GAS EXCHANGE OF OIL PALMS TRESS SUBMITTED TO LEAF-TEMPERATURE MODIFIED GROWN IN DIFFERENT PLANTATION SYSTEMS

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ABSTRACT: Studies on the influence of leaf temperature rise on gas exchange in tropical tree species grown in plantations are rare. With regard to the predicted increase in air temperature in the future in the Central Amazon, we investigated the influence of increasing leave temperature on the gas exchange of oil palms cultivated in monocultures as well as in mixed plantations with cassava or banana. This study was carried out at the Embrapa Experimental Station in Presidente Figueiredo – AM – Brazil, 60 km north of Manaus. The net photosynthesis (P_n), transpiration (*E*), stomatal conductance (g_s) and the water use efficiency (*WUE*) of the plants were quantified by a portable photosynthesis meter (CI-340). In all plantations increasing leaf temperatures caused a significant decrease of the net photosynthesis (P_n), stomatal conductance (g_s), and the water use efficiency (*WUE*) of the oil palms. Maximum transpiration rates (*E*) were observed at leaf temperatures between 38 and 46°C. In addition to the influence of leaf temperature rise, the planting system also had a significant influence on the gas exchange of palm plants.

Key words: E*laeis guineensis*; agroforestry system, CO_2 assimilation

TROCAS GASOSAS DE DENDEZEIRO SUBMETIDOS À MODIFICAÇÃO DA TEMPERATURA FOLIAR CULTIVADOS EM DIFERENTES SISTEMAS DE PLANTIO

RESUMO: São raros os estudos sobre a influência da elevação da temperatura foliar sobre as trocas gasosas em espécies arbóreas tropicais em plantios. Em consideração ao aumento previsto da temperatura do ar no futuro na Amazônia Central, investigamos a influência do aumento da temperatura sobre as trocas gasosas de plantas de dendezeiro cultivadas em monoculturas, bem como, em plantios mistos com mandioca e bananeira. Este estudo foi realizado na Estação Experimental da Embrapa em Presidente Figueiredo - AM - Brasil, 60 km ao norte de Manaus. A fotossíntese líquida (Pn), a transpiração (E), a condutância estomática (gs) e a eficiência no uso da água (WUE) das plantas foram quantificadas por meio de um analisador portátil de fotossíntese (CI-340). Em todos os sistemas de plantios o aumento da temperatura das folhas provocou uma diminuição significativa da fotossíntese líquida (Pn), da condutância estomática (gs) e da eficiência do uso da água (WUE) das plantas de dendezeiro. Foram observadas taxas máximas de transpiração (E) a temperaturas foliares entre 38 e 46°C. Além da influência da elevação da temperatura foliar, o sistema de plantio teve também influência significativa sobre as trocas gasosas das plantas de dendezeiro.

Palavras-chaves: E*laeis guineensis*; sistema agroflorestal, assimilação de CO_2

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INTRODUCTION

The oil palm (*Elaeis guineensis* Jacq.) is one of the most important commercial plants in tropical countries. The total area of oil palms in Brazil increased significantly during the last years. According Barcelos et al. (1999), the life of the palm lasts 20 to 30 years, with seed production throughout the year. Beside oil production, oil palm plantations are considered to be a great sink for carbon. Oil palms are often planted in monoculture systems, but oil palms are also planted in mixed plantation systems in order to improve the ecological stability and the productivity of the plantations.

Studies on the influence of the temperature on the gas exchange of tropical species are rare, even for commercial plant species, which are extremely important for the Brazilian agribusiness. Corresponding information is needed in order to improve agricultural production from the ecological and economic point of view. The air temperature and soil water conditions have a strong influence on the culture of the oil palm tree, because it influences the number of bunches, as well as the oil content in the fruit (CARR, 2011; ROLL et al., 2015; CHAGAS et al., 2019; AUCIQUE-PEREZ et al., 2020).

The temperature has a significant influence on the stomatal conductance, the photosynthetic apparatus, and with that on the gas exchange of plants (COSTA et al., 2002; MORAIS et al., 2017). According to Wise et al. (2004), high temperatures may damage the thylakoid membranes, the organizational structure, and the physicochemical properties of the photosynthetic apparatus. High temperatures can lead to increased mitochondrial respiration and photorespiration (DIAS & MARENCO, 2007).

Although the rate of $C0_2$ assimilation is a very sensitive parameter for the investigation of exogenous impact on plants, gas exchange measurements of oil palms have been carried out predominately with young plants under laboratory conditions (HONG & CORLEY, 1976), while only few studies were carried out under field conditions (DUFRENE & SAUGIER, 1989, 1993; HENSON & HARUN, 2005; LAMADE & BOUILLET, 2005; SEPTIWIBONO et al., 2019). However, field studies are necessary in order to understand the interactions between abiotic and biotic factors present in commercial plantations.

Therefore, in this study the influence of leaf temperature on the gas exchange of oil palms was studied in the field in monocultures and in plantations intercropped with cassava or banana. The study was carried out with special regard to predicted climate change scenarios in the Central Amazon.

MATERIAL AND METHODS

Experimental site

The study was carried out at the experimental station of the Embrapa Amazonia Ocidental, located in the Agricultural District SUFRAMA (DAS) in Presidente Figueiredo (BR-174 Manaus - Boa Vista, km 54; 2° 31' S and 60° 02' W). The soil of the site was classified as Oxisol álico with a clay texture. The annual average rainfall is 2500 mm per year with a 2-3 month dry season, and the mean annual temp is 26° C. The site was used as pasture for approximately 10 years and abandoned in 1990. The experiment was installed in 2004 in a completely randomized block design with three repeats. Three different plantation systems were installed (3 systems x 4 plots per system). Each plot contained 24 oil palms. System I: Oil palm (planted in equilateral triangle of side 9 meters, 9 m within row and 7.8 m between planting); System II: Palm intercropped with banana cv Thap Maeo planted between the palms (spacing 3 m x 2.5 m between plants in row); System III: Oil palms mixed with cassava butter planted in four rows between the lines (spacing of 1.0 m x 0.8 m between lines). The oil palms were created from seeds of intraspecific crosses of the type tenera (BRS 2501) from Rio Preta da Eva-AM located about 60 km west of Manaus.

Gas exchange measurement

The gas exchange measurements were carried out in March/April 2008 (rainy season in the Amazon region, plant age 4 years). The analysis was carried out at this time with good soil water availability, and therefore without interference with gas exchange due to lack of water in the soil. In each plot the gas exchange of three oil palms was quantified at leaf number 17 counted from the top of the plant, because it is the one that best expresses the physiological state, that is, it presents a defined structure and maximum metabolic activity (CORLEY, 1983; DUFRENE & SAUGIER, 1989; RODRIGUES et al., 2002). The net photosynthesis (P_n), the transpiration (E), and the stomatal conductance (g_s) of the leaves were quantified by means of a portable photosynthesis meter (CID, Model CI-340, Camas). In addition the water use efficiency (WUE = P_n / E) was calculated. The data of the response curve photosynthetic temperature variations were obtained in the intensity of photon flux (PPDF) 1000 $\mu mol.m^{-2}.s^{-1}$ foliar chamber fitted with CO_2 concentration of 400 $\mu mol.CO_2\ m^{-2}.\ s^{-1}$ and at temperatures of 30, 34, 38, 42, 46 and 50°C, obtained by means of the temperature control module coupled to the CI-510CS portable photosynthesis meter (CI-340, CID, Inc.). The sequence of measurements was always following order of increasing intensity, the minimum temperature predetermined for the stabilization of readings at each temperature level, and the maximum was 10 minutes to 20 minutes.

Statistics

The relationship between leaf temperature and leaf gas exchange were submitted to analysis of variance, adopting the level of significance of 1 and 5% for the F test. The variables were analyzed by means of Pearson correlations and regression analyses.

RESULTS AND DISCUSSION

The results showed that all plantation systems had a significant effect ($p \leq 0,01$) on P_n, E, g_s Wue rates in relation to the increase in leaf temperatures (Table 1). Regarding the regression analysis, observing the behaviour of gas exchange in relation to the effect of the increase in foliar temperatures, it was found that there were differences between the planting systems. For the monoculture oil palm system, the linear regressions were significant for the g_s and Wue variables, while the P_n and E rates were significant ($p \leq 0,01$) for the polynomial regressions. In the oil palm intercropped with banana system, the P_n and Wue rates were significant for both regressions, with differences between the stomatal conductance with significance for linear regression and the transpiration perspiration rates with significance for polynominal regression. For the oil palms mixed with cassava system, only the stomatal conductance rates were significant for the linear regression and the polynomial regression was significant for all the gas exchange variables (Table 1).

TABLE 1: Analysis of variance, regression and significance of the mean-squares (QM) of the leaf temperatures (TF) on the net assimilation rate of CO_2 (P_n), transpiration rate (E), stomatal conductance (g_s) and the efficient use of water (WUE) of oil palms in monoculture and two mixed plantations (mixed banana, mixed cassava).

Oil palm monoculture					
Factors	GL	QM			
		P_n	E	g_s	WUE
Leaf temperature	5	42,41**	3,74**	51580,47**	17,51**
Linear regression	1	26,35^{ns}	0,76^{ns}	31823,93**	13,37**
Polynominal regression	1	370,64**	19,77**	21694,85^{ns}	0,09^{ns}
Average		9,09	2,41	148,80	3,98
CV (%)		21,85	19,40	54,19	18,45
Oil palms mixed with bananas					
Factors	GL	QM			
		P_n	E	g_s	WUE
Leaf temperature	5	105,41**	3,62**	42665,29**	21,55**
Linear regression	1	94,98**	0,94^{ns}	34173,23**	21,26**
Polynominal regression	1	39,11**	35,17**	1641,15^{ns}	7,19**
Average		7,76	2,19	126,83	3,40
CV (%)		24,15	29,81	36,16	14,58
Oil palms mixed with cassava					
Factors	GL	QM			
		P_n	E	g_s	WUE
Leaf temperature	5	67,25**	7,02**	214272,93**	17,75**
Linear regression	1	86,02^{ns}	0,36^{ns}	223636,07**	15,64^{ns}
Polynominal regression	1	177,74**	85,56**	60628,10**	31,64**
Average		9,90	3,28	216,13	3,23
CV (%)		27,28	27,70	30,47	15,58

****, * Significant at 1 and 5%, respectively, ^{ns} Non-significant. CV (Coefficient of variation).**

In all plantations the rate of photosynthesis, the stomatal conductance and efficiency in water use were negatively correlated (($p \leq 0,01$). The rate of transpiration showed a significant positive correlation in monoculture oil palm and a significant negative correlation in oil palm intercropped with banana. In the system oil palms mixed with cassava, the transpiration rates showed no significant correlation (Table 2).

TABLE 2: Pearson correlation between the leaf temperature (LT), net photosynthesis (P_n), transpiration (E), stomatal conductance (g_s) and water use efficiency (WUE) of oil palms in monoculture and two mixed plantations (mixed banana, mixed cassava).

Monoculture.	P_n µmol.CO_2 m^{-2}. s^{-1}	E mmol.H_2O. s^{-1}	g_s mmol.H_2O. s^{-1}	WUE
LT (°C)	-0.4022**	0.6705**	-0.4867**	-0.9077**
Mixed banana	P_n µmol.CO_2 m^{-2}. s^{-1}	E mmol.H_2O. s^{-1}	g_s mmol.H_2O. s^{-1}	WUE
LT (°C)	-0.7998**	-0.2510*	-0.7780**	-0.9530**
Mixed cassava	P_n µmol.CO_2 m^{-2}. s^{-1}	E mmol.H_2O. s^{-1}	g_s mmol.H_2O. s^{-1}	WUE
LT(°C)	-0.5964**	0.2387 ^{ns}	-0.9545**	-0.9390**

****, * Significant at 1 and 5%, respectively, ^{ns} Non-significant. CV (Coefficient of variation).**

In figures 1, 2, 3 and 4 the equations of the curves are adjusted to explain the biological behaviour of the effect of leaf temperature elevation on the gas exchange of oil palm leaves in different planting systems.

Leaf temperatures higher than 42 °C had the strongest impact on the net photosynthesis of the oil palms. (up to 65% reduction of CO2 assimilation, Figure 1). The impact of increasing leaf temperatures on the net photosynthesis of the oil palms was more pronounced in the plantation system II (mixed with banana) than in the systems, I (monoculture) and III (mixed with cassava).

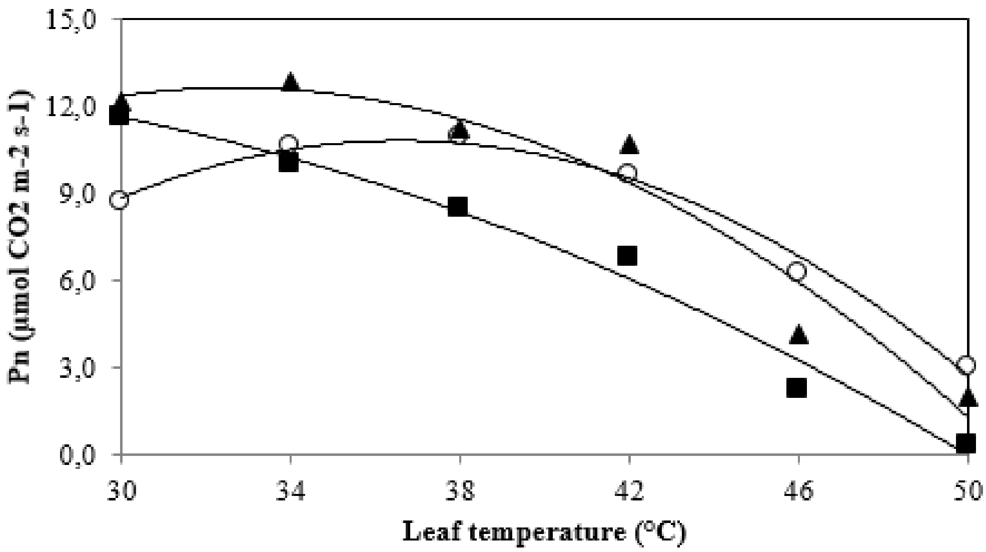

FIGURE 1: Relationship between leaf temperature (°C) and net photosynthesis (P_n) of 4-years-old oil palms: Monoculture (○), Oil palms mixed with bananas (■) and Oil palms mixed with cassava (▲). ***Means*** **(n=10. The relationship between leaf temperature and net photosynthesis was adjusted by the equations: y (○)= -0,0452x^2 + 3,3064x – 49,668 R^2 = 0.98, y (■)= -0,0147x^2 + 0,5936x + 7,0663 R^2 = 0,98, y (▲)= -0,0378x^2 + 2,4737x – 27,6 R^2 = 0,94.**

In the mixed plantations II and III transpiration rates were negatively correlated with the leaf temperature at temperatures higher than 38° C, while in the monoculture plantation I a significant impact of leaf temperature on the transpiration rate was exclusively found for leaf temperatures higher than 46° C (Figure 2).

The negative correlation between leaf temperature and net photosynthesis is caused by the increase in the rate of respiration, the decrease in stability of membranes, the decrease in carboxylation efficiency of Rubisco, and the accumulation of carbohydrates (starch) in chloroplasts at high temperatures. With the increase of the temperature in the leaves for a prolonged time, there can be damage to the photosynthetic apparatus in an irreversible way, because the process of CO_2 assimilation is damaged due to the enzymatic destructuring and denaturation involved in the process of CO_2 assimilation, causing photoinhibition or photodestruction (SIEBKE et al., 2002; KATTGE & KNOOR, 2007)

The maximum net photosynthesis of the oil palms observed in our study (12 µmol CO_2 m^{-2} s^{-1}) was lower than reported for oil palms grown in Cote d´Ivoire (DUFRENE & SAUGIER, 1989, 1993),(approximately 23 µmol CO_2 m^{-2} s^{-1} in plants with five years of age in leaflet number 10).

In the study conducted by Fonseca et al. (2018) on oil palm plantations in Pará, the average daytime values of CO_2 absorption reached a maximum around noon, with 22,3 (0,98) µmol m^{-2} s^{-1} in the rainy season and 21,0 (0,47) µmol m^{-2} s^{-1} in the less rainy season in agricultural cultivation in dry year in eastern Amazonian. This might be caused by the differences in leaf age and differing soil conditions in these studies.

Studies carried out by Schroth et al. (2001) show a strong competition for water and nutrients between plants in dense agroforestry systems. Other studies indicate a strong competition light in complex agroforestry systems, which also had a strong impact on the productivity of the plants (LAL, 1991; SALAZAR et al., 1993).

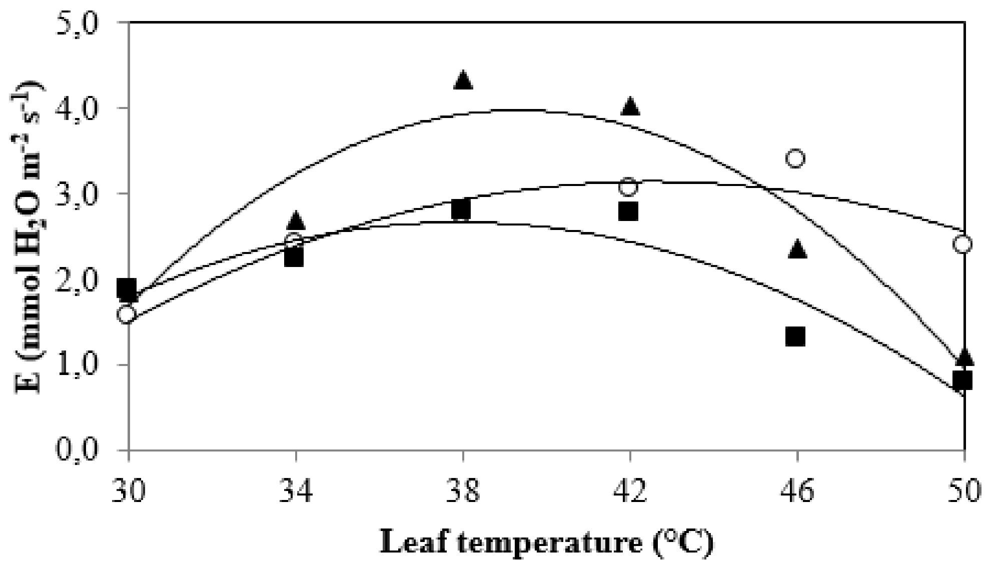

FIGURE 2: Relationship between leaf temperature (°C) and transpiration (E) of 4-years-old oil palms: Monoculture (○), Oil palms mixed with bananas (■) and Oil palms mixed with cassava (▲). ***Means*** **(n=10). The relationship between leaf temperature and transpiration was adjusted by the equations: y (○)= -0,0104x² + 0,8883x – 15,726 R² = 0,89, y (■)= -0,0139x² + 1,0558x – 17,337 R² = 0,87, y (▲)= -0,0264x² + 2,0766x – 36,84 R² = 0,90.**

Our results agree with results obtained by Dufrene & Saugier (1989) showing also maximum transpiration rates of oil palms in mixed plantations at leaf temperatures between 30 and 38 ° C. Transpiration has a strong cooling effect (at 25° C 44 kJ mol^{-1} to evaporate a water molecule) (TAIZ & ZEIGER, 2004) indicating an intercorrelation between the leaf temperature and the transpiration rate in our study. It is observed in this study that due to the good water availability of the soil due to the rainy season in the region, the transpiration rates had an increase up to 42° C, due a strategy used to reduce the leaf temperature, avoiding damage due to overheating of the photosynthetic apparatus, since the evaporation process of the water molecule by the plants causes substantial heat loss and is one of the most important means available to them to regulate temperature. In the studies of Mendez et al. (2012), it is observed that there is a strong influence of the water status of the oil palm plants on the gas exchange, with a drastic reduction of the parameters in low water availability of the soil.

Differences in transpiration in the three plantation systems are paralleled by differences in stomatal conductance (Figure 3). We suggest a lower vapor pressure deficit (VPD) in plantation system II (mixed with banana) compared to system I (monoculture) and III (mixed cassava) due to partial shading by the big banana leaves. Fifah & Haniff (2018) also evaluating the behavior of oil palm gas exchanges in different periods of precipitation found that the values of g_s decreased 54% during the dry period compared to the wet period, leading to a reduction of 59% 44% in the rates of photosynthesis and transpiration, respectively.

In mahogany trees, Dias & Marenco (2007) also detected a reduction in photosynthetic rate and stomatal conductance with increasing leaf temperatures. These authors suggest a significant influence of the increase in vapor pressure deficit (VPD) and a reduction in leaf water potential on the opening and closure of the stomata.

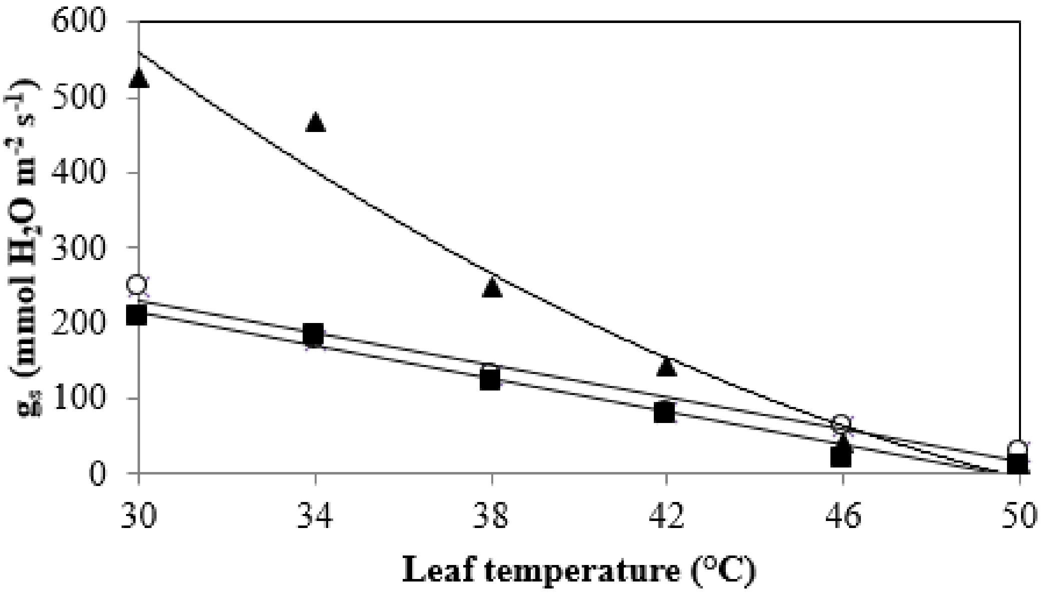

FIGURE 3: Relationship between leaf temperature (°C) and stomatal conductance (g_s) of 4-years-old oil palms: Monoculture (○), Oil palms mixed with bananas (■) and Oil palms mixed with cassava (▲). ***Means*** **(n=10). The relationship between leaf temperature and stomatal conductance was adjusted by the equations:y (○)= -10,66x + 548,1 R^2 = 0,96, y (■)= -11,04x + 545,6 R^2 = 0,97, y (▲)= $0{,}6986x^2 - 84{,}145x + 2455{,}8$ R^2 = 0,97.**

This might be due to the lower competition for soil water in system I compared to system II and III.

The reduced impact of high leaf temperatures on the net photosynthesis and the transpiration of oil palms grown in system I (monoculture) compared to system II (mixed banana) and III (mixed cassava) corresponds to a slighter decrease of the water use efficiency of the palms in system I compared to the mixed systems II and III at higher temperatures (Figure 4).

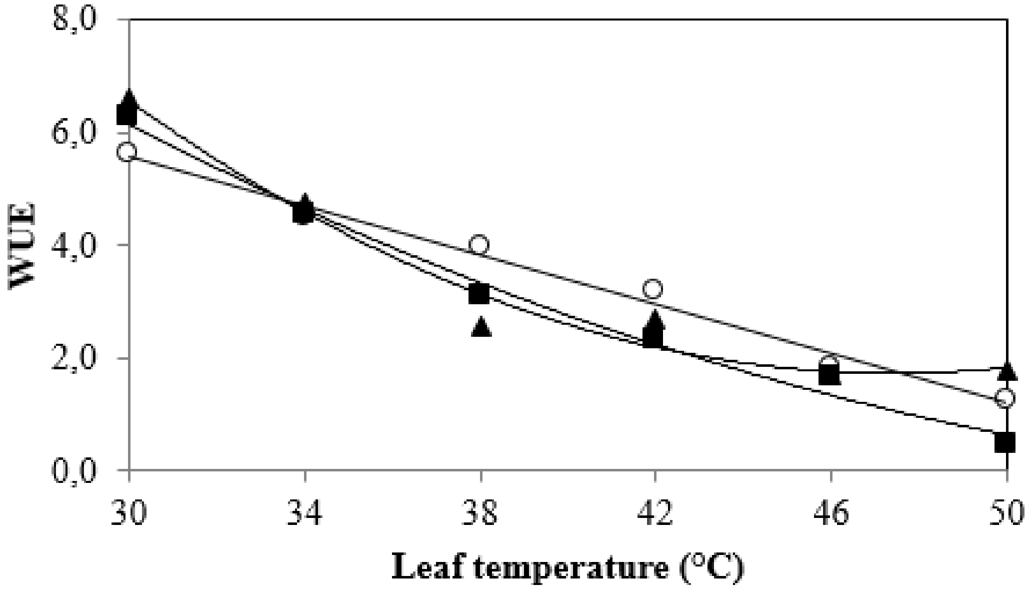

FIGURE 4: Relationship between leaf temperature and water use efficiency (WUE) of 4-years-old oil palms: Monoculture (○), Oil palms mixed with bananas (■) and Oil palms mixed with cassava (▲). *Means* (n=10). The relationship between leaf temperature and water use efficiency was adjusted by the equations:y (○)= -0,218x +12,13 R^2 = 0,98, y (■)= 0,0063x^2 – 0,7813x + 23,905 R^2 =0,99, y (▲)= 0,016x^2 – 1,5164x + 37,663 R^2 = 0,96.

This gives further evidence for the assumption that in the 4-years-old plantation the positive effect of reduced competition in the monoculture system I favors the primary production of the oil palms, while expected synergistic effects (nutrition, soil water conditions) in the mixed plantations are of less importance for the productivity of the palms.

CONCLUSION

From the results, it can be concluded that the leaf temperature is the dominant factor affecting the gas exchange of the oil palm, while the agricultural management in the different plantation systems is of less importance. Consequently, the layout of mixed plantations should concentrate on the light and temperature conditions of the plants considering a predicted increase of air temperature in the Amazon in the future.

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