Leaf Gas Exchange Measurement Under Land Use Changes in Jambi, Indonesia

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January, 2018

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Masterarbeit
Zur Erlangung des M.Sc. an der
Bioklimatologie Abteilung
Fakultät fur Forstwissenschaften und Waldökologie
Georg-August-Universität Göttingen
Januar, 2018

Abstract

Rapid deforestation is occurring in Indonesia, where the development of oil palm and rubber plantation are the main drivers. These transformations will have an impact on the carbon cycle; however, our understanding about these changes is incomplete partly because we have little data to date. Carbon cycle changes can be understood by Land Surface Models (LSMs). However, using LSM's to predict changes in carbon cycle remains uncertain. Highest uncertainty attributed to parametrization of photosynthetic activity, which is defined as the balance of carboxylation capacity (V_{cmax}) and electron transport capacity (J_{max}).

Therefore, in this study, we measured diurnal photosynthesis and photosynthetic capacity of various species under land use change systems in Jambi, Indonesia. We found that the rates of leaf net photosynthesis and evapotranspiration on oil palm in a large scale commercial plantation (PTPN VI) have similar pattern. Both showed a major inclining rate during mid-morning, followed by a slow declination rate throughout the day. We also found a stronger correlation of evapotranspiration and meteorological variables, especially light radiation. We found that Jungle rubber had the highest V_{cmax} and J_{max} across all land-use types. The high fertilized oil palm had a higher V_{cmax} and J_{max} than low fertilized oil palm. Fast growing species had a higher V_{cmax} and J_{max} than slow growing species. We also found that old plants had a higher V_{cmax} and J_{max} than young ones. V_{cmax} and J_{max} were strongly correlated while V_{cmax} and leaf nitrogen content moderately correlated. The data-sets collected in this study can be used to parametrize some of LSMs. Further, these data-sets can also be incorporated into large data-bases that examine global scale patterns.

Keywords: carboxylation capacity (V_{cmax}¬), electron transport capacity (J_{max}), photosynthetic activity, plantation, oil palm, rubber, tropical forest.

Zusammenfassung

In Indonesien schreitet die EntwaldungAbholzung von Regenwald und der Ersatz mitdurch Ölpalm- und Kautschukplantagen als den hauptsächlichen Triebkräften rasch voran. Die Umwandlung Transformation wird einen Einfluss auf den Kohlenstoffkreislauf haben, jedoch ist das Wissen über diese Veränderungen unvollständig, teilweise aufgrund mangelnder Daten. Änderungen im Kohlenstoffkreislauf können mithilfe von Landoberflächenmodellen (LSMs) verstanden werden. Die Verwendung von LSMs zur Vorhersage von Änderungen im Kohlenstoffkreiselauf ist jedoch mit großen Unsicherheiten behaftet, Jedoch gibt es weiterhin große Unsicherheiten in der Vorhersage von LSMs, die hauptsächlich mit der Parametrisierung der von Photosyntheseaktivität zusammenhängen, welche als das Geichgewicht aus Karboxylierungskapazität (V_{cmax}) und Elektronentransportkapazität (J_{max}) definiert ist.

Deshalb aher wurden in dieser Studie Tagesgänge der Tages-Photosynthese, sowie die und -Photosynthesekapazität verschiedener ABaumarten in Systemen mit Landnutzungsänderung in Jambi, Indonesien, gemessen. Es wurde herausgefunden, dass die Raten der Blatt-Netto-Photosynthese und Evapotranspiration der Ölpalmen in großflächigen kommerziellen Plantagen (PTPN VI) ähnlich waren wie große Steigerungen am Vormittag. Auch eine stärkere Korrelation von Klima und Evapotranspiration wurde nachgewiesen. In allen Landnutzungssystemen wurden für Dschungelkautschuk die höchsten V_{cmax} und J_{max}-Werte nachgewiesen. Stark gedüngte Ölpalmen zeigten höhere Werte für V_{cmax} und J_{max} als weniger gedüngte. Schnell wachsende Arten zeigten höhere Werte für V_{cmax} und J_{max} als langsam wachsende Arten. Ebenso zeigten alte Pflanzen höhere V_{cmax} und J_{max} -Werte als junge. V_{cmax} und J_{max} waren stark korreliert, während V_{cmax} und Blattstickstoffinhalt nur mäßig korreliert waren. Die in dieser Studie erhobenen Datensätze können zur Parametrisierung einiger LSMs verwendet werden. Außerdem können sie in umfassende Datenbanken eingegliedert werden, die globale Zusammenhänge untersuchen.

Schlüsselworte: Karboxylierungskapazität (V_{cmax}), Elektronentransportkapazität (J_{max}), Photosyntheseaktivität, Plantage, Ölpalme, Kautschuk, Tropenwald

Acknowledgement

I would like to thank my supervisor Prof. Dr. Alexander Knohl for the opportunity to conduct my master thesis under the bioclimatology department and as well for the remarkable insights and provision. I would also like to thank Dr. Ashehad Ali for the support, encouragement, comment, discussion and guidance throughout the fieldwork and writing period. Helps and comments from all colleagues of the Bioclimatology department are much appreciated. Special thanks to the fieldwork team, who made the data collecting possible.

My greatest gratitude for Indonesian Endowment Funds for Education (LPDP) for the full scholarship throughout the Tropical and International Forestry (TIF) master program. My sincere gratitude for the project from Collaborative Research Centre (CRC) 990: “Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia)” for giving me the access to the facilities and information during and after the fieldwork.

I would also like to acknowledge all my professors, lecturers, tutors, and classmates in TIF program. Special thanks for Indonesian big family living in Göttingen for the warmth and kindness. Especially for all of my best friends in Göttingen, Argi, Ka Onya, Gannady, Tania, Ari, Adit, Josia who have made 2 years of study very fun and memorable. Last but not least, I would like to thank my parents, family, and friends in Indonesia for the support and motivation.

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1. Introduction

1.1 Land Use Transformation

Globally, forests cover up to 3.9 billion hectares of land, which is about 30 % of the whole world's land surface (Food and Agriculture Organization 2006). This amount of forest cover is decreasing due to deforestation. The speed of deforestation in the world reached 12.9 million hectares annually during 2000-2005 as published by Intergovernmental Panel on Climate Change (IPCC) in fourth assessment report (AR4). The definition of deforestation is the transformation of forested lands to non-forested lands or a long-term canopy cover reduction, with a minimum 10% threshold (FAO 2010). The forest transformed into another land use such as agricultural, plantation, grassland, or urban land. United Nations Framework Convention on Climate Change (UNFCCC) categorized deforestation as one of the land use change which contributed to global emission. IPCC (2013) reported in their Fifth Assessment Report (AR5) that Forestry and Other Land Use (FOLU) contributed 11% of total annual anthropogenic greenhouse gas (GHG) emission. A large amount of forest loss is happening in tropical countries (FAO 2016).

Indonesia is one of the tropical countries in Southeast Asia that has a relatively large amount of forest. In Indonesia, forests stretch over -approximately- 187.84 million hectares, covering than 50% of the total land area (Ministry of Environment and Forestry of Indonesia 2014). Currently, rapid deforestation is occurring in Indonesia leading to a forest loss of around 6.02 million hectares of forest during 2000-2012 (Margono, Potapov, Turubanova, Stolle & Hansen 2014). Within Indonesia, Sumatra and Kalimantan are the two hotspots where most of the deforestation occurred (Margono *et al.* 2014). One of the main factors of deforestation is the transformation of forest to plantation area, mainly oil palm (Gilbert 2014). Most of the plantations in Indonesia are currently located in Sumatra and Kalimantan and are operated either by small-holder or commercial companies. Apart from Indonesia companies, there are also international companies in the oil palm business which plays a big role in

Indonesia's deforestation. The implemented moratorium has not slowed forest loss, but it is part of the prevention process (Gilbert 2014).

Sumatra lost approximately 550,000 hectares of forest annually from 1990 to 2007 (Laumonier *et al.* 2010), mostly due to transformation to the plantation. The transformation from tropical forest to rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis)* plantation were already reported by many research (Tilman *et al.* 2001; Fitzherbert *et al.* 2008; Koh, Miettinen, Liew & Ghazoul 2011; Villamor, Pontius & van Noordwijk 2014). The increasing number of the allocated land surface for oil palm reaches approximately 400,000 hectares per year, reaching a total of 10.6 million hectares in 2015 (USDA 2016). The transformation of forest to rubber agroforestry system in Sumatra started in 1900's, and oil palm plantation started ten years later under Dutch administration (Gouyon, de Foresta & Levang 1993; Corley & Tinker 2003). Since then, the potential profit of these two plantations was recognized and started dominating the land utilization.

1.2 Impacts of Land Use Transformation on Carbon Cycle

There will be an impact on the global carbon cycle caused by emissions produced from forest transformation (Houghton, Hall & Goetz 2009). The government of Indonesia reported to United Nations Framework – Convention on Climate Change (UNFCCC) in the Second National Communication (SNC) that land-use change in Indonesia contributed more than 50% of total carbon emission of the country (Ministry of Environment, 2010). The carbon cycle is the flow within a place in which carbon is stored (called carbon pool, storage, reservoir or stock) (University of New Hampshire 2014). Three important carbon stocks are the atmosphere, terrestrial, and ocean. These carbon stocks have their own characteristic and importance. The ocean is well known as the biggest containers of carbon. The atmosphere is the smallest yet very significant because of its role as the connecting line between the other two. Terrestrial is the most dynamic carbon stock, which includes forests and the organic carbon contained within the soil (Post *et al.* 1990).

Plants with their photosynthetic and respiration system is an important aspect in the carbon cycle through their leaf gas exchange activity with the atmosphere. Photosynthesis is a vital process for the plant to grow and survive during their growth cycle and is the starting point of the carbon cycle. Carbon fixed through photosynthesis fills around 40% of plant's dry mass. CO_2 absorbed by leaf through stomata is diffusing from intercellular spaces to the point of carboxylation inside the chloroplast (C_3 species) (Lambers, Chapin & Pons 2008). The optimum condition for photosynthesis includes a certain range of water supply, availability of nutrients for the plant, and ideal light and temperature conditions, as well as another minor affecting condition. The less favorable condition will change the rate of photosynthesis inside the plants, such as elevated CO_2 supply (Lambers *et al.* 2008). Moreover, the complete land use transformation from forest to non-forested land will result in extreme changes (Canadell & Raupach 2008; Churkina 2008; Vitousek, Mooney, Lubchenco & Melillo 2008). The release of CO_2 in tropical lands can be estimated using model, comparing carbon content with and without the transformation (Detwiler 1986). The intensive cultivation of tropical soil can reduce its carbon content down to 60% after five years of clearing (Olofsson & Hickler 2008).

The current trend of global-scale changes in the environment (especially elevated atmospheric CO_2 concentrations) might cause the change in NEP (Net Ecosystem Productivity) as well. In this case, photosynthesis will respond stronger to the atmospheric CO_2 concentration compared to heterotrophic respiration, which leads to the escalating net CO_2 uptake from elevated atmospheric CO_2 from fossil fuel burning and land use change emissions (Lambers *et al.* 2008). The changes in global carbon cycle can be predicted by Land Surface Models (LSMs). It is essential to understand the interaction of water and carbon cycles, the energy from terrestrial and vegetation, and how these might change due to eco-physiological responses to increasing CO_2 caused by changes in land use (IPCC 2001). Tropical forest is assumed to be vulnerable to the climate change caused by land use change (Phillips *et al.* 2010), yet we do not fully understand whether the tropical trees would be able to cope with the elevating atmospheric supply of CO_2 through photosynthetic carbon fixation (Bonan & Levis

2010). Moreover, LSMs have lots of uncertainties that are mainly caused by parameterization of the photosynthetic activity (Norby *et al.* 2016).

1.3 Photosynthetic Capacity

Photosynthetic capacity (A_{max}) is defined as the balance between carboxylation capacity (V_{cmax}) and electron transport capacity (J_{max}) (Hopkins & Huner 2009). It is also the rate of CO_2 assimilation at saturated light (Lambers *et al.* 2008). V_{cmax} and J_{max} are the most important parameters to evaluate the photosynthetic capacity plants with different characteristics. V_{cmax} is the maximum carboxylation rate (Lambers *et al.* 2008; De Kauwe *et al.* 2016; Norby *et al.* 2016), which resulted by the activity rate of the enzyme ribulose 1.5-bisphosphate carboxylase/oxygenase (RuBisCO) (Farquhar, von Caemmerer & Berry 1980; Domingues *et al.* 2010) while J_{max} is the maximum rate of photosynthetic electron transport (Caemmerer 2000; Lambers *et al.* 2008; De Kauwe *et al.* 2016). These two parameters are commonly used to measure the photosynthetic capacity as V_{cmax} shows the response to the CO_2 treatments while J_{max} to response the light treatments. There is also Dark Respiration (Rd) that is required to produce the essential carbon and energy to sustain plant growth (Lambers *et al.* 2008).

Photosynthesis has an important role in ecosystem carbon cycle, as well as in earth system model (Sellers 1997; Canadell *et al.* 2007; Block & Mauritsen 2013; Hurrell *et al.* 2013). Most of this model developed by Farquhar et al. (1980) are sensitive to photosynthetic capacity (Ali *et al.* 2016). It is essential to understand the responses to increasing CO_2 caused by land use change (IPCC 2001), so we will be able to predict a wider scope of changes in global environment condition. The elevated CO_2 is affecting the rate of photosynthesis (VAN OOSTEN, WILKINS & BESFORD 1994; Bert G. Drake and Miquel A. Gonzàlez-Meler 1997; Nakano, Makino & Mae 1997; Osborne, Drake, LaRoche & Long 1997; Curtis & Wang 1998; Theobald, Mitchell, Parry & Lawlor 1998; Würth, Winter & Körner 1998). Based on biochemical characteristics needed for CO_2 assimilation, there is a photosynthetic model developed by Farquhar et al. (1980). The model can demonstrate the basic principle of the biochemistry of photosynthesis using several photosynthetic parameters (Lambers *et al.* 2008).

Photosynthetic capacity can be measured in controlled measurement as well as in the field. There are several considerations before attempting the site measurement. High heterogeneities of environmental variable make it hard to conduct field measurement, moreover in an area with frequent changes of weather condition (Tian-gen *et al.* 2017). Measurement done in late-afternoon on the cloudy or overcast day will give a lower and inaccurate data (Chen, Yu, Chen & Xu 2006). Complexities and challenges such as difficulty to reach a certain area of the tree, the trees and bushes density of the tropical forest, and the threat from insects or wildlife, also need to be considered in the field measurement (Ehleringer & Cook 1980). Using controlled environment such as in the greenhouse or laboratory can be used as an option to overcome the mentioned problems. However, many research showed that there is a significant difference between the plants grown in the field and inside the controlled environment in the photosynthetic parameters (Mahon & Hobbs 1981; Mishra *et al.* 2012; Kolari *et al.* 2014). Compared to the plants in the field, plants in the greenhouse cannot capture well enough the changes of dynamics environments overtime (Tian-gen *et al.* 2017). Therefore, it is important to measure photosynthetic rates in the natural field condition.

1.4 Leaf Gas Exchange Measurements

Few studies of tropical forest have reported that diurnal photosynthetic patterns might be related to seasonal changes in microclimate and water availability (Koch, Amthor & Goulden 1994). It is important to understand the diurnal pattern of species photosynthesis as there is no data related to this aspect of highly demanded oil palm. Water use efficiency (WUE) and light use efficiency (LUE) are calculated from the collected data to understand how water and light are limiting the photosynthesis activity. Both are defined as the ratio of the light and water used productively in the photosynthesis process (Stanhill 1986).

The ratio between stomatal conductance and a function ($A/(C_a\sqrt{VPD}$) also will be calculated as it can visualize the fitting of optimal stomatal conductance (Medlyn *et al*. 2011). Measurement of photosynthetic capacity was done to compare to the different photosynthetic rate in plantation management (monoculture-polyculture), fertilization rate (high-low), leaf position (sunlit-shaded), age class (young-old), slow-growing and fast-growing species (ulin-pulai).

1.5 Hypothesis

Photosynthetic rate is changing over time during the day. There are several known types of diurnal photosynthetic pattern in the tropical rainforest: (1) Midday photosynthetic moderate depression (Brodribb & Holbrook 2007) and (2) continuous photosynthetic recession from late morning to the end of the daytime (Kenzo, Ichie, Ninomiya & Koike 2003; Brodribb & Holbrook 2007). The photosynthetic depression in tropical forest upper layer leads to the absorption of saturated light energy by chloroplast (Zhang, Meng & Cao 2009). Midday stagnancy in stomatal conductance (g_s) will limit CO_2 distribution to the mesophyll, thus photorespiration increases (Ishida, Nakano, Matsumoto, Sakoda & Ang 1999; Flexas & Medrano 2002).

Many important aspects remain uncertain regarding how different species with the different characters in respect of their photosynthetic capacity. Several species will be involved in this research such as oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*), and two forest species Ulin (*Eusideroxylon zwageri*) and Pulai (*Alstonia scholaris*). Ulin is a slow growing species; it needs around 120 years to get the 30 cm DBH (Kiyono & Hastaniah 2000). Pulai represents a fast-growing species, it can grow up to 30 meters high with the bole diameter around 30 cm in only ten years (Vincent 2006; Mashudi 2015). It is expected that fast-growing species favor having higher rates of photosynthesis, and also use respiratory energy more efficiently for growth and maintenance (Munns 2016). The effectiveness reflected in the energy-use proportion of whole-plant respiration to each specific growing process. However, reported by Van Der Werf et al. (1993), when existing differences in the plants' ability to absorb nutrients are eliminated, there will not be any significant differences in the primary physiological plant characteristic.

Differentiated as well as the rate of fertilization, the light availability for the leaf and the age class of the plants. Reported by Yong et al. (2010) that there’s a higher rate of photosynthesis obtained with the mature leaves with increased P and N nutrition level through fertilization. In addition, this rate of fertilization also indicates the quality of management in the oil palm plantation. The high fertilized oil palm plantation can receive up to 196 kg N ha−1 as urea (Meijide *et al*. 2017). The photosynthetic capacity of the sunlit and shaded leaf within the same species also will be compared.

The objectives of this study are to:

- To identify the diurnal photosynthetic pattern of oil palm tree
- To identify the water and light use efficiency pattern of oil palm tree
- To compare the rate of photosynthetic activity across species and land use
- To determine the relationship of photosynthetic rate and leaf nitrogen content

The hypothesis taken:

H1: The rate of photosynthesis will reach the peak at mid-morning.

H2: WUE and LUE will follow the pattern of leaf net photosynthesis.

H3: Sunlit leaves will have higher CO_2 assimilation compared to shaded leaves.

H3: Forest species will have a higher photosynthesis rate compared to plantation plants (oil palm and rubber)

H4: Fertilization rate, age class, leaf position, and silviculture management will have an impact on photosynthetic rate

2. Materials and Methods

2.1 Location and Data Design

This research is part of the Collaborative Research Center (CRC) 990 project: “Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems”. We conducted the study in Jambi, province of Indonesia, on the island of Sumatra. The total land area of Jambi province is 53,435 km^2, with approximately 21,000 km^2 of it covered by forest in 2015 (Badan Pusat Statistik 2016). Based on figures published by Jambi Plantation Agency (2014), oil palm and rubber make up most of the area covered by plantations in Jambi. Total area cover in that year for oil palm plantation and rubber plantation reached 662,846 hectares and 668,121 hectares respectively (Dinas Perkebunan Provinsi Jambi 2014).

Based on Köppen Climate Classification, Jambi classified as tropical rainforest climate (Af) with the monsoon. The rainy season runs from October to April, with the rest of the year being the dry season. Mean annual temperature is 26.7 ± 0.2°C and mean annual precipitation is 2,235 ± 381 mm (Allen, Corre, Kurniawan, Utami & Veldkamp 2016). During the last three years (2014-2016) the air humidity ranged from 73 to 94 % (Badu 2016).

Data were collected from four different locations within Jambi province. The first measurement location was PTPN VI Oil Palm Plantation (S 01°41'35.0" E 103°23'29.0"), a large commercial plantation with an average stand age of 13 years and high levels of fertilizer application (196 kg urea N ha^{-1} yr^{-1}, Meijide *et al.*, 2017). The second measurement location was Humusindo Oil Palm Plantation (S 01°54'39.5" E 103°16'00.1"), a smallholders-managed plantation. The stand age in Humusindo varying between 1 to 12 years, representing a plantation with low fertilizer application (48 to 138 kg N ha^{-1} per year, Allen et al., 2016). The third and fourth study areas were jungle rubber (polyculture) and rubber plantation (monoculture), located within the same area of Humusindo Oil Palm Plantation. The distance from PTPN VI to

Humusindo Oil Palm Plantation is roughly 50 kilometers. Both areas have the same dominant soil which loam Acrisol.

Observed variables in the collected data were species, land-use, fertilization rate, leaf position, and age class. Species observed were oil palm (*Elaeis guineensis* Jacq.), rubber (*Hevea brasiliensis*) in monoculture and polyculture plantation, ulin (*Eusideroxylon zwageri*) and pulai (*Alstonia scholaris*) in polyculture plantation. The rate of fertilization will be compared from two different oil palm plantations, PTPN VI (state-owned) and Humusindo (smallholders). The position of the measured leaf also will be compared between sunlit and shaded leaf. Sunlit leaves should be fully exposed to sunlight for the whole day. Shaded leaves should not be directly exposed to sunlight during daytime. The age class of the plant also will be compared for ulin and pulai. The trees under three years old, and haven’t been harvested were categorized as young, otherwise categorized as old. Three replicates were taken during the measurement of photosynthetic parameters. Particularly for oil palm in PTPN, diurnal photosynthetic patterns and light response also measured. Three replicates were measured every hour in oil palm diurnal measurement.

2.2 Instrumentation

There is an installed meteorological station (flux-net tower) in PTPN VI that records carbon, energy, and water fluxes. This tower also recorded the meteorological data. Since a 30m ladder is available in this tower, we were able to reach the top of the canopy and carry out our measurements at that canopy level. For other sites, we used a 5m ladder and did leaf measurements at this ladder height. We consider these measurements as the bottom of the canopy measurements. The campaign for data collection took place in May 2017, which was the beginning of the dry season in Indonesia.

The instrument used to measure the photosynthetic parameters was LI-6800 Portable Photosynthesis System (Li-COR Inc., Lincoln, NE, USA). This instrument produces the data for analysis of assimilation rate (A) and internal CO_2 concentration (Ci). The measurement for A-Ci done in the morning from 7 am to 12 pm. Each measurement took around 20-25 minutes. The measurement of diurnal photosynthetic patterns was done every hour from 7 am to 6 pm. There was occasional rain throughout our campaign period. Most of the rain was falling before 6 am and after 5 pm during that month.

During the leaf gas exchange measurement, we measured the CO_2 response and light response. The default LI-6800 environment setting was configured with the following guidance from LI-COR Inc and Stinziano (2017) with some adjustments: (1). Flow setpoint at 500 µmol s^{-1}, and Press. Valve: 0.1 kPa, (2) RH-air at 70-75%, (3) CO_2 injector setpoint 400 µmol s^{-1}, (4) Fan speed at 10,000 rpm, (5) Leaf temperature set at 27-30 ^{o}C, (6) Head light intensity at 1,500 µmol m^{-2} s^{-1}. Environment values such as relative humidity (RH) and leaf temperature were configured to the surrounding condition. Flow, valve pressure, and fan speed setpoint value configured to make sure the chamber condition is adequate to examine the photosynthetic activity through the reference and sample sensor. The light intensity from the head is configured at that point to make sure it is a saturated light condition for maximum photosynthetic activity.

In the CO_2 response curve measurement, the CO_2 setpoint was set to be automatically decreasing from 400 to 0 µmol s^{-1} then shortly back to 400 and shortly goes up to 1200 µmol s^{-1} with interval difference of 200 µmol s^{-1}. Light intensity curve measured with the same default setting, but with the decreasing amount of head light intensity. It started from 1500 µmol m^{-2} s^{-1} decreased to 0 µmol m^{-2} s^{-1} with interval changes of the difference of 200 µmol m^{-2} s^{-1}. All the measurement was done by using LI-6800 auto-program with minimum stabilizing waiting time of 60 to 180 seconds.

Following the gas exchange measurements, the leaves were taken as a sample in the dry paper envelope. The specific leaf area (SLA) was measured through the cutting disk with the size of 11.34 cm^2, then using a ratio of cut-area dry weight to total dry weight from the laboratory. The sampled leaves were brought to the laboratory in Jambi to be dried 24 hours for 105 ^oC. Then the leaves were brought to the University of Goettingen in Germany, and nutrient contents were examined using a Thermo Flash 11 12 Elemental Analyzer.

2.3 Data Analysis

Data collected from both CO_2 and light response then will be processed by using R-Studio. A-Ci curves were used to estimate the parameters, V_{cmax}, J_{max}, and R_d. V_{cmax} and R_d were derived from a part of A-C_i curves (in area that C_i was under 150 μmol mol^{-1}), because it is known that in this part A (leaf net photosynthesis) is limited by the maximum rate of carboxylation (Farquhar *et al.* 1980; Lambers *et al.* 2008). Fitted into this equation:

$$Ac = \frac{\left(1-\frac{0.5O}{\tau Ci}\right)*Vcmax*Ci}{Ci+Kc\left(1+\frac{O}{Ko}\right)} - Rd \qquad (1)$$

In this equation, O is the value of oxygen, Ci is the value of CO_2 in the intercellular, and τ as Rubisco specific factor ($V_{cmax}K_o/V_{cmax}K_c$). K_o and K_c are the Michaelis-Menten constants for O_2 and CO_2, and R_d is the dark respiration (Farquhar *et al.* 1980; Xu & Baldocchi 2003). In the area where higher C_i is expected, A is limited by the regeneration of RUBP (Ribulose 1,5-bisphosphate) through electron transport. Thus, J_{max} can be calculated when C_i in A-C_i curves higher than 250 μmol mol^{-1}. Fitted into this equation:

$$Aj = \frac{\left(1-\frac{0.5O}{\tau Ci}\right)*J*Ci}{4\left(Ci+\frac{O}{\tau}\right)} - Rd \qquad (2)$$

In this equation, J is the value of electron transport rate. J_{max} and photon flux composed J with this equation:

$$J = \frac{\propto I}{\sqrt{1+\left(\frac{\propto I}{Jmax}\right)^2}} \qquad (3)$$

In this equation, I is the absorbed (not intercepted) photon flux density. α is the value of light conversion efficiency (Xu & Baldocchi 2003).

The photosynthetic data were fitted to the model using a package developed by Duursma (2015) in R called plantecophys. The leaf temperature was changed to 25 ^{o}C to accommodate the global comparison data. Table 1 showed the list of model parameters and the units. Figure 1 shows the example of plots fitted using plantecophys package.

Light use efficiency (LUE) and water use efficiency (WUE) were calculated to understand when the plants have this optimized. Light use efficiency calculated from the ratio of leaf net photosynthesis to observed photosynthesis photon flux density (PPFD). Water use efficiency calculated through the ratio of net photosynthesis to leaf transpiration.

Stomatal conductance will be compared to the function of A/(Ca √VPD), a function developed by Medlyn *et al.* (2011). A is the leaf net photosynthesis, Ca is CO_2 in the ambiance, and VPD is vapor pressure deficit. The comparison aims to see how close the relationship between this function and stomatal conductance, so we know how this function can predict the stomatal conductance rate. Moreover, the slope value will be compared to global data published in the previous study.

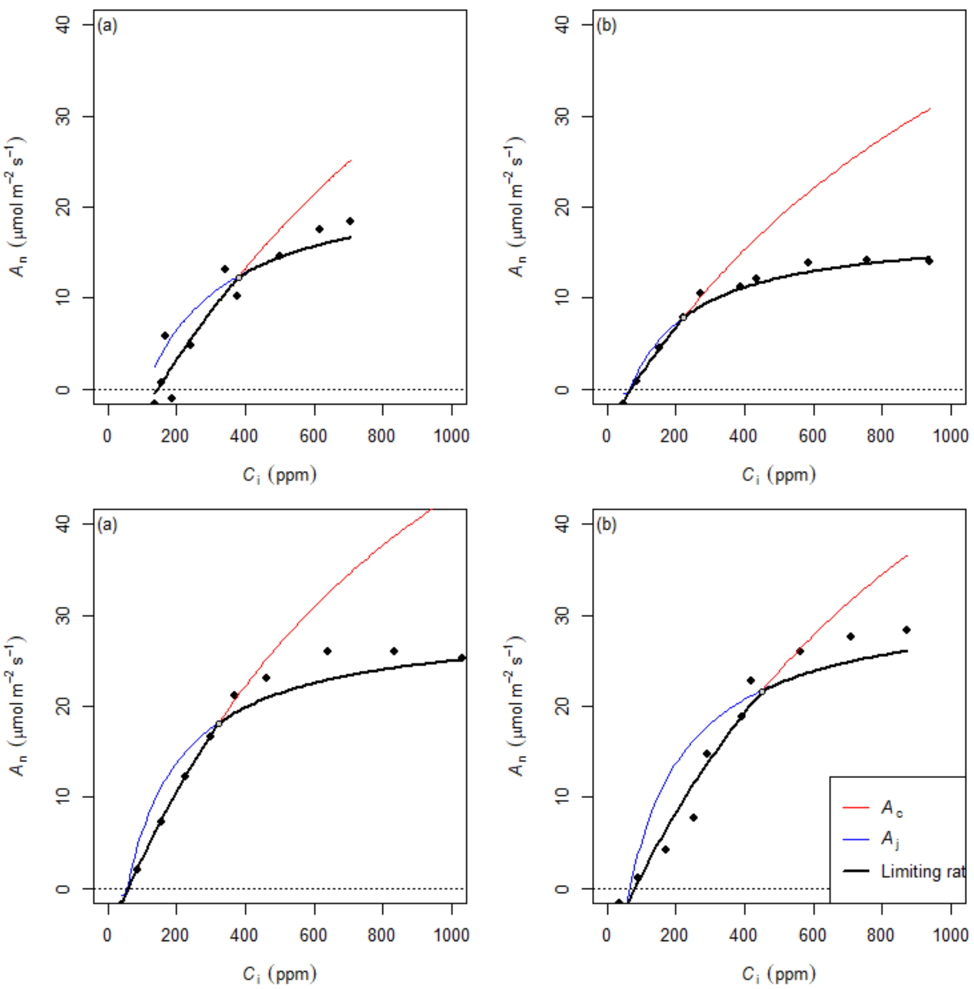

Figure 1 Fitted A-Ci curve with R using Plantecophys package for oil palm plantation and rubber plantation, each plantation divided into sunlit and shaded leaf. ACi curve for a) oil palm sunlit leaf, b) oil palm-shaded leaf, c) rubber sunlit leaf, and d) rubber shaded leaf

Table 1 List of model parameters and their units. Temperature-dependent values are from Bernacchi et al. (2001), and the rest of the parameters are from Harley et al. (1992).

Parameter	Description	Value	Unit
K_c	Michaelis-Menten constant for CO2 (25 °C)	275.0	μmol mol^{-1}
K_o	Michaelis-Menten constant for O2 (25 °C)	420.0	mmol mol^{-1}
τ	Specificity factor for Rubisco	2321	-
ΔHa(Kc)	Activation energy for temperature dependency	79.43	kJ mol^{-1}
ΔHa(Ko)		36.38	kJ mol^{-1}
ΔHa(τ)		-29.0	kJ mol^{-1}
ΔHa(Rd)		46.39	kJ mol^{-1}
ΔHa(Vcmax)		65.33	kJ mol^{-1}
ΔHa(Jmax)		79.5	kJ mol^{-1}
ΔHd(Vcmax)	Deactivation energy for temperature dependency	202.9	kJ mol^{-1}
ΔHd(Jmax)		201.0	kJ mol^{-1}
ΔS(Vcmax)	Entropy term for temperature dependency	0.65	kJ K^{-1} mol^{-1}
ΔS(Jmax)		0.65	kJ K^{-1} mol^{-1}

3. Results

3.1 PTPN VI Diurnal Variation of Photosynthetic and Light Response

3.1.1 PTPN VI Photosynthetic Parameters Pattern

The mean leaf net photosynthesis started to increase the value after 9 am in the morning with the value of 2.58 µmol m^{-2} s^{-1} and reached the peak at 12 noon with the value of 8.49 µmol m^{-2} s^{-1} (Figure 2). Continued to a slight decrease until 3 pm and declining sharply afterward. The average value of the leaf net photosynthesis is 5.65 µmol m^{-2} s^{-1} during the daytime.

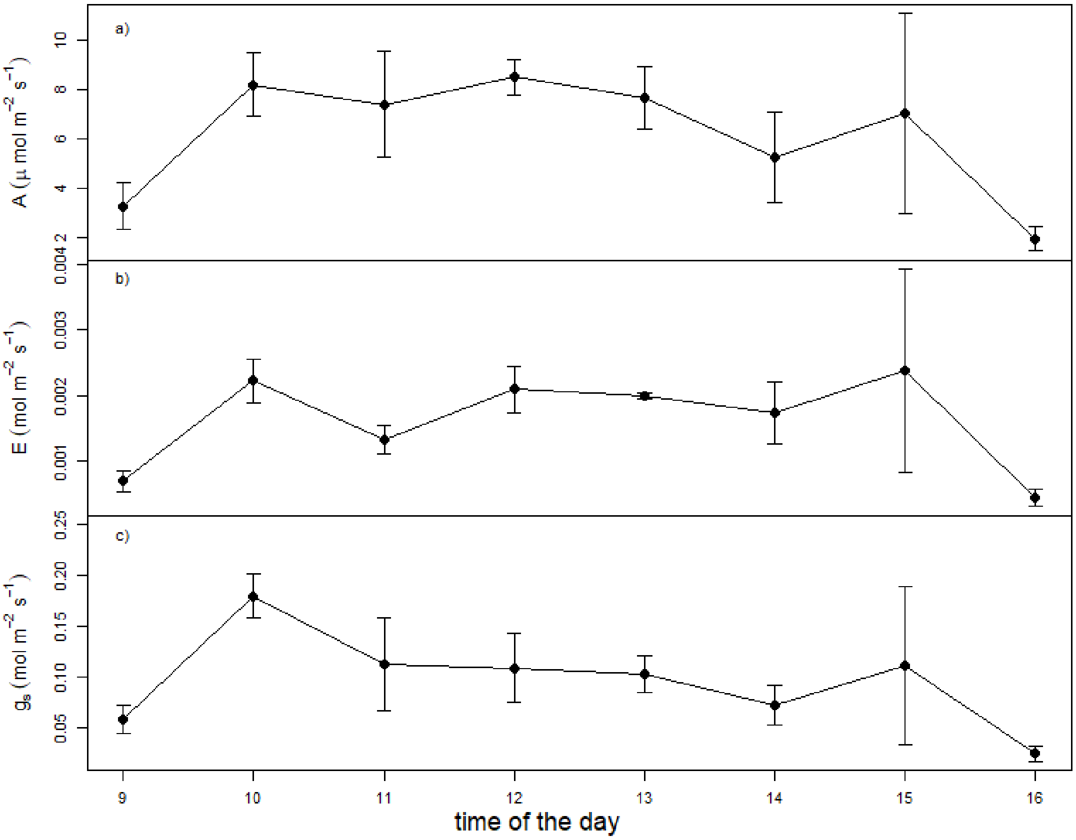

Figure 2 Diurnal course of leaf net photosynthesis (a), leaf transpiration (b), and stomatal conductance (c) for oil palm at PTPN VI measured at the top of the canopy. The points indicate means and bars indicate standard error across the replicates (n=3) at each hour

There is a similarity between A and E in this measurement. They showed the strong correlation during the course of the day (r^2=0.81; Figure 3). The similar trend also recorded in the mean leaf transpiration and stomatal conductance graph. It started to increase at 9 am with the value of 0.0005 mol m^{-2} s $^{-1}$. The inclination relatively slow and later reached the maximum mean leaf transpiration at 3 pm with the value of 0.00238 mol m^{-2} s $^{-1}$. The average value for leaf transpiration is 0.0015 mol m^{-2} s $^{-1}$ during the daytime.

The peak in mean stomatal conductance is reached earlier at 10 am with the value of 0.16 mol m^{-2} s $^{-1}$ after started to increase the value at 9 am with 0.05 mol m^{-2} s $^{-1}$. After reaching the peak, the value declining slowly throughout the day. The average value for stomatal conductance is 0.09 mol m^{-2} s $^{-1}$ during the daytime. All the data showed in the graph is a mean value from replicates taken at that particular time of the day. The daytime average of mean value from the replicates were shown in Table 2.

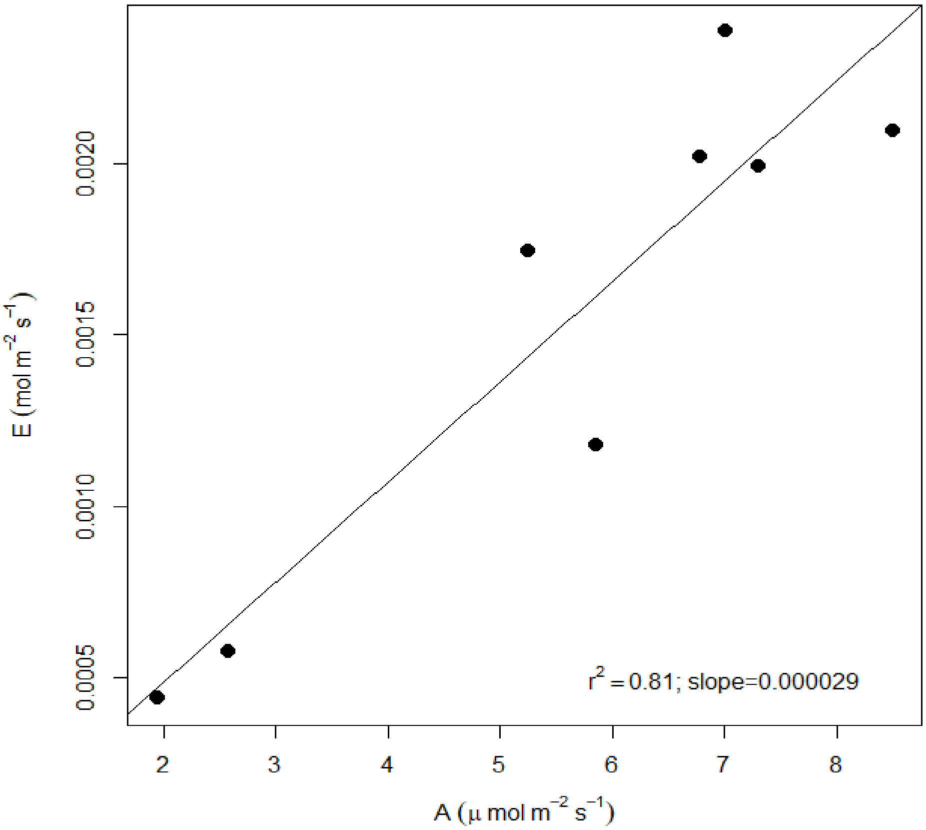

Figure 3 Relationship of A and E

Table 2 Daytime average value of the leaf-level photosynthetic parameters (Leaf Net Photosynthesis, Evapotranspiration, Stomatal Conductance, Light Use Efficiency and Water Use Efficiency)

Photosynthetic Parameter	**Daytime Average Value**	**Unit**
Leaf Net Photosynthesis (A)	5.65	µmol m^{-2} s^{-1}
Evaporation (E)	0.0015	mol m^{-2} s^{-1}
Stomatal Conductance (g_s)	0.087	mol m^{-2} s^{-1}
Light Use Efficiency (LUE)	7.85	mmol CO_2 / mol photon
Water Use Efficiency (WUE)	67.9	µmol CO_2 / mol H_20

The daily average value of light use and water use efficiency are given in Table 2. The mean light use efficiency started to increase from 9 am with the value of 5.13 m mol CO_2 for each mol photon and reached the peak at 10 am with the value of 17.68 m mol CO_2 / mol photons (Figure 4). Followed by a decrease towards the evening. The average light use efficiency during the daytime is 7.85 m mol CO_2 / mol photons.

Water use efficiency is showing a different trend with the slow increment in the morning. It started at 9 am with the value of 50.64 µmol CO_2 for each mol H_2O and reached the peak at 12 noon with the value of 80.8 µmol CO_2 / mol H_2O. The efficiency relatively stable before dropping sharply later in the evening. The average water use efficiency during the daytime is 67.99 µmol CO_2 / mol H_2O.

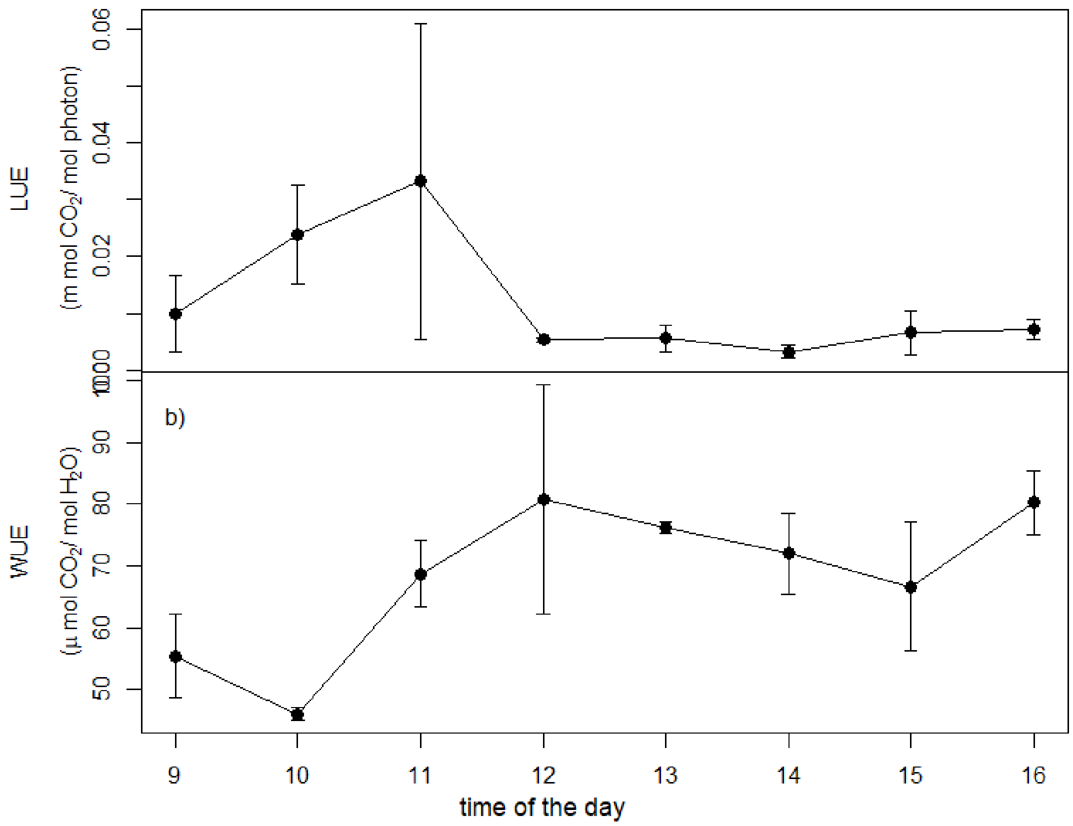

Figure 4 Diurnal change in leaf-level light use efficiency (a; LUE) and intrinsic water use efficiency (b; WUE) during the measurement day. LUE is calculated as the ratio of net photosynthesis to observed PPFD while WUE is calculated as the ratio of net photosynthesis to the leaf transpiration. The points indicate means and bars indicate standard error across the replicates (n=3) at each hour.

Stomatal conductance was linearly correlated to A/(Ca √VPD) with a positive slope of 8.5 and r^2=0.8 (p =, Figure 5).

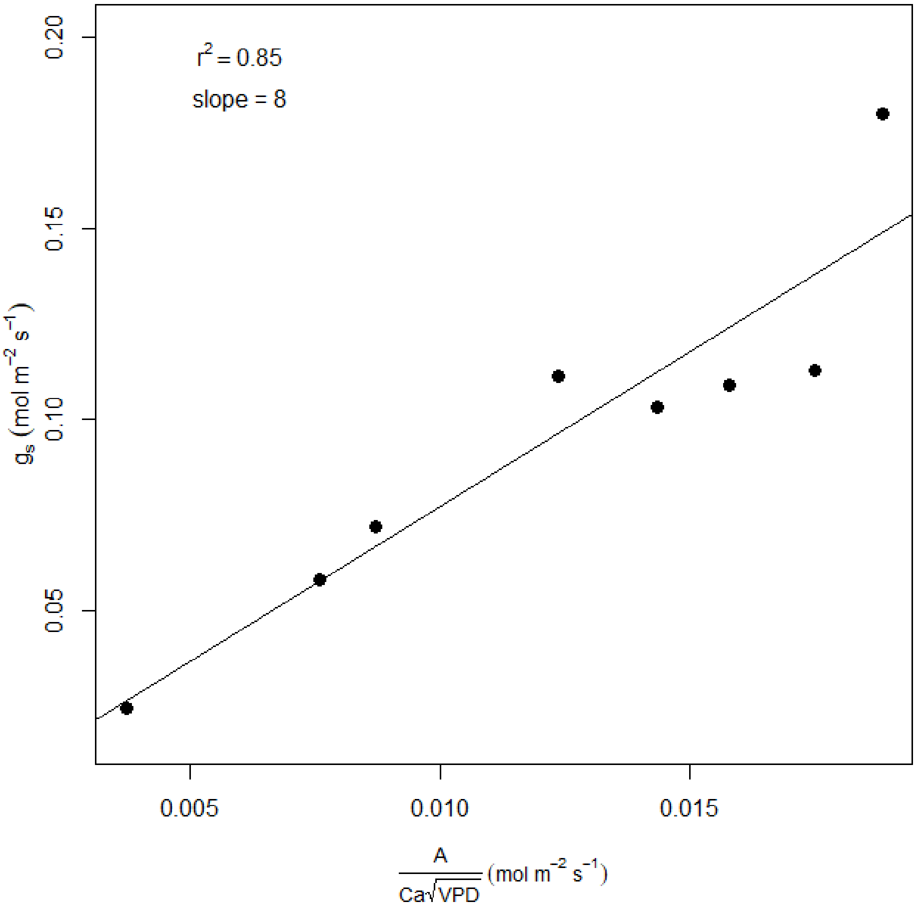

Figure 5 Relationship between stomatal conductance (g_s) and A/(Ca √VPD). The solid line is a linear fitted line across the measured data with the slope (8) and the r-square (0.85) statistics.

3.1.2 PTPN VI Diurnal Changes in Environmental Conditions

Mean air temperature is increasing slowly since the beginning of the morning and reached the peak at 2 pm with 36.5 °C (Figure 6). The daytime average for air temperature during the day was recorded at 33.5 °C. Light intensity in term of mean iPPFD showed a strong increase after 10 am and reached the peak at 1 pm with the value of 2044.9 µmol m^{-2} s^{-1}. The daytime average for mean iPPFD during the day is 1126.87 µmol m^{-2} s^{-1}. The vapor pressure deficit shows a very similar trend with air temperature. Started in the morning 9 am with the value of 1.16 kPa and reached the peak at 2 pm with the value of 2.32 kPa. The daytime average for vapor pressure deficit is 1.76 kPa.

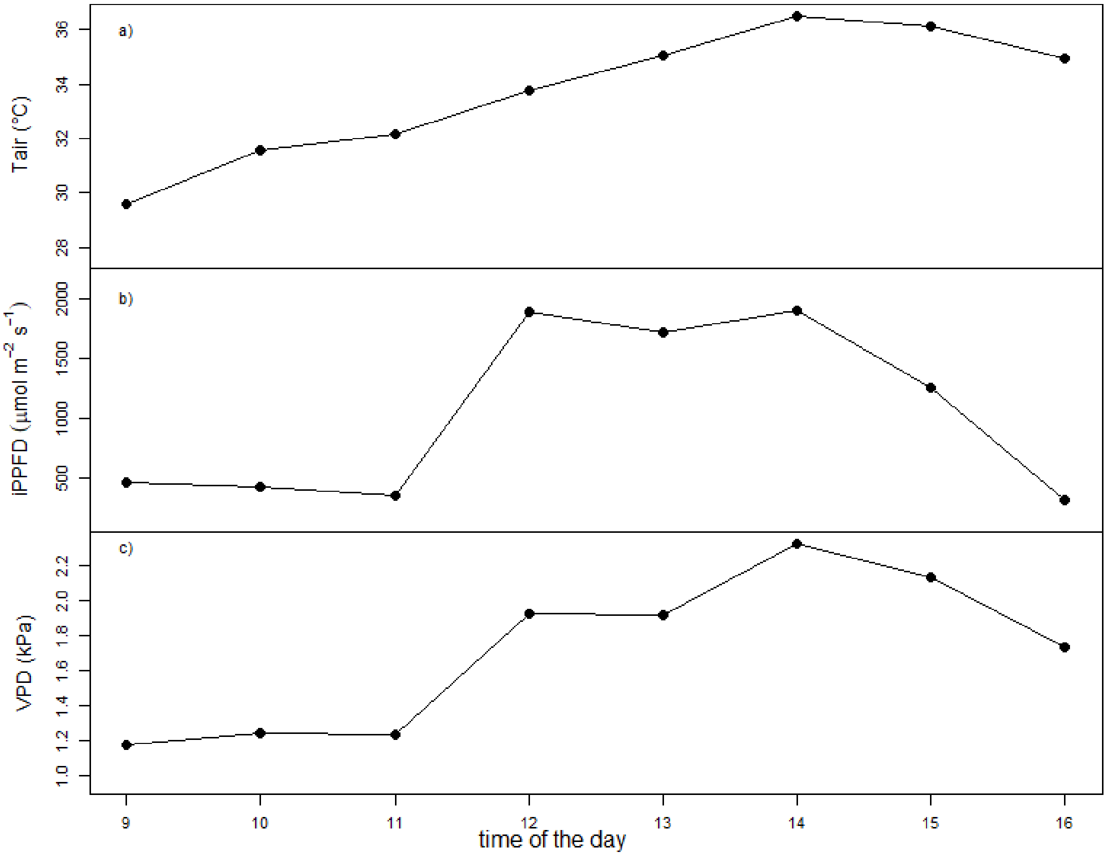

Figure 6 Environmental conditions at PTPN VI during the course of the day that included temperature (a; Tair), incident photosynthetic photon flux density (b; iPPFD) and leaf vapor pressure deficit (c; VPD). Each point is the average value (n=3).

Table 3 Daytime mean environmental condition (Air Temperature; Tair, incident photosynthetic photon flux density; iPPFD, Vapor Pressure Deficit; VPD and Relative humidity; RH) at PTPN VI during the measurement day.

Environmental Variable	**Daytime Average Value**	**Unit**
Air Temperature (Tair)	33.51	^{o}C
incident Photosynthetic Photon Flux Density (iPPFD)	1126.87	µmol m^{-2} s^{-1}
Vapor-Pressure-Deficit (VPD)	1.76	kPa
Relative Humidity (RH)	73.11	%

3.1.3 Relationship of Photosynthetic Parameters and Environment Condition

Leaf net photosynthesis shows the strongest dependence on intercepted photosynthesis photon flux density with r-squared value of 30% (Figure 7). Compared to the relation of A with air temperature and A with vapor pressure deficit which only has r-squared value of 5.6% and 8.6% respectively. The movement of the value also can be seen during the course of the day. The red arrow shows the trend during the morning, and the blue arrow shows the trend in the afternoon.

Leaf net photosynthesis tends to be higher when there is a higher supply of light, especially after mid-morning (Figure 7). The highest A with the value of 8.5 µmol m^{-2}s $^{-1}$ is reached when the iPPFD value is 1889.99 µmol m^{-2}s $^{-1}$, and it happened at 12 noon. The air temperature during the highest A is 33 ^{o}C, while the VPD is 1.9 kPa. The lowest A with the value of 1.95 µmol m^{-2}s $^{-1}$ occurs when the iPPFD value is 320 µmol m^{-2}s $^{-1}$ happened in the late afternoon. The air temperature during the lowest A is 34 ^{o}C, and the VPD is 1.73 kPa. The air temperature is still high after the whole day radiation from the sun.

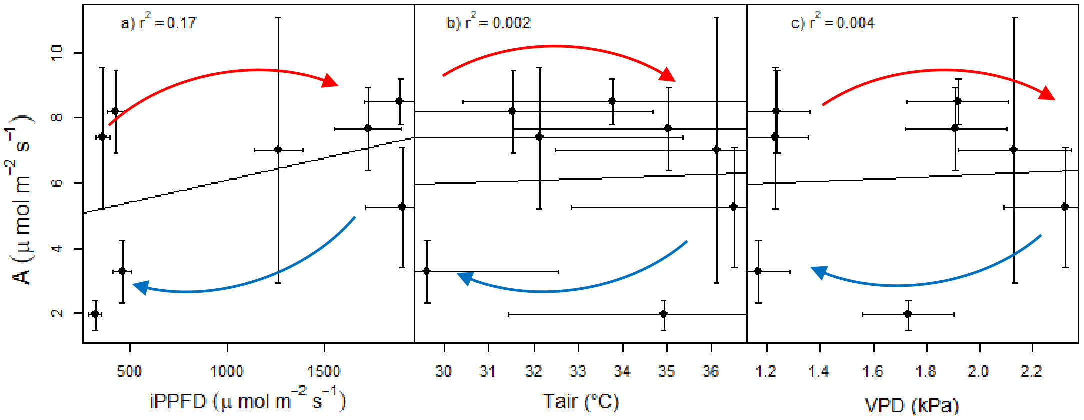

Figure 7 Linear regression among leaf net photosynthesis on incident photosynthetic photon flux density (a), air temperature (b), and vapor pressure deficit (c) on the sunlit leaves at the PTPN VI. The points indicate means and bars indicate standard error across the replicates at each hour. The arrow shows the cycle during the course of the day; red arrow shows the trend during the morning while the blue during the afternoon with the corresponding r-square values.

Leaf transpiration shows the strongest dependence on intercepted photosynthesis photon flux density with r-squared value of 43 % (Figure 8). However, the relation of E with air temperature and E with vapor pressure deficit are also not so different with r-squared value of 19 % and 26 % respectively. The movement of the value also can be seen during the course of the day. The red arrow shows the trend during the morning, and the blue arrow shows the trend in the afternoon.

Leaf transpiration tends to be higher when there is a higher supply of light, especially during mid-morning. The highest E with the value of 0.00238 mol m^{-2} s $^{-1}$ is reached when the iPPFD value is 1259.99 µmol m^{-2}s $^{-1}$, and it happened at 3 pm. The air temperature during the highest A is 36 ºC, while the VPD is 2.13 kPa. The lowest E with the value of 0.00044 mol m^{-2}s $^{-1}$ occurs when the iPPFD value is 320 µmol m^{-2}s $^{-1}$ happened in the late afternoon at 4 pm. The air temperature during the lowest A is 34 ºC, and the VPD is 1.73 kPa. Stomatal conductance shows weak dependence across three different environmental conditions (Figure 8). Strongest dependence on intercepted photosynthesis photon flux density with r-squared value of 2.8 %. The relation of E with air temperature and E with vapor pressure deficit are also not so different with r-squared value of 0.7 % and 0.6 % respectively. The movement of the value also can be seen during the course of the day. The red arrow shows the trend during the morning, and the blue arrow shows the trend in the afternoon.

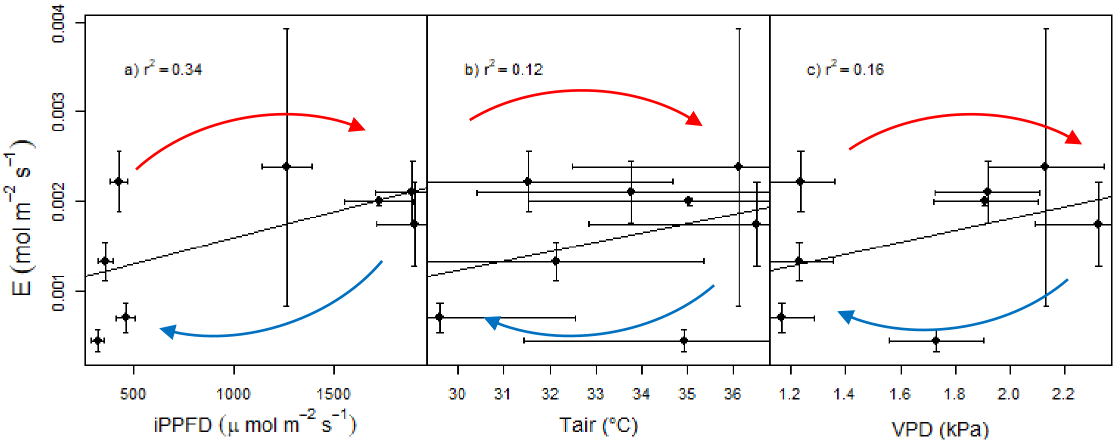

Figure 8 Relationship of leaf transpiration on the different environmental variable: incident photosynthetic photon flux density (a), air temperature (b), and vapor pressure deficit (c) on the uppermost-canopy leaves at the PTPN VI. The points indicate means and bars indicate standard error across the replicates at each hour. The arrow shows the cycle during the course of the day. The red arrow shows the trend during the morning and blue arrow during the afternoon with r-square values shown in each plot.

The highest g_s with the value of 0.16 mol m^{-2}s^{-1} is reached when the iPPFD value is 489.99 µmol m^{-2}s^{-1}, and it happened at 10 am (Figure 9). The air temperature during the highest A is 30 °C, while the VPD is 1.21 kPa. The lowest g_s with the value of 0.024 mol m^{-2}s^{-1} occurs when the iPPFD value is 320 µmol m^{-2} s^{-1} happened in the late afternoon at 4 pm. The air temperature during the lowest A is 34 °C, and the VPD is 1.73 kPa.

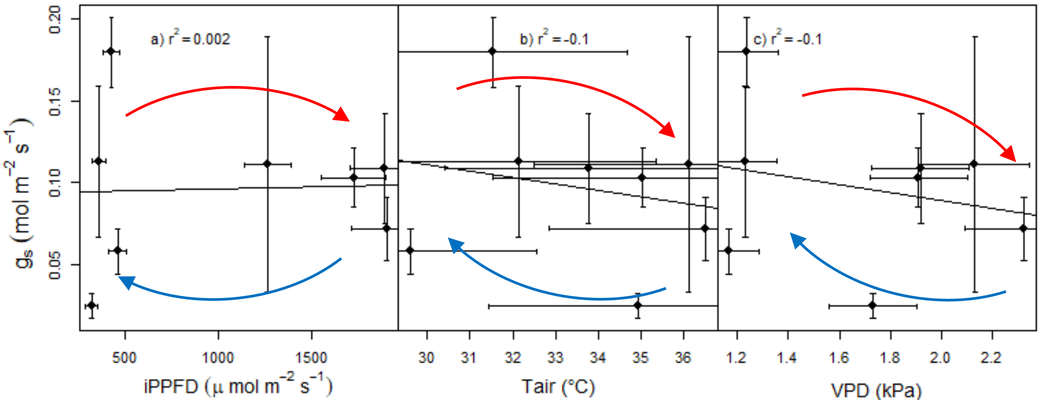

Figure 9 Dependence of stomatal conductance on a) incident photosynthetic photon flux density, b) air temperature, and c) vapor pressure deficit on the uppermost-canopy leaves at the PTPN VI. The points indicate means and bars indicate standard error across the replicates at each hour. The arrow shows the cycle during the course of the day. The red arrow shows the trend during the morning and blue arrow during the afternoon. The value of r-square shows the strength of the dependencies

The dependence of light and water use efficiency to environmental conditions also put together to be compared. Figure 10 shows the relation of water and light use efficiency each to iPPFD, Tair, and VPD. The highest light use efficiency with the value of 17.68 m mol CO2 / mol photons reached when the value of iPPFD is 489.99 µmol m-2 s -1, happened at 10 am. The air temperature during that time is 30.5 oC, and the VPD is 1.21 kPa. The lowest light use efficiency with the value of 3.27 m mol CO2 / mol photons reached when the value of iPPFD is 1899.99 µmol m-2 s -1, happened at 2 pm. The air temperature during that time is 36.5 oC, and the VPD is 2.32 kPa.

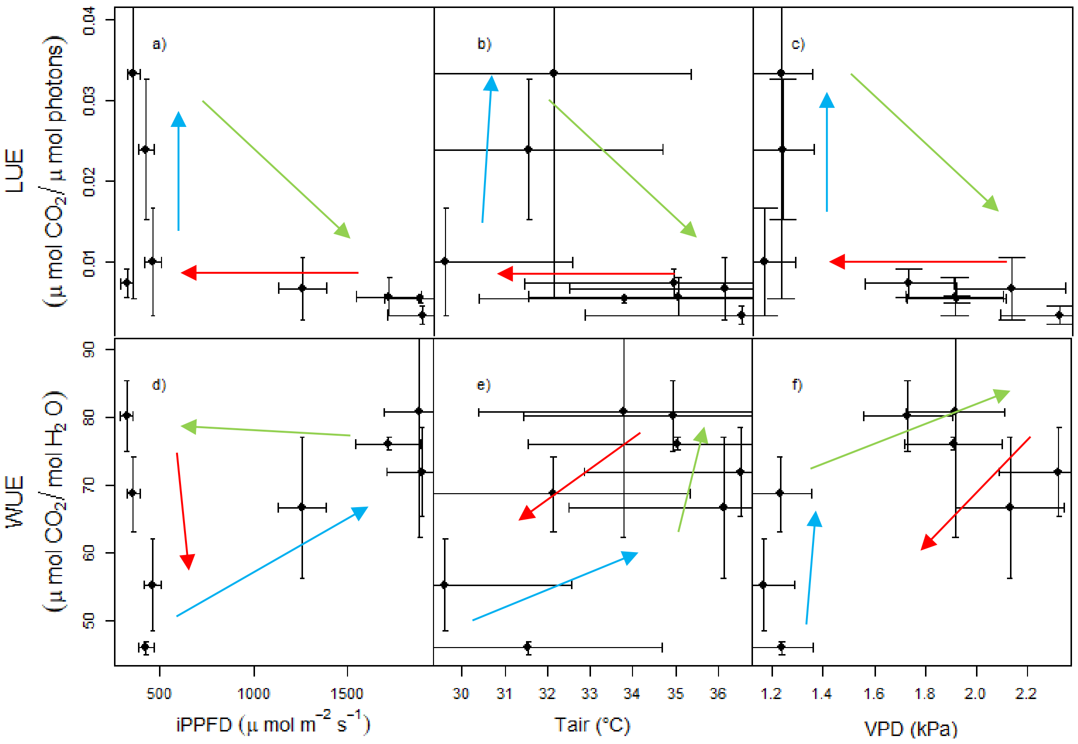

Figure 10 The response of leaf-level light use efficiency (a, b, c) and intrinsic water use efficiency (d, e, f) to incident photosynthesis photon flux density (a, d), air temperature (b, e) and vapor-pressure deficit (c, f). The arrow shows the cycle during the day. Blue arrow shows the morning (9 -11 am) trend, green arrow shows the midday (11 am - 1 pm) trend, red arrow shows the afternoon (2 – 4 pm) trend.

The highest water use efficiency with the value of 80.8 µmol CO_2 / mol H_2O reached when the value of iPPFD is 1889.99 µmol m^{-2} s^{-1}, happened at 12 noon. The air temperature during that time is 33.7 °C, and the VPD is 1.91 kPa. The lowest light use efficiency with the value of 45.4 µmol CO_2 / mol H_2O reached when the value of iPPFD is 489.99 µmol m^{-2} s^{-1}, happened at 10 am. The air temperature during that time is 30.5 °C, and the VPD is 1.21 kPa.

3.1.4 PTPN VI Oil Palm Light Response

There are two light response curves for the sunlit leaf, and one light response curve for the shaded leaf (Figure 11). Light response curves from sunlit leaves show a very similar pattern and value. The first curve of sunlit leaf started at iPPFD=0 and the A value is below zero. It went to the compensation point with the value of 50.76 µmol m^{-2} s^{-1} when leaf net photosynthesis is 0. The first area where the photosynthesis limited by light, stop at around 500 µmol m^{-2} s^{-1}. Afterwards, it became relatively flat with a maximum value of A is 11.63 µmol m^{-2} s^{-1}.

The second curve of sunlit leaf started at iPPFD=0 and the A value is below zero. It went to the compensation point with the value of 52.79 µmol m^{-2} s^{-1} when leaf net photosynthesis is 0. The first area where the photosynthesis limited by light, stop at around 500 µmol m^{-2} s^{-1}. Afterwards, it became relatively flat with a maximum value of A is 12.46 µmol m^{-2} s^{-1}.

Table 4 Leaf-level parameters (A_{max}; light-saturated photosynthetic rate; Slope; quantum yield, theta; angle of curvature, Rd; dark respiration and light compensation point) obtained from fitting the light response curve to absorbed PPFD at PTPN VI

Light status	**A_{max}**	**Slope (Φ)**	**Theta (θ)**	**Rd**	**Light Compensation Point**
	µmol m^{-2} s^{-1}			µmol m^{-2} s^{-1}	µmol m^{-2} s^{-1}
Sunlit 1	11.635	0.035	0.923	1.756	50.764
Sunlit 2	12.466	0.039	0.989	2.058	52.791
Shaded	4.393	0.079	0.079	0.594	6.833

The light response curve of shaded leaf started at iPPFD=0 and the A value is below zero. It went to the compensation point with the value of 162.071 µmol m^{-2} s^{-1} when leaf net photosynthesis is 0, very high compared to the first two curves. The first area where the photosynthesis limited by light, stop at around 200 µmol m^{-2} s^{-1}. Afterwards, it became relatively flat with a maximum value of A is 4.39 µmol m^{-2} s^{-1}, very low compared to the sunlit curves. The complete values derived from the curves showed in Table 4.

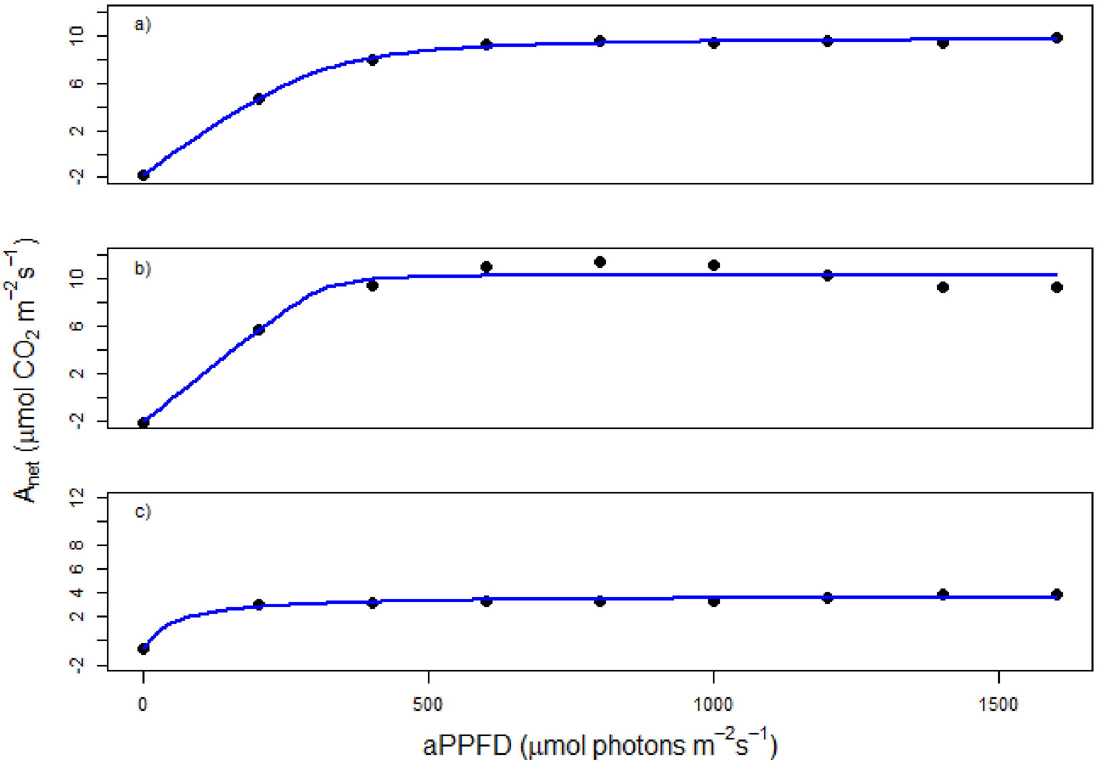

Figure 11 Fitting the light response curve of oil palm at PTPN VI to the absorbed PPFD for first sunlit leaf (a), second sunlit leaf (b) and a shaded leaf (c).

3.2 Photosynthetic Parameters of CO2 Response

3.2.1 V_{cmax} and J_{max} Comparison Across Land-Use Type

Sunlit leaves of Jungle rubber showed the highest V_{cmax} and J_{max} across all land-use types (Figure 12; a, b). On the other hand, sunlit and shaded leaves of Ulin had the least V_{cmax} and J_{max} among other species (Figure 12; a, b). Mostly, sunlit leaves had a higher V_{cmax} and J_{max} than shaded leaves (Figure 12; a, b). Both V_{cmax} and J_{max} differed significantly among the land-use types (Figure 12; a, b). The range of V_{cmax} varied between 5 – 70 µ mol m^{-2} s^{-1} while J_{max} lied 10 – 160 µ mol m^{-2} s^{-1} between across sunlit and shaded leaves. Species means of V_{cmax} varied more than sevenfold (Figure 12 a, from 10 to 70 µ mol m^{-2} s^{-1}).

Jungle rubber had a higher V_{cmax} and J_{max} than monoculture rubber plantation (Figure 12; a, b). Sunlit and shaded leaves of ulin and monoculture rubber had the least difference (Figure 12; a). High fertilized oil palm had a higher V_{cmax} and J_{max} than low fertilized (Figure 12; a, Table 1). The rates of dark respiration from sunlit and shaded leaves differed significantly across low and high fertilized oil palms (Table 5), ranging from 1.5 to 4.4 µ mol m^{-2} s^{-1}. Low fertilized oil palm showed a larger variation in V_{cmax} and J_{max} than high fertilized oil palm (Table 5). Between the forest species, Pulai - a fast growing species had a higher V_{cmax} and J_{max} than Ulin – a slow growing species (Figure 12; a, Table 6).

Values of leaf nitrogen content of sunlit and shaded leaves differed significantly among species, ranging from 0.6 to 2 g m^{-2} (Figure 12; c). Across all land-use types, Jungle rubber had the highest leaf nitrogen content while Ulin had the least (Figure 12; c). Both for sunlit and shaded leaves, the spatial trend across species in V_{cmax} and J_{max} matches with the trend in the leaf nitrogen content (Figure 12; a, b, c).

Old plants had a higher V_{cmax} than young ones (Figure 13). Old Jungle rubber showed the highest V_{cmax} across all land-use types (Figure 13). Among the old plants, there was a little difference in the V_{cmax} of Pulai and monoculture rubber (Figure 13).

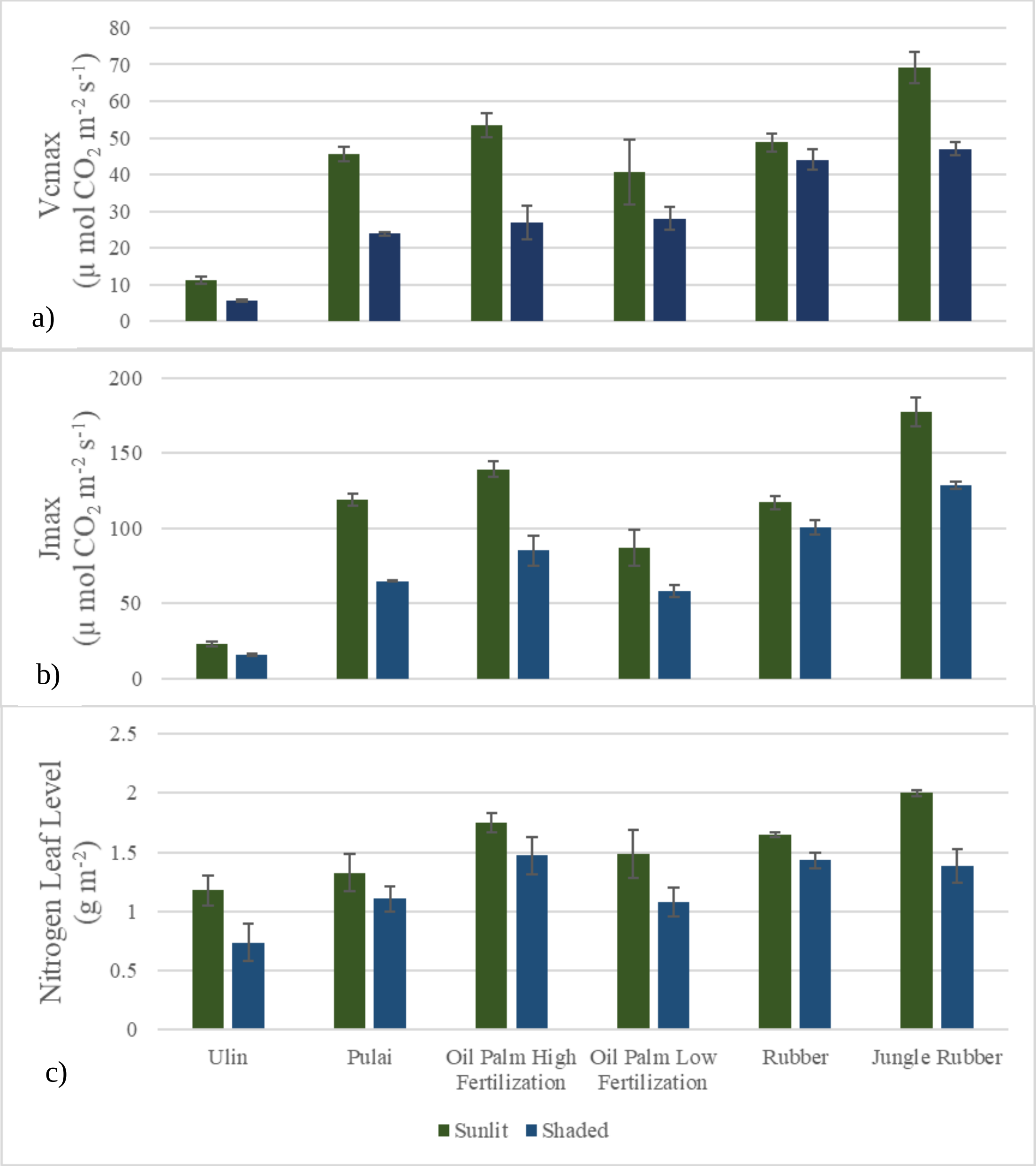

Figure 12 Trends in the mean values of maximum carboxylation velocity (V_{cmax}; top), maximum electron transport rate (J_{max}; middle) and leaf nitrogen content (bottom) of sunlit (dark green) and shaded (dark blue) leaves of four old species (Ulin, Pulai, Oil Palm, Rubber) from various land-use types. The vertical bars indicate the error bars.

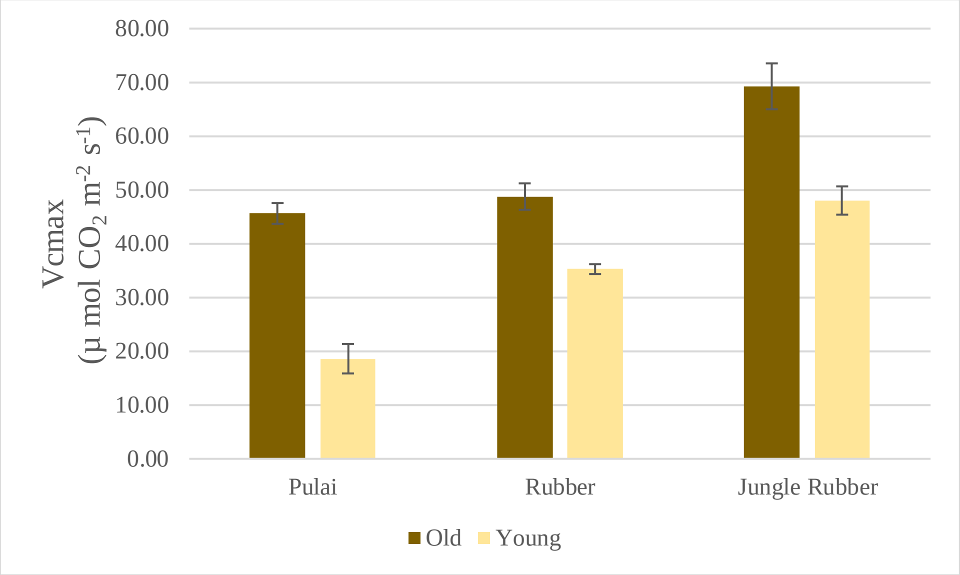

Figure 13 Comparison of the average values of maximum carboxylation rate (V_{cmax}) for sunlit leaves of young (dark brown) and old (light brown) plants of forest (Pulai, Ulin) and jungle rubber species. The vertical bars are the error bars.

Table 5 Means and the standard error (SE) for the maximum carboxylation rate (V_{cmax}), maximum electron transport rate (J_{max}), and dark respiration rate (Rd) for low and high fertilized oil palms with varying light status (sunlit, shaded).

Fertilization Rate	Light Level	V_{cmax}	SE	J_{max}	SE	R_d	SE
High	Sunlit	53.33	3.32	139.21	5.20	1.06	0.85
High	Shaded	29.59	4.89	83.87	10.61	2.69	1.59
Low	Sunlit	40.79	8.84	87.18	11.85	4.35	2.02
Low	Shaded	28.05	3.08	58.17	4.35	1.10	0.82

Table 6 Means and the standard error (SE) for the maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) for two forest species (pulai and ulin), for different light conditions (sunlit leaf, shaded leaf) and age status of the tree (young, old).

Characteristic	V_{cmax}	SE	J_{max}	SE
Pulai Old Sunlit	45.63	1.94	118.83	3.76
Pulai Old Shaded	23.83	0.38	64.86	0.56
Ulin Old Sunlit	11.21	1.10	23.11	1.48
Ulin Old Shaded	5.70	0.35	16.02	0.62

3.2.2 Relationship Between V_{cmax}, J_{max} and Leaf Nitrogen Across Land Use Types

There was a strong positive correlation between J_{max} and V_{cmax} ($r^2 = 0.87$, Figure 14) across land use types. The J_{max}/V_{cmax} ratio was 2.36 (Figure 14). Lower values of V_{cmax} and J_{max} were associated with forests (Figure 14) while rubber appears to have higher values of V_{cmax} and J_{max} (Figure 14). The V_{cmax} and J_{max} of forests were least scattered about the fitted line (Figure 14) while there was a considerable variability of V_{cmax} and J_{max} in rubber and oil palm (Figure 14).

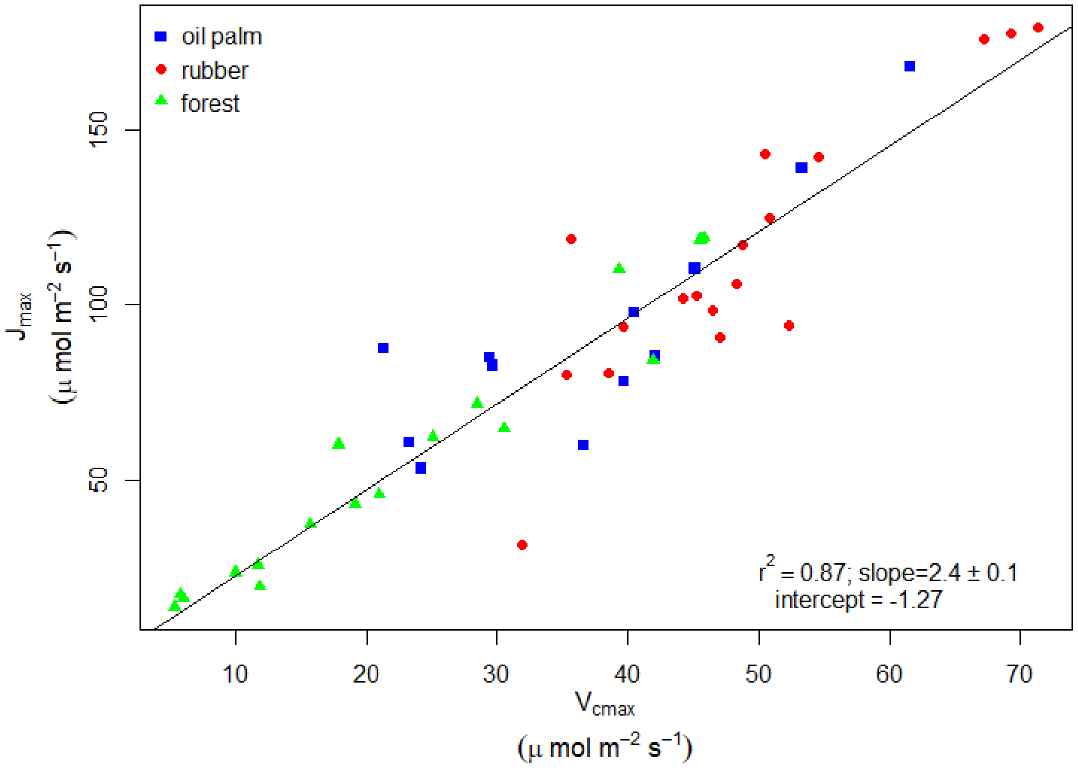

Figure 14 Relationship between the maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) for various species across different land-use types. The data are represented by blue squares, oil palm; red points, rubber trees; and green triangle forest species. Each point represents the individual leaf, and the black line is the fitted line. The goodness of the fit ($r^2 = 87\%$) and the regression parameters are shown.

We found that leaf nitrogen content was linearly and positively correlated with V_{cmax} across land use types (slope = 25.8, Figure 15). Since there was a lot of scattering in the data, we did not find a strong correlation ($r^2 = 0.38$, Figure 15). Indeed, there was considerable variability in the relationship between V_{cmax} and J_{max} of oil palm (Table 7). Forest species have the strongest correlation of V_{cmax} and J_{max} compared to oil palm and rubber.

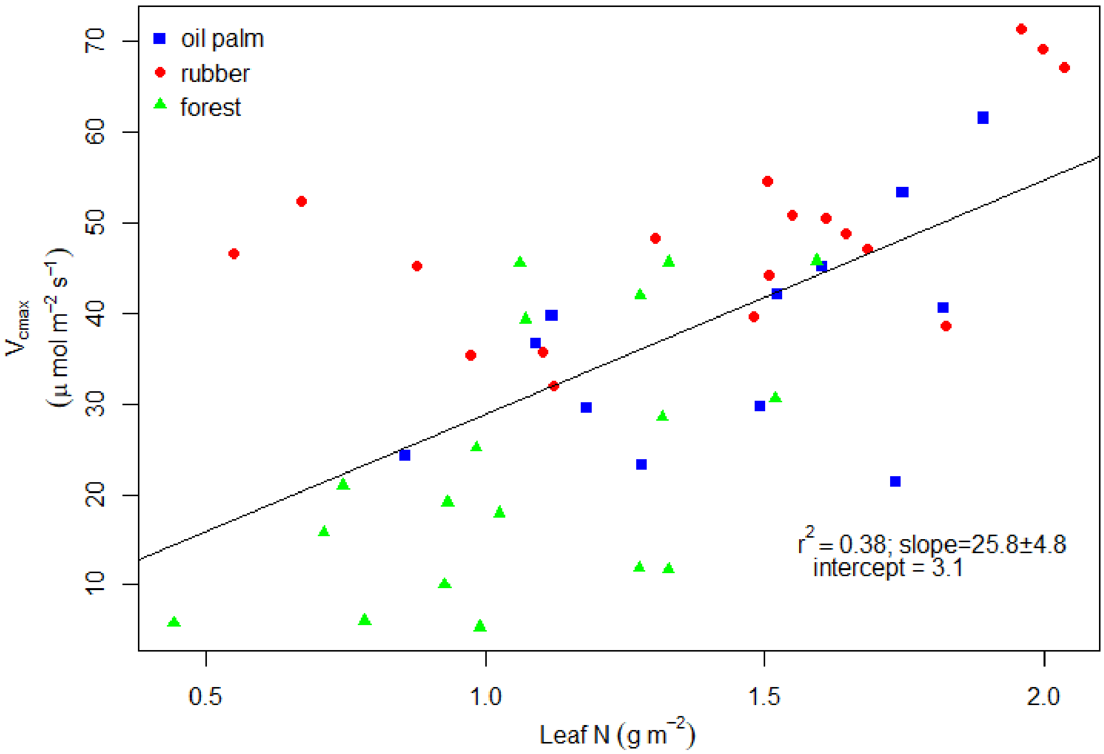

Figure 15 Relationship between the maximum carboxylation rate (V_{cmax}) and the amount of leaf nitrogen per unit area (Leaf N) for different species across land-use types. The data are represented by blue squares, oil palm; red points, rubber trees; and green triangle forest species. Each point represents the individual leaf, and the black line is the fitted line. Simple linear regressions were applied to the data.

Table 7 Linear regression (y=a+bx), level of significant (p-value), the coefficient of determination (r^2) between maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) among oil palm, rubber, and forest species (Ulin and Pulai).

Species	a	b	r^2	p-value
Oil Palm	7.4	2.2	0.71	<0.01
Rubber	-31.2	2.9	0.79	<0.01
Forest Species	-1.25	2.5	0.95	<0.01

Table 8 Correlation among oil palm, rubber, and forest species (ulin and pulai). The value of linear regression (y=a+bx), level of significant (p-value), coefficient of determination (r^2) between maximum carboxylation rate (V_{cmax}) and nitrogen per leaf area (N).

Species	a	b	r^2	p-value
Oil Palm	7.7	20.4	0.30	<0.05
Rubber	28.9	14	0.30	<0.05
Forest Species	-7.2	28.8	0.35	<0.05

3.2.3 Effects of Fertilization and Age on V_{cmax}, J_{max} and Leaf Nitrogen Relations

Among oil palms, there was a strong positive correlation between J_{max} and V_{cmax} (r^2 = 0.71 Figure 16a). The ratio of J_{max} to V_{cmax} was 2.2 (Figure 16a). Forest species have the strongest correlation (r^2 = 0.95; slope = 2.5, Table 8) compared to the plantation species. Within the oil palm data, the high fertilized plantation has higher correlation and slope (r^2 = 0.90; slope = 2.1, Table 9), compared to low fertilized plantation (r^2 = 0.63; slope = 1.6, Table 9). There was also a strong positive correlation between J_{max} and V_{cmax} in rubber plantation (r^2 = 0.79; slope = 2.9, Table 8), so we distinguished the age class of the tree. Furthermore, we found out that the old tree has a higher correlation (r^2 = 0.86; slope = 3.0, Table 11) than the young tree (r^2 = 0.62; slope = 2.6, Table 11).

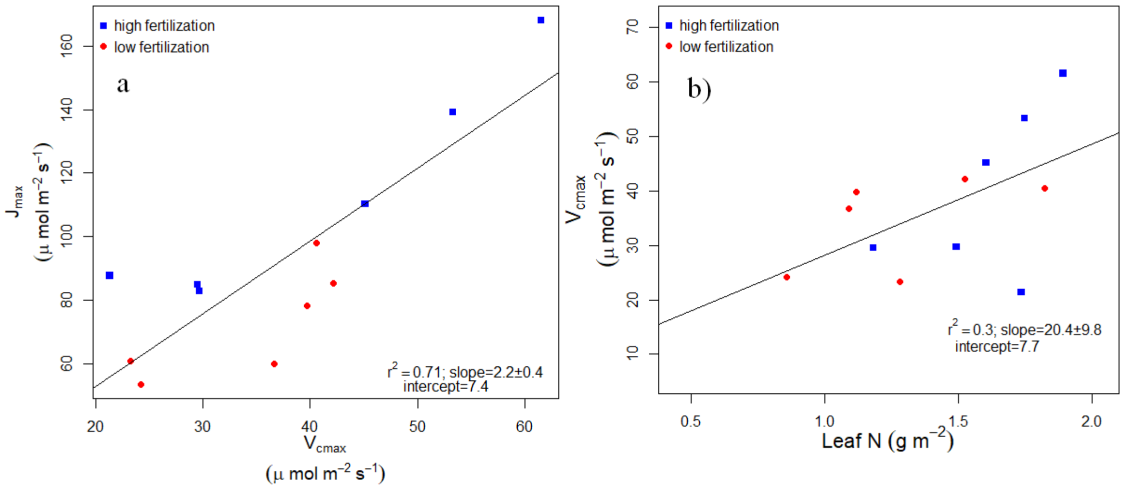

Figure 16 Relationship between the maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) for high fertilization (red points) and low fertilization (blue squares) on oil palm. Each point represents the individual leaf. Regression parameters and the fitted line (black) are shown.

V_{cmax} increased linearly with increasing leaf nitrogen content with a moderate correlation (Figure 15b, $r^2 = 0.38$). In this V_{cmax} and leaf nitrogen content relationship, forest species have the strongest correlation ($r^2 = 0.35$; slope = 28.8, Table 8) compared to oil palm and rubber. Particularly for oil palm, the high fertilized plantation has a higher value of V_{cmax} per leaf nitrogen content (30.53, Table 11) than the low fertilized plantation (27.4, Table 11).

Table 9 Value of linear regression (y=a+bx), level of significant, coefficient of determination (r^2) between maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) in PTPN VI oil palm plantation.

Relationship	Fertilization Rate	a	b	r^2	p-value
J_{max} - V_{cmax}	High	27.7	2.1	0.90	<0.01
J_{max} - V_{cmax}	Low	16.9	1.6	0.63	<0.05

Table 10 Comparison of different fertilization rate to the maximum carboxylation rate (V_{cmax}), maximum electron transport rate (J_{max}), and the nitrogen per leaf area.

Fertilization Rate	V_{cmax}	J_{max}	Leaf N	V_{cmax} / Leaf N	J_{max} / Leaf N
High	53.33	139.21	1.75	30.53	79.68
Low	40.79	87.17	1.48	27.4	58.6

Table 11 Comparison of old and young plants in rubber plantation (monoculture and polyculture). Showed in the table are a linear regression (y=a+bx), level of significant, coefficient of determination (r^2) between maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}).

Age Class	a	b	r^2	p-value
Old	-31.3	3.0	0.86	<0.01
Young	-29.6	2.6	0.62	<0.05

4. Discussions

We found that rates of Leaf net photosynthesis and evapotranspiration were similar. Mostly, light use efficiency (LUE) decreased while water use efficiency (WUE) increased over the course of the day. We also found that the parameter, g_1, was relatively high. Further, Evapotranspiration not leaf net photosynthesis had stronger correlations with the climate. Light-saturated leaf net photosynthesis was strongly limited by light at the top of the canopy.

We found that Jungle rubber had the highest V_{cmax} and J_{max} across all land-use types. The high fertilized oil palm had a higher V_{cmax} and J_{max} than low fertilized oil palm. Pulai species had a higher V_{cmax} and J_{max} than Ulin species. Mixed jungle rubber showed a higher photosynthetic parameter compared to monoculture rubber plantation. We also found that old plants had a higher V_{cmax} and J_{max} than young ones. V_{cmax} and J_{max} were strongly correlated while V_{cmax} and leaf nitrogen content moderately correlated.

4.1 Diurnal Variation of Photosynthesis and Evapotranspiration

The diurnal patterns of the leaf gas-exchange followed the pattern described in Tucci et al. (2010), where the leaf net photosynthesis was found to be low in the early morning, reached a maximum around midday and then decreased strongly in the afternoon. The decrease in the late afternoon leaf net photosynthesis could be related to a higher afternoon temperature and VPD. Similar patterns were reported for other palm studies such as coconut (Prado, Passos & de Moraes 2001; Passos, Prado & Aragao 2009), tropical deciduous and evergreen trees (Brodribb & Holbrook 2007), dipterocarp trees (Zhang *et al.* 2009) and peach (Tucci *et al.*, 2010). In the afternoon (between 12 noon to 2 pm), the decrease in stomatal conductance was related to the increase in leaf VPD (Fig. 4c), a response that was observed in Eucalyptus (Prior, Eamus & Duff 1997) to prevent excessive shoot dehydration.

The rates of Leaf net photosynthesis and evapotranspiration were similar because in our study we found a strong correlation between Leaf net photosynthesis and evapotranspiration (r^2 >80%, statistic not shown). Our finding suggests that carbon uptake and water loss from oil palms are likely to be tightly coupled. The magnitudes of A_{net} (8.49 µmol $m^{-2}s^{-1}$) and g_s (0.16 mol $m^{-2}s^{-1}$) found in our study reconciles with Zhang et al. (2009) and Raschke & Resemann (1986).

The higher light use efficiency in the morning could be due to low irradiance. Similar results have been reported widely before (Roderick, Farquhar, Berry & Noble 2001). The low values of light use efficiency around noon time were probably due to saturation of photosynthesis or photoinhibition at higher PPFDs.

WUE was lower in the morning than in the afternoon because photosynthesis (A_{net}) and stomatal conductance were low as the environmental conditions (in particular, irradiance) were low. The lower values of stomatal conductance reduced the relative differences between A_{net} and g_s and thus intrinsic WUE was low in the morning.

We posit that the diurnal trend of leaf-level WUE observed in our study could scale up to the ecosystem level. We hypothesize that at the ecosystem-level, diurnal changes in WUE would be lower in the morning than in the noon-time or afternoon, and therefore we suggest that our hypothesis merit further investigation.

The parameter g_1 was high indicating that oil-palms are likely to have low WUE. The value of g_1 found in our study is in the range as found in other studies (Lin, Medlyn & Duursma 2015). Crops have been shown to have low WUE – at least at the leaf-level (Medlyn *et al.* 2011). The low WUE pattern observed at the leaf-level holds at a larger scale (e.g., at the ecosystem-level) needs to be also examined as there could be a large source of uncertainties associated with the carbon and water fluxes at such levels (Medlyn *et al.* 2017).

In our study, the A_{net} of oil palms was strongly modulated by stomata, which in this study was not that sensitive to climatic conditions. One reason could be that atmospheric conditions such as temperature and VPD did not vary that much in our study unlike other studies (Brodribb & Holbrook 2007). The stomatal sensitivity to environmental fluctuations has been shown to modulate palm gas exchange (Oliveira *et al.* 2002). We advocate that changes in the diurnal pattern of photosynthesis in oil palms of very tropical sites like ours could occur if there is a strong seasonality, especially strong wet and dry seasons.

4.2 Relationship between Photosynthesis, Evapotranspiration, and Climate

In general, we did not find a large diurnal variation in the climate, especially for temperature. Our VPD values are similar in magnitude to a study by Röll et al. (2015). Photosynthesis was positively related to leaf temperature in the morning while negatively related to leaf temperature in the afternoon. Photosynthesis had stronger correlations with the leaf temperature in the afternoon than in the morning (r^2 ~70% versus $r^2 > 90\%$, statistic not shown).

Evapotranspiration, not leaf net photosynthesis had stronger correlations with the climate. Of the climate variables, iPPFD explained the largest amount of variation in both Evapotranspiration and leaf net photosynthesis, indicating that irradiance has strong control over carbon uptake and water loss of oil palms.

4.3 Light limitation on Photosynthesis

At the top of the canopy, light-saturated photosynthetic rates of shaded leaves were approximately 1/3 of the sun-lit leaves. Even lower in the light compensation point (1/8 of the sun-lit leaves). These findings match with the research from Ellsworth & Reich (1993) where the sunlit leaves considered to have higher light compensation point. Sunlit plants will have a higher capacity for electron transport and ATP synthesis per chlorophyll unit compared to shaded one. Eventually, these higher capacities will be able to process more sunlight into ATP and NADH during CO_2 assimilation (Munns 2016). Our results suggest that oil palms have the potential to partition light climate differentially even within the top canopy layers.

4.4 Comparison of V_{cmax} and J_{max} Values

Our values of V_{cmax} and J_{max} across the different land use types are in the range of published values for rubber and oil palm (42.00 ± 2.42 m^{-2} s^{-1}, Meijide *et al.*, 2017), and also within the range of global data for tropical forest species (30-50 m^{-2} s^{-1}, Ali *et al.*, 2015). The mean J_{max}/V_{cmax} ratio reported by (Wullschleger 1993; Walker *et al.* 2014) is also similar to ours. Meijide *et al.* (2017) computed V_{cmax} and J_{max} from the A/Ci curve by a method suggested by Remko Duursma (2015), which we also used. Note that at species-level, in our study we have a species that had a substantially lower V_{cmax} value. This species can be considered as a slow-growing species. It is equivalent to the research comparing the fast and growing species of Poa by Atkin et al. (1997), where the rate of photosynthesis is correlated positively with the relative growth rate.

A number of photosynthetic measurements on tropical species have been carried out (e.g., Domingues *et al.* (2010), Cernusak *et al.* (2013), Norby *et al.* (2016)). Our V_{cmax} values for the two tropical species ranged from 10 – 40 u mol m^{-2} s^{-1}, this value is slightly lower than what has been reported (Walker *et al.* 2014; Ali *et al.* 2015). The difference in V_{cmax} values maybe is associated with interannual variability (Tucci *et al.* 2010) or spatial variability (e.g., canopy depths; Ali *et al.* (2015)). Despite the extensive research on land use change systems, photosynthetic measurements on species under rainforest transformations are rare and we know of very little data from Southeast Asia on crops and natural forests.

Rubber polyculture (jungle rubber) showed a higher both V_{cmax} and J_{max} compared to rubber monoculture. The same result occurred in both sunlit and shaded leaf. This is a different finding compared to previous research regarding polyculture and monoculture (Klasen *et al.* 2016). Many large-scale oil palm plantation company applied an extreme homogeneity to enhance the yield per hectare, means better productivity (Azhar *et al.* 2015). This uniformity is usually produced less beneficial for the environment and ecosystem services (Klasen *et al.* 2016). However, the reason why in this research the photosynthetic productivity is showing another trend is that there was no difference in plantation management between these two plantation areas. Both are a plantation owned by a smallholding, run by local people.

4.5 Effects of N fertilization and Age of Plants on V_{cmax}

Research from Maier *et al.* (2008) investigated the increase of photosynthetic capacity caused by the application of fertilization. Maier *et al.* (2008) reported that there is an increase in V_{cmax} and J_{max} for loblolly pine (*Pinus taeda* L.) after the application of 112 kg ha^{-1} of elemental N. Our research showed the matching finding. Oil palm plantation with high fertilization has a higher both V_{cmax} and J_{max} compared to the low one. This relationship between fertilization and photosynthetic activity is because the energy from photosynthesis is essentials to reserve N in the leaf (Kull & Kruijt 1999).

Our findings showed the old plants in forest species and rubber tree have higher V_{cmax} compared to the young plants. Most of the trees reached the optimum point of the photosynthetic rate during their mature age and decreased towards the end of their lifespan (Freeland 1952). This explains the reason for higher photosynthetic parameter of old plants compared to the young one across land-use in our measurement. The relationship of V_{cmax} and J_{max} is also increasing over the age of the plant.

4.6 Relationships of V_{cmax} with J_{max} and Leaf Nitrogen Content

The strong relationship of V_{cmax} and J_{max} already reported in several studies from different characteristics such as tropical species (slope = 2.1; Walker *et al.*, 2014) and 109 C_3 plant species (slope = 1.63; Wullschleger, 1993). Our data showed a similar number with a bit of stronger relationship and slope (2.44; Fig. 3). The relationship between V_{cmax} and J_{max} allocates the resources of Calvin-Benson cycle and the electron transport (Walker *et al.* 2014), and this relationship is maintained to be close to optimizing the use of the resource for photosynthesis.

Carboxylation rate tends to go linearly with leaf nitrogen content (Evans 1989; Lambers *et al.* 2008). The slope value of leaf nitrogen content and V_{cmax} correlation derived from our data is 25.8, which is higher than the value reported by Ali *et al.* (slope = 17.8; 2015). After we segregated the correlation based on the species, then the slope from forest species will show a higher value, while oil palm and rubber show a similar value with Ali *et al.* (2015). There's a moderate correlation between leaf nitrogen and V_{cmax} in our data, especially in forest species ($r^2 = 0.35$, Table 4). So N is a limiting factor in forest species because there was no fertilization applied for this plant.

4.7 Data Usage and Limitations

The correlation of $V_{cmax} - J_{max}$ and leaf nitrogen – V_{cmax} across different species and land-use in this research can be used as parameterization in a global model (LUNA V1.0; Ali *et al.*, 2016) and dataset (Wullschleger 1993; Kattge, Knorr, Raddatz & Wirth 2009; Domingues *et al.* 2010; Walker *et al.* 2014; Norby *et al.* 2016). As well as the comparison of V_{cmax} on different age class. The impact of fertilization rate on V_{cmax} also can be used in the global dataset parameterization.

Some of the limitations of this research are the seasonality along the year. We found out that even a short rain during the day was affecting the data significantly. Thus, we doubt that during the months where high precipitation occurs the leaf gas exchange measurement can be successfully done, especially photosynthetic diurnal measurement.

Data collection for diurnal measurements in PTPN VI Oil Palm Plantation were done in the top of the canopy. However, the rest of sunlit leaves from another land-use type were taken from 3-4 meter high. The average height of the tree canopy ranged from 10 m (oil palm) to 48 m (forest species) (Kotowska, Leuschner, Triadiati, Meriem & Hertel 2015). Installing a crane in the study area would be an ideal condition for this measurement.

4.8 Future Works

There are a couple of room for improvement in this research topic. Future research can consider more species in the V_{cmax} comparison, especially forest species. Comparing shade-tolerant and shade-intolerant species in the future study is advisable. A previous study (Craine & Reich 2005) reported that there is a difference between this two types of species. However, their measurement was done for seedlings for temperate species. Measuring the diurnal photosynthetic pattern on rubber and dominant forest species also strongly recommended.

This research was done only in one month, at the beginning of dry season. Having additional data during the different time of the year is also advisable to capture seasonal variability (Tucci *et al.* 2010). Previous research (Xu & Baldocchi 2003) showed that prolonged summer drought had an impact on photosynthesis for plants in the greenhouse. How the plants in the field react to this condition is yet to be answered.

There is a strong impact of soil type on A_{net} reported on the previous study (Maire *et al.* 2015), yet very few studies have looked at the effects of soil on V_{cmax} (from A/Ci curve) (Kattge *et al.* 2009; Ali *et al.* 2015). One of the reason might be because it takes way longer to capture A/Ci curve data compared to A_{net}.

The only soil type being used is loam acrisol in this research. Taking replicates in the different soil type will be good to capture more spatial variability (Ali *et al.* 2015). In this research, there were only three replicates. Adding more replicates will capture more variance (Domingues *et al.* 2010).

Taking phosphorus (P) into account also should be considered in the future work as reported on the previous study that P content in the leaf could also modify the relationship between V_{cmax} and leaf N (Coste *et al.* 2005; Domingues *et al.* 2010). N and P concentrations successfully predict V_{cmax} and J_{max} through a model even though it was found to be that P was not significantly affecting V_{cmax} per unit N (Norby *et al.* 2016).

5. Conclusion

We found that rates of Leaf net photosynthesis and evapotranspiration were similar in oil palm, but evapotranspiration had stronger correlations with the climate, compared to leaf net photosynthesis with the climate. This implies that in oil palm, it is simpler to create a model of evapotranspiration from climate, and rather more complex with the leaf net photosynthesis. It is also concluded that with the increase of climate variables, the water use efficiency will be lower.

Most of the photosynthetic parameters reached the peak during mid-morning. Mostly, light use efficiency (LUE) decreased while water use efficiency (WUE) increased over the course of the day Light saturated leaf net photosynthesis was strongly limited by light at the top of the canopy.

Our findings showed that Jungle rubber had higher V_{cmax} and J_{max} compared to monoculture rubber plantation. This means higher productivity in the tree wise, but also means lower productivity in area wise due to the share with other forest species. The high fertilized oil palm had a higher V_{cmax} and J_{max} than low fertilized oil palm. Pulai species had a higher V_{cmax} and J_{max} than Ulin species. Mixed jungle rubber showed a higher photosynthetic parameter compared to monoculture rubber plantation. We also found that old plants had a higher V_{cmax} and J_{max} than young ones. V_{cmax} and J_{max} were strongly correlated while V_{cmax} and leaf nitrogen content moderately correlated.

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7. Statement of declaration

I hereby assure that this thesis is the result of my own work and investigations, except where otherwise stated. This work has not been submitted before to any other university for any kind of degree.

Signed: …………………….. (Braninditya Nugroho)
Date: ……………………..