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Research Article

Photosynthetic activities of oil palm and its understory cover crops under shade

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Abstract

Photosynthesis is a key part of how oil palm ecosystems store carbon. The net CO_2 *assimilation rate is greatly affected by the concentration of* CO_2 *between cells (Ci). Nonetheless, data on the assimilation–intercellular* CO_2 *(A/Ci) response of oil palm and understory vegetation in shaded mineral soil conditions remain inadequate. This study aimed to assess the A/Ci response characteristics and essential photosynthetic variables of oil palm (Elaeis guineensis Jacq.) and two understory cover crops, Asystasia gangetica and Nephrolepis biserrata, cultivated beneath mature oil palm canopies. The study was conducted at the Cikabayan Teaching Farm, IPB University, Bogor, Indonesia. A portable photosynthesis system was used to measure gas exchange variables at different times of the day. These included net* CO_2 *assimilation rate (A), stomatal conductance, transpiration rate, and intercellular* CO_2 *concentration (Ci). The results indicated clear physiological differences in the responses of canopy and understory vegetation. The Ci values of oil palm remained fairly stable throughout the observation period. On the other hand, understory species showed greater changes, requiring more Ci in the morning and less in the afternoon. Nephrolepis biserrata exhibited higher net assimilation than A. gangetica, indicating greater photosynthetic efficacy in shaded environments. These findings underscore the divergent photosynthetic regulation between canopy and understory vegetation, underscoring the significance of understory plants in facilitating carbon assimilation dynamics in shaded oil palm ecosystems.*

Keywords: absorption of CO_2; *Asystasia gangetica*; *Nephrolepis biserrata*; stomatal conductances

Introduction

Indonesia is one of the world's largest producers of palm oil. The total area of oil palm plantations in Indonesia was 9,144.7 thousand hectares in 2023 (BPS, 2025a). In

2024, the country produced 30,996.28 thousand tons of palm oil (BPS, 2025b). Mineral soils are the most common type of soil for growing oil palm, but peatlands can also be used for plantation development. Some studies report that oil palm production on mineral soils is usually higher than on peatlands (Hillari 2022; Sitompul 2024), whereas others report no significant differences between the two soil types (Ansyori et al., 2017; Budianto et al., 2016).

A significant factor influencing oil palm productivity is the plant's capacity for photosynthesis and carbon assimilation. In photosynthesis, plants assimilate carbon dioxide (CO_2) and transform it into carbohydrates that facilitate growth and productivity. Oil palm plantations are documented to serve as substantial carbon sinks, exhibiting a net CO_2 absorption of roughly 64 ton CO_2 ha^{-1} per year and an oxygen output of nearly 18 ton per hectare (Uning et al., 2020). Likewise, Borbon et al. (2020) projected that carbon sequestration in oil palm farms might attain 4.55 ton C ha^{-1} per year. Additional research corroborates that oil palm plantations can serve as net carbon sinks, aiding in climate change mitigation (Siallagan et al., 2025). Moreover, Indonesia ranks among the top 15 nations capable of sequestering at least 1 Mt CO_2 annually through soil organic carbon sequestration (FAO, 2022).

Even though this is possible, environmental factors, especially the amount of water and light the oil palm trees receive, have a significant effect on how well they can take in carbon. Water supply is one of the biggest challenges in growing oil palms on mineral soils, especially during the dry season, when production usually declines. Rianjes et al. (2023) said that not having enough water can lower the productivity of oil palms, but it takes about a year for this to happen. This means that if there isn't enough water in one year, the yields may be lower in the next year. Limiting water also increases the likelihood of oil palm plants having damaged and dried-out fronds (Evizal et al., 2021). Physiologically, water stress reduces photosynthetic rates and stomatal conductance (Filho et al., 2021), thereby limiting carbon assimilation and ultimately affecting plant growth and productivity.

Light availability in the plantation canopy is also important for photosynthetic performance, along with the availability of water. As oil palm trees grow, the structure of their canopies changes, which changes the microclimate below the canopy. Young oil palm trees let more light through to the soil surface, while mature oil palm canopies block more light from reaching the understory layer. These small changes in the environment affect how oil palm leaves grow and how understory plants grow.

The photosynthetic performance of oil palm has been studied under various conditions, including nurseries, immature stands, and mature plantations. Apichatmeta et al. (2017) found that oil palm has a high photosynthetic efficiency and requires ample light, especially as trees age. Romero et al. (2022) showed that planting density also affects photosynthesis. They found that a planting density of 115 trees ha^{-1} gave the best photosynthetic characteristics and the highest total fresh fruit bunch (FFB) yield. Genetic differences also affect how well plants photosynthesize under stress. Montoya et al. (2024) found that *Elaeis guineensis* genotypes are better at keeping photosynthesis going during drought than *Elaeis oleifera* and OxG hybrids. Environmental factors, including the duration of water immersion, affect photosynthesis, respiration, and stomatal conductance in oil palm seedlings (Andesmora et al., 2025).

In oil palm ecosystems, carbon sequestration is not only determined by the oil palm trees. Vegetation growing under the oil palm canopy, especially cover crops or weeds, also helps plants take in carbon through photosynthesis. Sahari et al. (2023)

reported that different weed types differ in their ability to adapt to changes in the microenvironment in oil palm plantations. For example, Satriawan et al. (2021) found that *Nephrolepis biserrata* and *Asystasia intrusa* can produce biomass of 21.2-27.1 ton C ha^{-1} and 17.6-17.9 ton C ha^{-1}, respectively. They also found that these plants can store carbon at rates of 0.6 and 0.9 ton C ha^{-1} per year. Additional research indicates that species including *Nephrolepis biserrata, Asystasia gangetica, Paspalum conjugatum*, and *Ageratum conyzoides* have potential as ground cover plants in established oil palm plantations, owing to their rapid growth, ability to cover soil surfaces, and role in nutrient cycling (Asbur et al., 2018).

Research on weed photosynthesis has demonstrated that environmental factors significantly affect their physiological responses. Zhang and Wen (2008) found that the invasive weed *Micania micrantha* has a weaker photosynthetic response to light and CO_2 when it is infected by whiteflies (*Bemisia tabaci*). Chadha et al. (2019) similarly found that water scarcity reduced the net assimilation rate of *Lactuca serriola* by approximately 25%. Conversely, Naidoo and Naidoo (2023) demonstrated that *Chromolaena odorata* can tolerate shaded environments and enhance carbon sequestration under reduced light.

The assimilation–intercellular CO_2 (A/Ci) response curve is a common way to study how photosynthesis responds to environmental conditions. The A/Ci curve shows how the net photosynthetic assimilation rate (A) and the intracellular CO_2 concentration (Ci) are related. This provides important information on the biochemical limits and controls of photosynthesis (Farquhar et al., 1980). This method can also be used to see how plants respond to changes in their environment and to estimate how much carbon they will take up in the future by modeling (Stinziano et al., 2019; Tejera-Nieves et al., 2024a).

However, research on the A/Ci response characteristics of oil palm and understory vegetation in shaded conditions in mineral soil plantations remains scarce. Understanding these physiological responses is crucial to clarifying the collaborative role of canopy and understory vegetation in carbon assimilation in oil palm ecosystems. This study aimed to assess the A/Ci response characteristics and essential photosynthetic variables of oil palm (*Elaeis guineensis* Jacq.) and two understory species, *Asystasia gangetica* and *Nephrolepis biserrata*, cultivated beneath the canopy of mature oil palm on mineral soils.

Material and methods

Study site and experimental period

This research was conducted from January to April 2025 at the Cikabayan Teaching Farm in Bogor, Indonesia (250 m above sea level; coordinates: −6.54787, 106.7157). Soil and plant analyses were performed at the Laboratory of the Department of Agronomy and Horticulture, IPB University.

Plant materials and field conditions

The plant material utilized in this study comprised oil palm (*Elaeis guineensis* Jacq.) and understory vegetation flourishing beneath the palm canopy. The oil palm plantation had 12-year-old Tenera palms that were planted 9 m × 9 m apart in an equilateral triangle pattern. This made the population density about 143 palms per hectare. Twice a year, the palms were fertilized with NPK Phonska fertilizer at a rate of 2 kg per tree. *Asystasia gangetica* and *Nephrolepis biserrata* were the two most common understory plants. They grow naturally around the oil palm trees.

Sampling procedure

Three oil palm trees were randomly chosen from Block 26 to represent the rest of the palm trees in the area. Five individual samples of *A. gangetica* and five samples of *N. biserrata* growing beneath the palm canopy were chosen for the understory vegetation. Monthly field observations were made in January, February, and April 2025. In April 2025, we took photosynthetic measurements of oil palm six times a day: at 07:00 am, 08:00 am, 09:00 am, 11:00 am, 01:00 pm, and 03:00 pm. We took photosynthetic measurements from the 17th frond of the oil palm, focusing on the middle leaflet section. Here, the youngest oil palm frond was considered the first frond. Measurements were taken on both the right and left leaflets, so there were two data points for each frond. For understory vegetation, measurements were taken on the third leaf.

Observed variables

The experimental variables included growth variables (plant height, stem diameter, number of fronds, leaf area, number of spear leaves), production variables (fresh fruit bunch (FFB) yield, FFB moisture content, number of male and female flowers), and physiological variables (net assimilation, stomatal conductance, transpiration, intracellular CO_2 concentration (Ci), air humidity, air temperature, leaf chlorophyll content, anthocyanin content, carotene content, stomatal density, and leaf greenness).

Instruments and measurements

The LI-6800 Portable Photosynthesis System (LI-COR Biosciences) was used to measure photosynthetic variables. A Konica Minolta SPAD-502 Plus Chlorophyll Meter was used to find out how much chlorophyll was in the leaves. A skylift vehicle was used to reach the oil palm canopy. To evaluate stomata, a microscope was used after preparing the sample with clear adhesive tape, nail polish to make stomatal imprints.

Data analysis

All measurements were conducted with two replications. The obtained data were expressed as mean ± standard deviation (SD) and analyzed using SAS version 9.1.3.

Results and discussion

Table 1 shows the results of measuring the greenness of the leaves of *A. gangetica* and *N. biserrata* plants that were growing in the shade of oil palm trees. The data show that the greenness values changed over time during the three months of observation and at the three oil palm sampling points. The average greenness of *A. gangetica* went down a little from 40.47 in January to 35.91 in February. It stayed pretty steady at 35.80 in April. *N. biserrata*, on the other hand, had a different pattern. Its value went up from 35.84 in January to 41.33 in February and then to 42.48 in April. These results show that the two species react differently to shaded microenvironmental conditions under the oil palm canopy. In general, the greenness of a leaf is closely linked to the amount of chlorophyll it has. This shows how well the plant can absorb light and photosynthesize in places where there isn't much radiation.

The standard deviation values also showed that the greenness values varied, which means that different species are better or worse at adapting to microhabitat conditions. *A. gangetica* had less variation, with standard deviation values between 1.75 and 4.13. This suggests that the physiological response is more stable when the plants are in the shade of oil palms. *N. biserrata,* on the other hand, showed more variation, especially in April when the standard deviation was 10.76. This means that the sampling locations were more sensitive to changes in the environment. Baligar et al. (2021) say that higher levels of CO_2 in the atmosphere in the future may help some cover crops grow even in low-light conditions. This could lead to more biomass and agroecological benefits. Additionally, environmentally friendly management practices in oil palm plantations that let understory plants grow can help the ecosystem without adding to greenhouse gas emissions (Drewer et al., 2024). Rani et al. (2025) also said that cover crops are important for improving soil quality, making farming more sustainable, and making it more resistant to climate change.

Table 1. Leaf greenness of *A. gangetica* and *N. biserrata* under the shade of oil palm

Sample plant	*A. gangetica*			*N. biserrata*		
	January	February	April	January	February	April
T1	39.23	39.87	39.63	43.42	46.02	54.91
T2	39.71	34.85	36.35	29.81	40.65	36.09
T3	42.47	33.01	31.42	34.29	37.32	36.44
Average	40.47	35.91	35.80	35.84	41.33	42.48
Standard deviation	1.75	3.55	4.13	6.94	4.39	10.76

According to Table 2, the greenness of oil palm leaves got less and less from January to April. In January, the average leaf greenness value was 97.03 units. In February, it dropped to 73.32 units, and in April, it dropped even more to 68.69 units. This pattern of getting lower was seen in all of the sample plants. For instance, T2 went down from 99.51 units in January to 72.78 units in February and then to 66.35 units in April. The standard deviation of 0.79 in February was lower than in January (2.86) and April (2.41), which suggests that the observed plants had a more uniform leaf greenness condition during that time. The amount of nitrogen available to a plant is closely linked to the color of its leaves. So, changes in SPAD values may mean that the plant is under nutrient stress. Rendana et al. (2015) say that the best way to find nutrient stress in the field is to use both remote sensing techniques and in-situ measurements with a SPAD Chlorophyll Meter.

At the same time, the density of stomata showed a slight downward trend over the course of the study. In January, the average number of stomata was 226.79 stomata mm^{-2}. This number dropped to 206.91 stomata mm^{-2} in February and 201.30 stomata mm^{-2} in April. T2 had the highest stomatal density in January (258.89 stomata mm^{-2}), but it dropped sharply to 190.60 stomata mm^{-2} in April. T3, on the other hand, had values that stayed fairly stable, ranging from 211.50 to 210.99 stomata mm^{-2} during the whole observation period. The variability of stomatal density decreased from 27.82 in January to 9.76 in February and 10.23 in April, showing that the sample plants had a more even distribution over time. Stomatal density is very important for controlling the movement of gases and water through stomata, which affects how well plants use water. Pan et al. (2024) elucidate that the configuration of leaf stomata, encompassing stomatal density and size, governs stomatal conductance and CO_2 assimilation capacity, ultimately influencing water use efficiency. Additionally, elevated CO_2 levels can enhance intrinsic water use efficiency (iWUE) by decreasing stomatal conductance and promoting photosynthesis (Zhan et al., 2025). In contrast, elevated leaf temperatures can markedly diminish photosynthesis, respiration, stomatal conductance, and water use efficiency in oil palm plants (de Morais et al., 2020).

Table 2. Leaf greenness and stomatal density of oil palm

Sample plant	Leaf greenness (unit)			Stomata density (unit mm^{-2})		
	January	February	April	January	February	April
T1	93.90	72.94	71.17	209.97	202.32	202.32
T2	99.51	72.78	66.35	258.89	218.12	190.60
T3	97.68	74.23	68.55	211.50	200.29	210.99
Average	97.03	73.32	68.69	226.79	206.91	201.30
Standard deviation	2.86	0.79	2.41	27.82	9.76	10.23

Table 3 shows the results of photosynthetic measurements in oil palm plants. It shows that net assimilation, stomatal conductance, and transpiration changed depending on when the measurements were taken. Net assimilation went up from 5.55 μmol CO_2 m^{-2} s^{-1} at 07.00 a.m. to a high of 11.15 μmol CO_2 m^{-2} s^{-1} at 11.00 a.m. (approximately 101% more), then went down to 6.86 μmol CO_2 m^{-2} s^{-1} at 01.00 p.m. and 5.23 μmol CO_2 m^{-2} s^{-1} at 03.00 p.m. Stomatal conductance followed a similar pattern, peaking at 08:00 a.m. (0.39 mol H_2O m^{-2} s^{-1}) and dropping to 0.22 mol H_2O m^{-2} s^{-1} at 01:00 p.m., which is a drop of almost 44%. The average values for net assimilation, stomatal conductance, and transpiration were 7.97 μmol CO_2 m^{-2} s^{-1}, 0.31 mol H_2O m^{-2} s^{-1}, and 0.01 mol H_2O m^{-2} s^{-1}, respectively. The standard deviations were 2.37, 0.06, and 0.00, indicating that assimilation and stomatal conductance varied moderately, whereas transpiration did not. Syarovy et al. (2018) assert that transpiration and photosynthesis rates increase in normal oil palm seedlings; however, such increases are undetected in chimaera seedlings due to the lack of chlorophyll. Moreover, Munir et al. (2022) indicated that the mean stomatal pore width in oil palm seedlings augmented with the application of KCl fertilizer and elevated soil moisture levels, whereas Sukmawan and Riniarti (2020) demonstrated that the mass of desiccated oil palm bunches and the frequency of irrigation are correlated with the rates of transpiration and photosynthesis in oil palm seedlings.

Table 3. Net assimilation, stomatal conductance, and transpiration of oil palm plants based on the observation period

Observation time	Net assimilation (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Transpiration (mol H_2O m^{-2} s^{-1})
07.00 a.m.	5.55	0.33	0.01
08.00 a.m.	8.05	0.39	0.01
09.00 a.m.	10.97	0.36	0.01
11.00 a.m.	11.15	0.28	0.01
01.00 p.m.	6.86	0.22	0.01
03.00 p.m.	5.23	NA	NA
Average	7.97	0.31	0.01
Standard deviation	2.37	0.06	0.00

Note: NA-not detected

The findings of Jaredi et al. (2024) demonstrate that photosynthetic rate declines as drought stress intensifies, underscoring the critical roles of chlorophyll and intercellular CO_2 concentration (Ci) in sustaining photosynthetic activity. Table 4 shows that the Ci values for oil palm trees changed with time, going from 307.28 to 405.02 µmol CO_2 mol^{-1}, with an average of 341.38 µmol CO_2 mol^{-1}. At 03:00 p.m., the Ci value was the highest (405.02 µmol CO_2 mol^{-1}), while at 11:00 a.m., it was the lowest (307.28 µmol CO_2 mol^{-1}). The changes in these values were linked to changes in the weather. For example, the relative humidity dropped from 65.8% at 07:00 a.m. to around 54.5% in the middle of the day and afternoon, and the air temperature rose from 27.6°C to about 29.5°C. The average temperature and relative humidity during the observation period were 28.71°C and 58.44%, respectively. Neoh et al. (2019) found that oil palm trees that produce more oil also store more carbon at higher Ci levels, which is linked to higher stomatal conductance and transpiration rates. Shi et al. (2024) have found that air humidity impacts photosynthetic rates. When relative humidity is low, stomata are less permeable, reducing net assimilation in plants.

Table 4. Intercellular CO_2 concentration (Ci), air humidity, and air temperature of oil palm plants based on observation time

Observation time	Intercellular CO_2 (Ci) (µmol CO_2 mol^{-1})	Relative humidity (%)	Temperature (°C)
07.00 a.m.	351.19	65.80	27.60
08.00 a.m.	344.88	63.13	27.97
09.00 a.m.	323.52	58.71	28.44
11.00 a.m.	307.28	53.97	29.55
01.00 p.m.	316.41	54.53	29.22
03.00 p.m.	405.02	54.51	29.47
Average	341.38	58.44	28.71
Standard deviation	32.31	4.60	0.75

Results of measurements of photosynthetic activity for *N. biserrata* and *A. gangetica* soil cover plants are shown in Table 5. Like most plants, the photosynthetic rate of both plants increased at noon, as the intensity of sunlight and temperature increased. According to Saputri et al. (2020), temperature is one of the abiotic factors affecting photosynthesis, as it makes photosynthesis susceptible to temperature stress. Results of Listia et al. (2020) study state that physiological characteristics of the plant, such as photosynthesis rate, respiration rate, intracellular CO_2 concentration, and stomatal dimensions of oil palm plants grown at high altitude are lower than those of oil palm plants grown at lower altitude. In addition to temperature, photosynthesis is also affected by light, as shown by the results of the Nasution et al. (2025) study, which states that light and $NaHCO_3$ both play a major role in the rate of photosynthesis, but that there is an optimum limit at which further increases will not yield significant results.

Table 5 shows the findings of measuring how photosynthetic activity affected the soil cover plants *Nephrolepis biserrata* and *Asystasia gangetica*. Like most plants, the photosynthetic rates of both species increased at noon as temperature and light levels rose. The net assimilation rate for *N. biserrata* went up a lot, from 0.90 µmol CO_2 m^{-2} s^{-1} at 09:00 a.m. to 18.11 µmol CO_2 m^{-2} s^{-1} at 01:00 p.m. The average value was 9.50 µmol CO_2 m^{-2} s^{-1}, and the standard deviation was 12.17, indicating substantial variance across observation times. In the same way, *A. gangetica* net assimilation went up from 1.92 to 10.94 µmol CO_2 m^{-2} s^{-1}, giving it an average of 6.43 µmol CO_2 m^{-2} s^{-1}

with a standard deviation of 6.38. However, its total assimilation rate was still lower than that of *N. biserrata.* In terms of stomatal conductance, *N. biserrata* increased from 0.12 to 0.90 mol H_2O m^{-2} s^{-1} (average 0.51 mol H_2O m^{-2} s^{-1}), whereas *A. gangetica* declined from 0.52 to 0.19 mol H_2O m^{-2} s^{-1} (average 0.36 mol H_2O m^{-2} s^{-1}). This suggests that the two species respond differently to changes in their surroundings. In the meantime, the transpiration rates of both species stayed rather modest and steady, at about 0.00–0.01 mol H_2O m^{-2} s^{-1}. These data show that higher temperatures and light levels in the environment are associated with greater photosynthesis during midday. Saputri et al. (2020) state that temperature is one of the abiotic factors that affect photosynthesis, as it can cause plants to become stressed by heat. Listia et al. (2020) also reported that physiological traits such as photosynthetic rate, respiratory rate, intracellular CO_2 concentration, and stomatal size vary with the environment. According to Nasution et al. (2025), light is just as important as temperature for photosynthesis. They said that light and $NaHCO_3$ have a significant effect on photosynthesis, but adding more than the optimal amount doesn't always have a significant effect.

Table 5. Net assimilation, stomatal conductance, and transpiration of *Nephrolepis biserrata* and *Asystasia gangetica* based on observation time

Observation time	Net assimilation (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Transpiration (mol H_2O m^{-2} s^{-1})
N. biserrata			
09.00 a.m.	0.90	0.12	0.00
01.00 p.m.	18.11	0.90	0.01
Average	9.50	0.51	0.01
Standard deviation	12.17	0.55	0.01
A. gangetica			
09.00 a.m.	1.92	0.52	0.01
01.00 p.m.	10.94	0.19	0.01
Average	6.43	0.36	0.01
Standard deviation	6.38	0.23	0.00

Mature oil palm fields tend to be damp and do not get much sunlight. Table 6 shows that the intercellular CO_2 concentration (Ci) of both weed species decreased from morning to afternoon. In *N. biserrata,* Ci dropped from 373.09 μmol CO_2 mol^{-1} at 09:00 a.m. to 245.02 μmol CO_2 mol^{-1} at 01:00 p.m., which is a drop of 128.07 μmol CO_2 mol^{-1} (34.3%). In *A. gangetica,* it dropped from 379.54 to 259.32 μmol CO_2 mol^{-1}, which is a drop of 120.22 μmol CO_2 mol^{-1} (31.7%). Relative humidity rose from morning to afternoon, from 56.87% to 63.44% in *N. biserrata* (average 60.16%) and from 56.53% to 61.47% in *A. gangetica* (average 59.00%). The temperature also rose, from 27.88°C to 30.33°C in *N. biserrata* (average 29.11°C; SD 1.73) and from 27.69 °C to 29.04 °C in *A. gangetica* (average 28.37 °C). These results show that the microclimatic conditions were quite constant, with high humidity and moderate temperatures. Tulva et al. (2024) state that higher stomatal density increases stomatal conductivity, yet low relative humidity and high stomatal density both inhibit plant growth on their own. The relatively high humidity observed in this study supports the adaptability of shade-tolerant weeds such as *N. biserrata* and *A. gangetica* under oil palm canopies, which is consistent with the findings of Asbur et al. (2024), who demonstrated that four weeks post-planting, both species achieved 100% soil coverage.

Table 6. Intercellular CO_2 concentration (Ci), relative humidity, and temperature in *Nephrolepis biserrata* and *Asystasia gangetica* based on observation time

Observation time	Intercellular CO_2 (Ci) (μmol CO_2 mol^{-1})	Relative humidity (%)	Temperature (°C)
N. biserrata			
09.00 a.m.	373.09	56.87	27.88
01.00 p.m.	245.02	63.44	30.33
Average	309.06	60.16	29.11
Standard deviation	90.56	4.65	1.73
A. gangetica			
09.00 a.m.	379.54	56.53	27.69
01.00 p.m.	259.32	61.47	29.04
Average	319.43	59.00	28.37
Standard deviation	85.01	3.49	0.95

Table 7 displays the findings for chlorophyll a, chlorophyll b, anthocyanins, carotenoids, and total chlorophyll. Chlorophyll a is the main pigment that plants use to turn light energy into chemical energy. Chlorophyll b is a secondary pigment that collects light at different wavelengths and sends it to chlorophyll a. When measured, oil palm leaves had more pigments than the weeds that were seen. The average chlorophyll a content in oil palm was 0.070 mg cm^{-2}, with a range of 0.066–0.073 mg cm^{-2}. The average chlorophyll b content was 0.024 mg cm^{-2}, with a range of 0.022–0.025 mg cm^{-2}. The highest total chlorophyll was found in treatment T3 (0.097 mg cm^{-2}), followed by T2 (0.095 mg cm^{-2}) and T1 (0.088 mg cm^{-2}). The overall average was 0.093 mg cm^{-2}, with a standard deviation of 0.005.

Table 7. Levels of chlorophyll a, chlorophyll b, anthocyanin, carotene, and total chlorophyll in oil palm and weeds of the genera *N. biserrata* and *A. gangetica*

Sample plant	Chlorophyll a (mg cm^{-2})	Chlorophyll b (mg cm^{-2})	Anthocyanin (μmol cm^{-2})	Carotene (mg cm^{-2})	Total chlorophyll (mg cm^{-2})
Oil palm					
T1	0.066	0.022	0.025	0.025	0.088
T2	0.070	0.025	0.026	0.026	0.095
T3	0.073	0.024	0.025	0.026	0.097
Average	0.070	0.024	0.025	0.026	0.093
Standard deviation	0.004	0.001	0.001	0.001	0.005
Cover crop					
N. biserrata	0.028	0.011	0.010	0.011	0.039
A. gangetica	0.025	0.008	0.004	0.008	0.033
Average	0.026	0.010	0.007	0.009	0.036
Standard deviation	0.002	0.002	0.004	0.002	0.004

The amounts of anthocyanin and carotenoid in oil palm were quite steady, with averages of 0.025 μmol cm^{-2} and 0.026 mg cm^{-2}, respectively (Table 7). The weeds, on the other hand, had lower pigment concentrations. For example, *N. biserrata* had chlorophyll a and b levels of 0.028 mg cm^{-2} and 0.011 mg cm^{-2}, respectively. *A. gangetica* had slightly lower levels, at 0.025 mg cm^{-2} and 0.008 mg cm^{-2}. Total chlorophyll levels ranged from 0.033 to 0.039 mg cm^{-2}, with an average of 0.036 mg cm^{-2}. Even though oil palm had more pigments, the differences between treatments were not large, indicating that the amounts of chlorophyll a and b were not very different between treatments. Astutik et al. (2019) reported that potassium affects maize plants' chlorophyll a, b, total chlorophyll, and root surface area 4 weeks after planting. The leaves of oil palm trees contain a lot of chlorophyll, which affects the amount of oil palm fruit they produce (Juanda et al., 2020). Fatmawaty et al. (2024) also reported that the total chlorophyll variable did not depend on seedling age or the amount of light received.

According to Table 8, the growth metrics of the 12-year-old oil palm trees didn't change much from sample to sample. The average plant height was 659.7 cm, with a range of 651.0 to 675.0 cm and a standard deviation of 13.3 cm. The average stem diameter was 217.0 cm, with a range of 196.0 to 249.0 cm and a standard deviation of 28.2 cm. The average number of fronds per plant was 35.7, with a range of 34 to 37. The average leaf area was 12.4 m^2, with a range of 12.0 to 13.1 m^2. The leaf area index (LAI) ranged from 5.9 to 6.8, with an average of 6.3 and a standard deviation of 0.5. This means the canopy was relatively dense and could block sunlight effectively to support photosynthesis. This finding aligns with other research: leaf area and the number of fronds can be used to estimate daily carbon input via LAI and to predict microclimate and plant productivity (Manurung et al., 2024; Hardwick et al., 2015). The LAI is also affected by the number of leaves per plant, leaf size, and planting density. These factors affect how well the canopy absorbs light and boosts photosynthesis and dry matter production (Noor & Harun, 2004).

Table 8. Growth variables and leaf area index (LAI) in oil palm plant samples

Plant sample	Plant height (cm)	Stem diameter (cm)	Number of fronds	Leaf area (m^2)	Number of spear leaves	Leaf area index (LAI)
T1	675.0	196.0	37.0	12.1	1.0	6.4
T2	653.0	206.0	34.0	12.0	1.0	5.9
T3	651.0	249.0	36.0	13.1	1.0	6.8
Average	659.7	217.0	35.7	12.4	1.0	6.3
Standard deviation	13.3	28.2	1.5	0.6	0.0	0.5

According to Table 9, each plant made between 22.85 and 32.68 kg of fresh fruit bunches (FFB), with an average of 28.9 kg and a standard deviation of 5.3 kg. T2 had the most production (32.68 kg), and T3 had the least (22.85 kg). The water content of FFB didn't change much; it ranged from 22.55% to 24.24%, with an average of 23.5%. This means that the plants had similar physiological conditions. The number of female flowers to male flowers was very different in each sample. In T1, there were four female flowers to one male flower; in T2, three female flowers to two male flowers; and in T3, two female flowers to one male flower. This meant that the sex ratios were 80.00%, 40.00%, and 66.67%, with an overall average of 62.2%. This difference shows that plants have different reproductive potential. A higher percentage of female flowers may make it more likely that fruit will form and, in the end, FFB will be produced. Overall, the FFB output observed in this study is similar to that reported in prior studies with planting distances of 8 × 8 m and 9 × 9 m, which also showed similar levels of oil palm productivity (Hayata et al., 2020).

Table 9. Production variables in oil palm plant samples

Plant sample	Average weight of FFB per plant (kg)	Water content of FFB (%)	Female:male flower ratio	Sex ratio
T1	31.23	23.80	4:1	80.00
T2	32.68	24.24	2:3	40.00
T3	22.85	22.55	2:1	66.67
Average	28.9	23.5	-	62.20
Standard deviation	5.3	0.9	-	20.40

Figure 1 shows the relationship between the net photosynthetic rate (A) and the concentration of CO_2 in the cells (Ci) of oil palm, *A. gangetica*, and *N. biserrata*. This was measured at 9:00 a.m. and 1:00 p.m. The A/Ci curve shows a nonlinear response, with photosynthesis rising quickly at first as Ci goes up, especially when Ci is around 300–350 μmol mol^{-1} in oil palm. When Ci is low, the rise in A means that Rubisco carboxylation activity controls the rate of carbon fixation. As Ci increases, the curve gradually approaches a peak or saturation point, indicating that photosynthesis is limited by biochemical processes, such as electron transport and RuBP regeneration, as described in the Farquhar-von Caemmerer-Berry (FvCB) photosynthesis model. The A/Ci curve is widely used to evaluate how photosynthetic traits respond to changes in the environment and to predict how much carbon plants will take in in the future through modeling (Stinziano et al., 2019). Cheah and Teh (2020) identified critical variables of the FvCB model and their thermal dependence in oil palm, enabling more precise modeling of photosynthetic carbon assimilation, particularly under elevated temperature and CO_2 conditions.

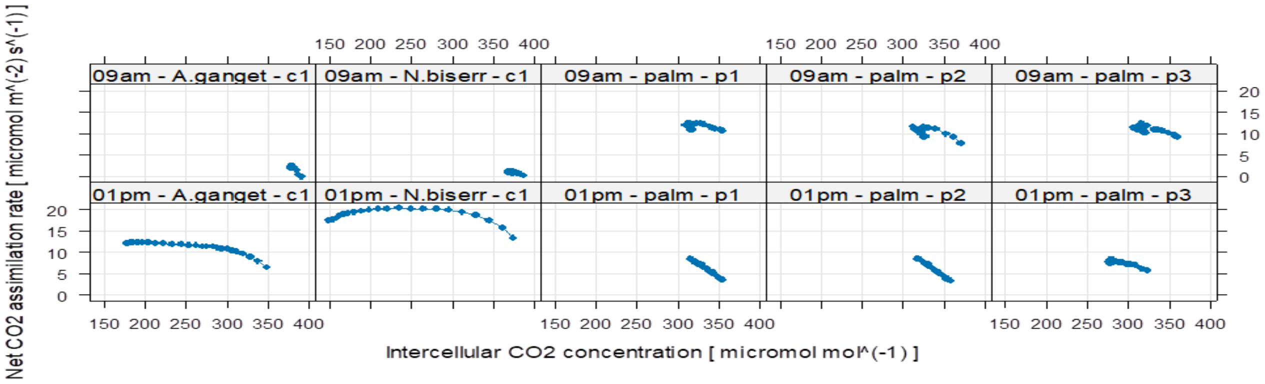

Figure 1. A/Ci curve in oil palm, *A. gangetica*, and *N. biserrata* plants during photosynthesis measurements at 9:00 a.m. and 1:00 p.m.

The line's curve and the peak show the transition from photosynthesis limited by CO_2 to photosynthesis limited by biochemistry. The curve levels off when increases in Ci no longer significantly improve photosynthetic assimilation. This is because the capacities for enzymes and electron transport become limiting. In some cases, there may be a small drop in the curve after the peak. This could be due to physiological constraints, such as lower photosynthetic efficiency, stomatal limitation, or metabolic regulation at higher internal CO_2 levels. The relationship between A and Ci should ideally look like a saturating curve, where photosynthesis rises quickly at low Ci levels, levels off over time, and then levels off again as biochemical limits take over. This pattern shows the balance among Rubisco activity, electron transport in the leaf, and CO_2 availability within the leaf (Sharkey, 2016).

Figure 1 also shows that the photosynthetic response patterns of oil palm and the ground cover species differ, even though they are both C3 plants. Oil palm shows a stronger increase in absorption as Ci rises, which means it has a better ability to photosynthesize than the understory species *A. gangetica* and *N. biserrata*, which respond more slowly. These differences likely reflect differences in physiological traits and ecological adaptations, such as how understory plants adapt to living in the shade. The Farquhar-von Caemmerer-Berry model remains important today because it links biological processes to direct gas-exchange data (Sharkey, 2016). Yin and Struik (2009) advocate integrating the FvCB model into plant development models for both C3 and C4 species to improve predictions of plant responses to CO_2, light, temperature, and climate change. Furthermore, recent innovations in A/Ci measurement protocols employing Dynamic Assimilation Techniques (DAT) within the LI-6800 system have reduced measurement duration while maintaining comparable accuracy to steady-state methods across various plant species (Burnett et al., 2019; Tejera-Nieves et al., 2024a; Tejera-Nieves et al., 2024b).

Conclusions

The photosynthetic performance of oil palm and understory vegetation in mineral soil plantations was significantly affected by microclimatic factors, such as temperature, light availability, and humidity. Oil palm exhibited relatively stable intercellular CO_2 concentrations over the observation period, suggesting more consistent regulation of photosynthesis across canopy microclimates. The understory species, on the other hand, showed more dynamic responses, had higher Ci in the morning and lower in the afternoon. *Nephrolepis biserrata* had a higher net CO_2 assimilation rate than *Asystasia gangetica*, which suggests that it is better at photosynthesis in shaded areas. Since understory vegetation might help oil palm plantations to maintain carbon dynamics, maintaining the understory layer can make oil palm agroecosystems more stable.

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