inside the chamber. The volume of the chamber was approximately 60 L. As the sample taken for measurement was around 200 mL it can be assumed that this did not lead to a sufficient drop in pressure to 'pump' CO_2 from the soil to introduce a bias into the result (Kucera and Kirkham, 1971). The cylinder was connected to the analyzer via a 3 mm diameter butyl rubber tube with the appropriate specifications (Bloom et al., 1980). Prior to analysis, the air sample was dried using a magnesium perchlorate drier, in order to protect the analyzer and limit water vapour interference with the CO_2 during measurement (Long and Hallgren, 1982). The first sample was taken when the cylinder was fitted hermetically on its support and served as a reference. Two samples were then taken five minutes apart.

The equations used to calculate respiration were those conventionally used for closed circuit measurements (Long and Hallgren, 1982).

Along with these in situ measurements, soil was sampled down to a depth of 15 cm. Once the roots had been removed from the soil (dry extraction), a first set of samples were directly incubated in a thermostatically controlled bath at 25 °C (Anderson and Ingram, 1993), while a second set was incubated with moisture content raised to field capacity. CO_2 release was measured on two air samples taken one hour apart. Respiration of the root compartment was then estimated by the difference between the measurements taken in situ and those taken in the laboratory on root-free soil. This deduction is arrived at by estimating the weight of soil 'contained' under the cylinder and effectively participating in CO_2 release, by applying a bulk density of 1.51 and assuming that a soil depth of 15 cm represents the maximum depth of organic matter accumulation (Djegui et al., 1992). Nonetheless, it has to be clearly noticed that this method of estimating roots respiration is an estimation. It has inherent difficulties that are not easily overcome but is the only practical approach in intact ecosystem studies. The problem is the disturbance of soil samples in laboratory when the roots are removed for the 'root-free' soil respiration measurements.

Sampling procedure

Four variable factors likely to be involved in CO_2 flux from the soil were taken into account: soil organic matter content, root density, humidity, and time of measurement. The depth, though playing a role in the variation of CO_2 release (Dyer and Brook, 1991), was not considered to be a determining variable. In our opinion, the depth effect is a consequence of both root density and of the depth profile of organic matter.

As for organic matter and root density, the elementary network concept defined by Djegui et al. (1992) was used. This involves five measurement positions (Fig. 2). (i) at the foot of the trunk: T (*Trunk*); (ii) at the edge of the 'fertilizer' circle (The fertilizer circle

corresponds to the circular zone of 1 m wide around the trunk and in which inorganic fertilizers are applied) towards the frond pile: CFP (*Circle Frond Pile*); (iii) between the edge of the circle and the interrow: CIR (*Circle Inter Row*); (iv) in the middle of the free interrow, mid-way between two palms: IR (*InterRow*); (v) in the middle of the frond pile: FP (*Frond Pile*). With these five points, it is possible to cover the full range of root density and organic matter variability at a constant depth. This set of five measurements was replicated five times in the study plot. Table 1 shows the root density measurements measured at each point, as well as the soil carbon content (Djegui et al., 1992).

The effect of moisture was studied by taking measurements in situ and in the laboratory on dry soil and on soil at field capacity. At the time of year when the study was conducted, the soil was dry with a moisture content close to that of the permanent wilting point (pF 4.2). The field capacity was obtained by soil rehydration in the laboratory and in situ down to a depth at least 15 cm by watering, following methods determined in preliminary trials. These two levels of soil moisture content – dry and moist – corresponded well to those found, in the upper horizon, for 9 and 3 months of the year, respectively (this arbitrary choice gives, in our opinion, a good balance of all the moisture conditions during a year).

As there is a peak in the diurnal rate of leaf gas exchanges in the middle of the day (Smith, 1989), measurements were spread throughout the day to check whether the same pattern applied to the root system.

Principle for estimating the quantity of carbon allocated to the roots

We used the calculation principle described by Raich and Nadelhoffer (1989). Considering the results of Ollagnier et al. (1978) pointing out the equilibrium of the organic stock of the soil in an oil palm plantation over 14 years old, the total amount of carbon returned to the soil by plant residue should be equal to the amount of carbon in the soil mineralized by heterotrophic respiration (Rh). Let Pa and Pb represent the carbon supplied to the soil in the form of aboveground parts (Pa) and below-ground parts (Pb) respectively, then:

$$Rh = Pa + Pb \quad (1)$$

Moreover, if Rs represents the total CO_2 release from the soil and Rr root respiration, then:

$$Rs = Rh + Rr \quad (2)$$

Combining (1) and (2) gives:

$$Rs - Pa = Pb + Rr \quad (3)$$

where Pb + Rr represents the overall carbon allocation to the root system, under the hypothesis that there is very little growth in a mature root system that has reached maximum expansion. At the most, root growth may only amount to renewal of dead roots (Pb).

In order to use this method of estimation, we have to make the following three assumptions. First, the carbon inputs into the soil come only from leaf litter and root litter: supplies of carbon leached by rainfall are therefore considered negligible. Second, carbon removal from the soil is only due to mineralization of litter, root residues, and organic matter; losses due to erosion and leaching are considered negligible. Third, the interactions between microbial activity and carbon supply, e.g. by the litter, on decomposition of soil organic matter (*priming effect*) are not taken into account.

Results

Spatial variation in - in situ - CO_2 release

Under dry conditions, the variation in CO_2, flux from one point to another was relatively law, from 3.2 μmol m^{-2} s^{-1} in the interrow to 5.1 μmol m^{-2} s^{-1} at the foot of the trunk (Table 2). This variation increased substantially when the soil was rehydrated: from 4.1 μmol m^{-2} s^{-1} in the interrow, to 10.0 μmol m^{-2} s^{-1} in the middle of the frond pile. Soil rehydration had the greatest effect in the frond pile, where CO_2 flow was multiplied by more than 2. The extent of these variations was about the same as that observed for the total carbon content of the soil (Table 1).

Respiration of root-free soil in the laboratory

The measurements of root-free soil respiration in the laboratory (Table 2) revealed relatively stable and low values for dry soil, reflecting low microbial activity. After rehydration, the values observed in the frond pile were 6 times greater than under dry conditions. Those near the trunk (T, CFP, CIR) were 2.7 to 3 times greater than under dry conditions. The moisture content had little effect in the interrow (IR) with a multiplication factor of 1.1 compared to the dry conditions. Once again, these results were consistent with the carbon contents measured in the soil as shown in Table 1.

Table 2. Measurement of CO_2 release from soil in situ and from root-free soil in the laboratory, either dry or rehydrated. Estimation of root respiration in each measurement zone

		Trunk	Circle Frond Pile	Circle InterRow	Inter--Row	Frond Pile
		(mean in μmol m^{-2} s^{-1})				
CO_2 release from the soil in situ, *dry* conditions	A	5.06 0.69* a**	4.40 0.72 ab	3.22 0.25 c	3.16 0.26 c	4.28 0.31 b
CO_2 release from the soil in situ after *rehydration*	B	6.34 0.35 c	8.55 0.51 b	4.87 0.31 d	4.11 0.29 e	9.97 0.60 a
CO_2 release from *root-free* soil *dry* conditions	C	1.29	0.95	0.78	0.79	0.86
CO_2 release from *root-free* soil after *rehydration*	D (1)[a] (2)	3.81 4.26	2.72 3.04	2.08 2/32	0.90 1.02	5.71 7.02
Multiplication coefficient (dry to moist) for CO_2 release from *root-free* soil (E = D/C)	E	2.95	2.86	2.67	1.14	6.64
Root respiration estimated when *dry* (F = A-C)	F	3.77	3.45	2.44	2.37	3.42
Root respiration estimated when *rehydration* (G = B-D)	G (2)	2.08	5.51	2.55	3.09	2.95
Mean root respiration (H = (F+G)/2)	H (2)	2.93	4.48	2.61	2.58	3.18
Contribution of root respiration to CO_2 release from the soil when *dry* (I=F/A)	I	0.75	0.78	0.76	0.75	0.80
Contribution of root respiration to CO_2 release from the soil when *rehydration* (J=G/B)	J (2)	0.33	0.64	0.52	0.75	0.30

* Confident interval at 95%.

** Student test for mean comparisons (5% risk), in the same row, the value allocated the same letter are not significantly different.

[a] (1) results of measurements at 25 °C; (2) data on moist soil corrected at 27 °C.

Table 3. CO_2 release from soil in situ for the main three zones : InterRow, Frond Pile and Circle. 'Circle' is defined as : (T+CIR+CFP)/3. Determination of CO_2 quantities allocated to the root compartment. Calculation per ha and per year of amounts of CO_2 released by the soil and roots

	InterRow	Frond Pile	Circle
	(μmol m^{-2} s^{-1})		
CO_2 release from soil in situ			
Under dry conditions	3.16	4.28	4.23
Under moist conditions (27 °C)	4.11	9.97	6.59
Estimated root respiration			
Under dry conditions	2.37	3.42	3.22
Under moist conditions (27 °C)	3.09	2.95	3.38
	(g CO_2 yr^{-1} m^{-2})		
Annual CO_2 release*			
Total CO_2 release from soil (27 °C)	4714.30	7912.67	6688.14
CO_2 release from roots (27 °C)	3567.59	4750.05	4581.12
Roots respiration/soil respiration	0.76	0.60	0.68
	(Mg CO_2 yr^{-1} ha^{-1})		
Mean release from plot**			
Total CO_2 release from soil (Rs)	57.11		
CO_2 release from roots (Rr)	39.65		
Roots respiration/soil respiration	0.69		
	(Mg CH_2O yr^{-1} ha^{-1})		
Weight of leaf litter returned to soil annually (143 palms × 22 leaves × 9 m^2 × 110 g m^{-2})	3.11		
	(Mg CO_2 yr^{-1} ha^{-1})		
Pa***	4.56		
	(Mg CO_2 yr^{-1} ha^{-1})		
Overall carbon allocation to roots			
Pb + Rr (= Rs-Pa)***	52.55		
	(Mg CO_2 yr^{-1} ha^{-1})		
Weight of root litter returned to soil annually			
Pb***	12.91		
Pb/(Pb + Rr)***	0.25		

* Dry conditions for 9 months and humid for 3 months.
** 65% from IR, 25% from FP, 10% from C.
*** From Raich and Nadelhoffer's formula.

Diurnal variation in - in situ - soil respiration

Soil respiration was measured at 5 points (T, IR, GIR, CFP and FP), 8 times a the day for 25 days, under dry conditions and after rehydration. Figure 3 shows the mean diurnal variations in CO_2 release from dry to moist soil and with changes in soil temperature along the day.

Dry soil respiration was relatively constant throughout the day around a mean value of 4 μmol m^{-2} s^{-1}. The significant increase in respiratory flux for moist soil between 7:30 am and 11:45 am corresponded to an increase in soil temperature. A slight depression. at 12:30 pm was associated with a slowing of the temperature increase. From 1:45 pm onwards, CO_2 release dropped in line with the temperature.

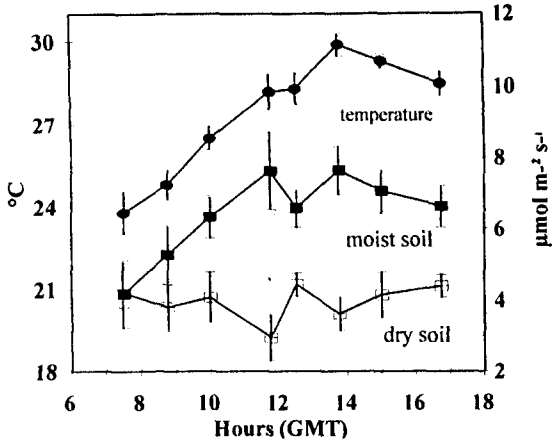

Figure 3. Variations in soil temperature and CO_2 release from both dry and moist soil during the day (mean values and confidence intervals at 95%).

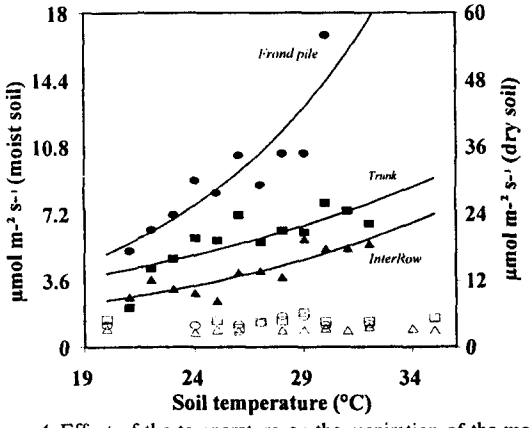

Figure 4. Effect of the temperature on the respiration of the moist soil (■ : T (*Trunk*); ▲ : IR (*InterRow*); ● : FP (*Frond Pile*) and the dry soil (□ : T, Δ: IR, ○: FP). Non-linear fitting (SAS Inst. Inc., 1990) for 3 locations IR, T, FP with the equation : R= A × exp(B× T°C). Estimation of the parameters A and B with confident interval at 95%. FP : A=0.631 [−0.144; 1.407] B= 0.104 [0.059; 0.149] and r^2 = 0.79 (p <1%); IR : A = 0.620 [0.119; 1.121] B = 0.070 [0.041; 0.098] and r^2= 0.76 (p <1%); T : A = 1.33 [0.114; 2.54] B = 0.05 [0.022; 0.09] and r^2 = 0.62 (p <1%). Points plotted on the graphs are the mean per class of degree Celsius.

Effect of the temperature on the respiration of the moist soil

As shown by the above results, soil respiration is strongly related to the soil temperature. For our data, the best fit was obtained with a simple empirical expression, the exponential curve (R = A × exp(B×T°C)) often used to describe many biological processes (Thornley and Johnson, 1990). Plots and fits to our data are given in Figure 4. For clarity, the results of the 3 most representative of measuring positions ((T), (IR), (FP)) have been plotted together with the mean points per temperature. It was obvious that temperature had an effect only on the 'moist' soil because the same phenomena could not be observed on dry soil (Fig. 4). Furthermore, this temperature effect was mainly related to the measuring position and therefore to the microbial activity. The effect of soil temperature was considerable on the soil of the frond pile and relatively small on soils from both the circle and interrow positions. Hence, it may be essential to make allowances for the fact that there is an effect of temperature on soil respiration only when the level of moisture is sufficient to permit a substantial activity by the microbial population. From these results, corrections taking into account the temperature were made to the values of CO_2 released from humidified soil measured in the laboratory at 25 °C. All the results were adjusted to 27 °C which represents both the annual mean value of the air temperature in Benin and also the mean temperature during our in situ measurements. On Table 2, relative corrections have been made for each measuring position for the measurements in laboratory, equivalent to their respective in situ pattern. Subsequently, all estimates have been presented for a temperature of 27 °C.

Root respiration

Root respiration was deduced from the difference in CO_2 release from the soil in situ and from root-free soil in the laboratory at a temperature of 27 °C (Table 2). Although not significant, slightly higher values were recorded with humid soil (average estimated respiration after humidification at all locations was equal to 3.24 µmol m^{-2} s^{-1} at 27 °C compared to 3.09 µmol m^{-2} s^{-1} under dry conditions). However, the moist soil:dry soil ratio was much lower (1.05) than that observed ratio for total soil respiration (3.78). Consequently changes in moisture content seem to affect root activity much less than microbial activity in the soil.

If the mean root respiration value estimated at each point is considered, for both dry and moist soil at 27 °C, the mean is seen to be linked to the measured root density (Fig. 5). Therefore, it seems possible to estimate root respiratory flux from their biomass.

Consequently, the contribution of roots to total CO_2 release from the soil seems to be highly variable depending on moisture conditions and on location (Table 2). For zones with a low organic matter content (IR), root respiration was dominant, irrespective of soil moisture content. It is very clear that for the interrow, the moisture content has no effect on the contribution

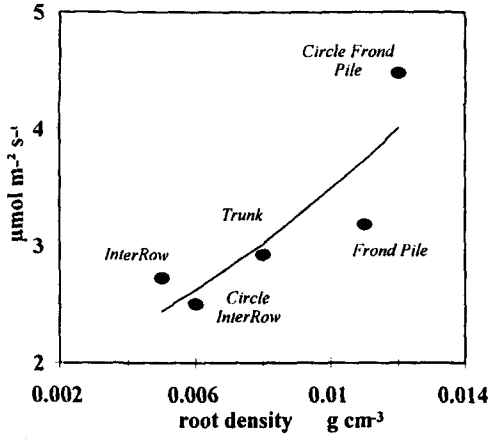

Figure 5. Relationship observed between estimated root respiration and root density measured at each sampling point IR, CFP, FP, CIR and T. Non linear fitting (SAS Inst. Inc., 1990) with equation : R = A × exp(B × dens), estimations of the parameters with confident interval at 95%, A = 1.712 [0.903; 2.520] ; B = 70.892 [22.865; 118.918] and $r^2 = 0.74$ (n.s.).

of root respiration to the gross flux. In (IR), root respiration represents around 75% of the total release.

Annual carbon allocation to the roots

Using Raich and Nadelhoffer's principle (1989) and in accordance with the points mentioned before, we estimated total carbon allocation to the root compartment, In order to obtain a year-long estimate, we combined the various estimates so as to integrate the variations in soil moisture content throughout the year. Given the mean values of the water deficit observed at Ouidah (Fig. 1), we considered as an order of magnitude that the top 15 cm of soil were close to field capacity for 3 months of the year (primarily in May, June and July) and near to the permanent wilt point (pF = 4.2) for 9 months. As for the temperature effect, it was decided that it may possibly play a slight role only during the months of May and June.

We considered that leaf litter was nil in the 'circle' and interrow, since it was concentrated in the frond pile, which represents around 30% (This percentage is slightly higher than the 25% usually quoted in this area (Djegui et al., 1992)) of the plot area. As we had no direct measurements of either the litter biomass returned to the soil each year, or of the speed with which it decomposes and is incorporated back into the soil,, three main points had to be taken into consideration in estimating Pa:

(i) the mass of litter returned to the soil each year is proportional to the leaf mass. According to Ziller et al. (1955), the ratio of the number of leaves in oil palm plantations at Pobè (under similar ecological conditions to those at Ouidah) to that at La Mé (Ivory Coast) is 0.8. In addition, the water deficit at Ouidah is likely to substantially reduce leaf size; de Berchoux (personal communication) noted that a moderate water deficit (270 mm) reduced leaf length by 6%. We therefore assumed a 30% reduction in leaf litter mass for the conditions in Benin compared to those at La Mé which is already observed at the yield level. At the latter site, leaf litter was estimated to be between 9 (Hirsch, 1980) and 11 Mg DM ha^{-1} (Dufrêne, 1989). We therefore assumed a leaf litter value of 7 Mg DM ha^{-1} which seems adequate for Benin conditions (estimation of a litter of 9.4 t ha^{-1} by Sokpon and Lejoly (1991 in the forest near the plantation of Pobè) taking into account the percentage of leaves exported by the people for firewood. Concentrated in the frond pile, which represents 30% of the area, this mass amounts to 2300 g DM m^{-2} in the frond pile.

(ii) the leaf litter returned to the soil is made up of leaflets, rachis and petioles. The absence of incorporation into the soil and the dry conditions at Ouidah considerably reduce the rate of litter decomposition: the petioles and rachis remain on the soil for a very long time, so the frond pile ends up very voluminous (3 m wide, 1 to 1.5 m high). We therefore assumed that only leaflets decomposed within a year; according to Dufrêne (1989), these account for about 25% of total leaf mass.

We thus estimated Pa as:

- 0 in the interrow (IR) and in the circle (C)
- 575 g DM m^{-2} yr^{-1} in the frond pile, i.e. 843 g of CO_2 m^{-2} yr^{-1}

The measured results integrated over time are shown in Table 3 for each zone considered. Under these conditions, on a year basis, root respiration would seem to account for 60% (FP) to 76% (IR) of total CO_2 flux from the soil. CO_2 allocation to the roots varied from 3568 to 4750 g (CO_2) m^{-2}, 24 to 31% of which are for root renewal (Pb).

We calculated the plot mean by allocating a weighing factor to each zone equivalent to its relative area ((IR) : 60%; (FP) : 30%; (C) : 10%) (Table 3). Root respiration thus amounted to 70% of CO_2 release from the soil (39.65 Mg ha^{-1} yr^{-1}). Total carbon allocation to the roots was 52.55 Mg CO_2 ha^{-1} yr^{-1}, 25% for renewal and 75% for respiration.

Discussion

The carbon allocated to the root system is used for growth and respiration (Buwalda, 1993). Due to the size of this root sink, a direct estimation is needed in order to validate carbon functioning models for the ecosystem, rather than an evaluation, frequently made by taking the simple difference in calculating the carbon balance, usually leading to substantial errors.

Direct measurement of root growth poses numerous methodological problems due to difficult access. In situ measurement of root respiration also poses many problems since it is so difficult to separate from the heterotrophic CO_2 flux resulting from the organic matter decomposition and microbial activity. This methodological difficulty has been illustrated and more or less solved by numerous authors, ranging from a simple protocol comparing soils in situ and soils from which roots have been removed (Coleman, 1973; Kucera and Kirkham, 1971; Singh and Gupta, 1977) to the use of radio-isotopes such as ^{14}C (Cheng et al., 1993; Warembourg and Paul, 1973) or gas chromatography (Silvola et al., 1992). Some have worked on direct estimation of the amount of organic matter likely to be involved in CO_2 flux from the soil (Maggs and Hewett, 1990; Raich and Nadelhaffer, 1989). Our simple method is based on comparative protocols, but provides a large number of measurements by using a portable infrared analyzer. This technique is increasingly being used (Howard and Howard, 1993; Kanemasu et al., 1974; Kiozumi, 1991; Pajari, 1995), and gives better results (Nakadai et al., 1993) than CO_2 capture with soda lime (Anderson and Ingram, 1993; Gunadi, 1994) or sodium hydroxide (Henson, 1992; De Jong et al., 1974; Rout and Gupta, 1989). Still, this technique brings little bias compared to theoretical calculations based on classical formula such as the Fick's law (Nay et al., 1994). The fact that a large number of measurements can easily be done, allows a quantification of variations in CO_2 release depending on environmental factors and an integration of the spatial variability of the cultivated ecosystem.

Our in situ results on soil confirmed the effects of environmental factors such as soil moisture content (Hanson et al., 1993; Howard and Howard, 1993; Rout and Gupta, 1989) and temperature (Kucera and Kirkham, 1971; Llyod and Tailor, 1994). Furthermore, our results showed that there is a strong interrelation between these two factors. A strong effect of the temperature on soil respiration is observed, only when the moisture content of soil is adequate for microbial activity. These data revealed some variability due to the spatial distribution of organic matter and of the roots in the soil. Much of the work in this field has been geared more toward the comparative study of the CO_2 flux in different types of ecosystems, either cultivated or not (Ceulemans et al., 1987; Fernandez et al., 1993; Raich and Schlesinger, 1992; Schlesinger, 1977; Singh and Gupta, 1977). Little work has been done on the analysis of spatial heterogeneity within the same system: Hanson et al. (1993) attempted to analyze the effect of topography whereas Dyer and Brook (1991) showed variation with the depth, consequence of the soil carbon content distribution. Our results, on the other hand, clearly revealed the major role played by the type of cropping practices, like leaf pruning and planting pattern, on the spatial distribution of soil respiration.

An attempt to establish a balance over a period of one year revealed that total CO_2 release from the soil amounted to about 57 Mg of CO_2 ha^{-1} yr^{-1}, i.e. approximately 1610 g of carbon per m^2 per year. This value tallies with those observed for CO_2 release in tropical forests, ranging from 400 to 2100 g of C m^{-2} yr^{-1} (Schlesinger, 1977). However, comparison with a more recent review (Raich and Schlesinger, 1992) shows that our values are much higher even than those encountered in humid tropical forests. On the other hand, recent results from Le Roux and Mordelet (1995) on a savanna soil in the Ivory Coast were comparable to ours (for instantaneous values, results ranging from 4.0 μmol m^{-2} s^{-1} to 9.6 μmol m^{-2} s^{-1} from October to April). Hanson et al. (1993) found much lower values (around 850 g of C m^{-2} yr^{-1}) for temperate forests, where the annual average temperature is much lower. Obvious temporal variations have been demonstrated by some studies (Dyer and Brook, 1991; Gunadi, 1994). In our opinion, these variations are mainly caused by moisture and temperature variations.

In the present study, total carbon allocation to the roots amounted to about 53 Mg of CO_2 ha^{-1} yr^{-1} (1445 g of C m^{-2} yr^{-1}), including about 13 Mg CO_2 ha^{-1} yr^{-1} for renewal (25%) and 42 Mg CO_2 ha^{-1} yr^{-1} (75%) for respiration. In comparison, using the total carbon budget established for an oil palm plantation in the Ivory Coast by Dufrêne et al. (1990), we arrive at 62 Mg of CO_2 ha^{-1} yr^{-1}, allocated to the roots, with around 15% for renewal and 85% for respiration. The orders of magnitude therefore seem to be highly comparable, and the differences observed between the two estimates could result from differences in either the methods used or the different eco-

logical conditions at the 2 sites. Under the conditions of Dufrêne, overall assimilation corresponded to 154 Mg of CO_2 ha^{-1} yr^{-1}, which is much higher than in southern Benin. The bunch production calculated by Dufrêne et al. (1990) was 23 Mg ha^{-1} yr^{-1}, whereas barely more than 4 Mg ha^{-1} yr^{-1} can be expected under the conditions at Ouidah (Chaillard et al., 1983). Therefore, it seems that carbon allocation to the different plant organs differ at the 2 sites: bunch yields seem to be much more affected by the poor ecological conditions found at Ouidah (4 Mg ha^{-1} yr^{-1} as opposed to 23 Mg ha^{-1} yr^{-1}) than by the amounts of carbon allocated to the roots (53 Mg ha^{-1} yr^{-1} as opposed to 62 Mg ha^{-1} yr^{-1}). This is another illustration of the functional balance concept developed in 1969 by Brower and de Wit (quoted by Klepper, 1991): a larger reduction in quantities of carbon allocated to the aerial parts than to underground parts is observed in response to nutritional stress and particularly water stress.

The values (33 Mg CO_2 ha^{-1} yr^{-1}) for total CO_2 release from the soil obtained by Henson (1992) for oil palm, in Malaysia, were lower than our estimations. These measurements were taken under water supply conditions that were not restrictive most of the time, hence the contribution made by organic matter in the soil was probably high. Without information on organic matter content and mineralisation rate at the Malaysian study sites, it is difficult to make a direct comparison with our measurements of overall CO_2 release. However, it is worth noting that the potential assimilation measurements made by Henson (1992) under saturated radiation conditions, were around 35% lower than those estimated by Dufrêne (1990) or by ourselves (CIRAD, 1995).

In conclusion, the importance of the root sink and the root respiration are clearly shown in this study. A correct estimation of its dynamics is essential for any attempt at establishing a carbon balance an the scale of a whole plant or an oil palm plantation. To do so, it will be necessary to validate the methodology, and to make sure that the measurements taken in the laboratory on samples of root-free soil are representative of how the soil performs in situ. Furthermore, our estimations are based on the hypothesis of a stable organic matter content in the soil, which enables us to calculate the carbon allocated to the roots by simple subtraction. This assumption is probably acceptable on a plot scale, but it should be checked for different zones characterized by different ways of returning organic matter to the soil.

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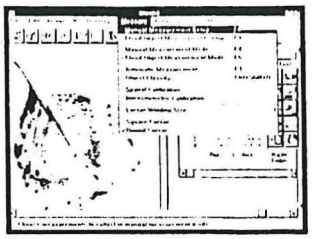

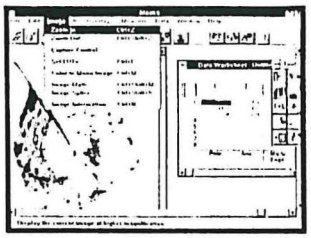

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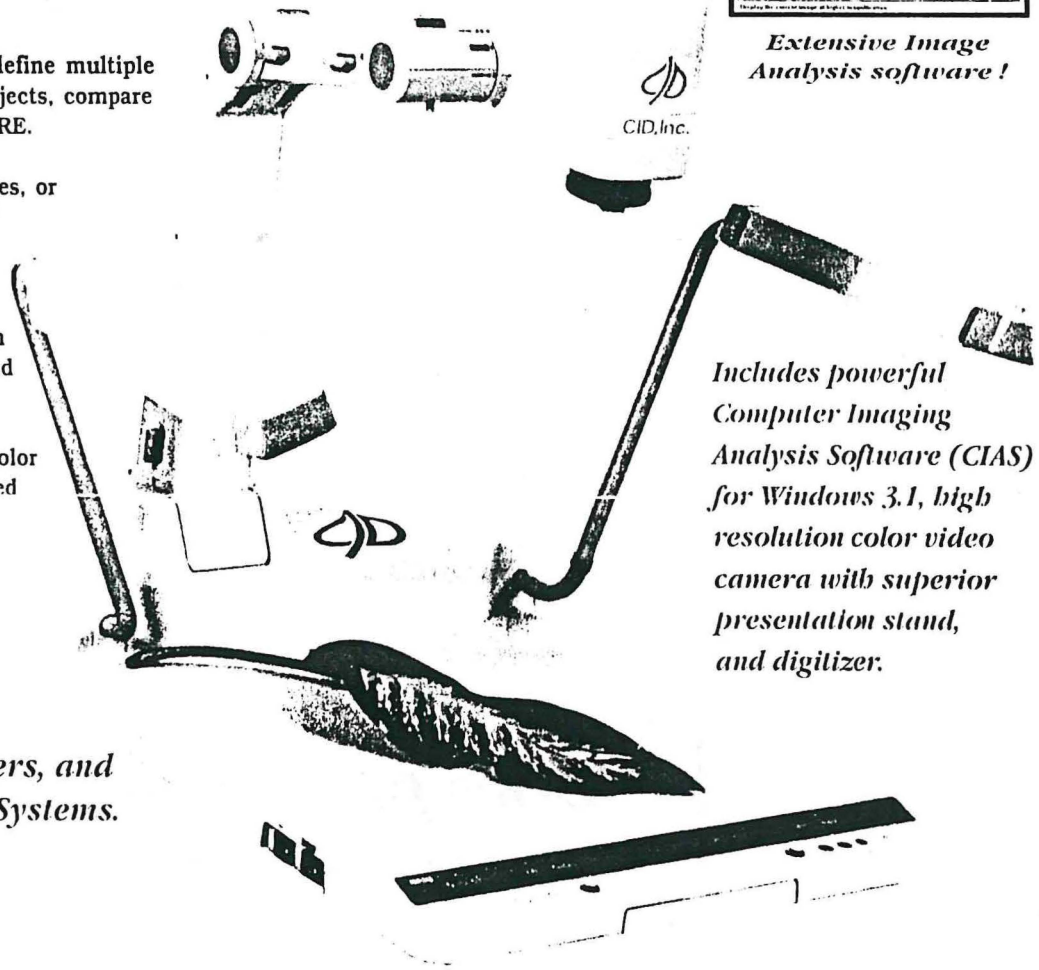

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