Journal of Tropical Crop Science Vol. 13 No. 3, October 2026
www.j-tropical-crops.com

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Photosynthetic Gas Exchange and Carbon Assimilation of Oil Palm (*Elaeis guineensis* Jacq.) and Understory Vegetation on Drained Tropical Peatlands

Jumena Adijaya[1], Herdhata Agusta*[2], Sudradjat[2], Supiandi Sabiham[3], and Triadiati[4]

[1] Agronomy and Horticulture Study Program, Graduate School, IPB University, Indonesia
[2] Department of Agronomy and Horticulture, Faculty of Agriculture, IPB University, Indonesia
[3] Department of Soil Science and Land Resources, Faculty of Agriculture, IPB University, Indonesia
[4] Department of Biology, Faculty of Mathematics and Natural Science, IPB University, Indonesia

*Corresponding author; email: agusta@ipb.ac.id

Abstract

This study evaluated the photosynthetic gas exchange of mature oil palm and understory vegetation in a drained tropical peatland plantation located in Riau, Indonesia. Measurements were taken six times a day on the 17th frond of 16-year-old palms and two dominant understory species (*Asystasia gangetica* and *Nephrolepis biserrata*) over six periods from February 2020 to March 2022. The photosynthetic rate of oil palm ranged from 18.44 to 43.47 µmol CO_2/m^2/s, and its stomatal conductance ranged from 0.050 to 0.067 mol H_2O/m^2/s. The transpiration rate ranged from 577.83 to 1,189.31 µmol H_2O/m^2/s. Stomatal conductance was strongly linked to transpiration ($r = 0.775$, $p < 0.001$). Understory species also showed high photosynthetic rates, with *N. biserrata* at 25.31–31.49 µmol CO_2/m^2/s and *A. gangetica* at 23.53–36.37 µmol CO_2/m^2/s. Diurnal patterns showed that physiological activity generally increased from morning to noon. These results demonstrate variation in leaf physiology and photosynthetic carbon assimilation in both canopy and understory plants on drained peatlands.

Keywords: *Asystasia gangetica*, CO_2 emissions, *Nephrolepis biserrata*, water table

Introduction

Indonesia is one of the largest producers of palm oil in the world. According to the Food and Agriculture Organization (FAO), Indonesia's palm oil production exceeded 240 million tonnes in 2023 (Food and Agriculture Organization, 2025). While most oil palm plantations are established on mineral soils, a substantial proportion has also been established on peatlands. The expansion of oil palm cultivation on peat soils has raised environmental concerns, as peatlands are major global carbon reservoirs. Poor management practices can accelerate peat decomposition and increase greenhouse gas emissions (Lourenco et al., 2023). Furthermore, climate change and increasing drought frequency in tropical regions may intensify carbon release from peat ecosystems (Swails et al., 2018).

Peatlands play a critical role in the global carbon cycle due to their capacity to store large amounts of organic carbon. Indonesia's peatlands are estimated to contain approximately 55–57 billion tonnes of carbon (Miller et al., 2022), much of which is concentrated in the upper soil layers, particularly within the top 30 cm (Huang et al., 2022). Conversion of peat swamp forests to agricultural land, including oil palm plantations, results in substantial carbon losses from both biomass and peat soils (Uning et al., 2020). This trend aligns with findings that peatlands are frequently converted for oil palm cultivation due to their perceived agricultural

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

suitability (Cook et al., 2018).

Effective water management is essential in oil palm plantations established on peatlands, particularly for maintaining appropriate groundwater levels. Drainage systems, typically consisting of canals, are used to regulate water levels to support crop growth while preventing excessive peat drying. During dry periods, water gates are often closed to retain moisture and reduce the risk of peat oxidation. However, excessive drainage can lower the water table, increase soil aeration, and stimulate heterotrophic respiration, which releases carbon dioxide (CO_2) from peat soils (Ma et al., 2022; Stuart et al., 2022). Maintaining optimal groundwater levels is therefore critical to minimizing peat decomposition and preserving ecosystem stability (Sulaiman et al., 2022). Moreover, over-drainage of tropical peatlands can lead to increased CO_2 emissions, land subsidence, and a higher risk of fire (Urzainki et al., 2022).

Concerns about the environmental impacts of oil palm cultivation on peatlands have influenced international policy discussions. For example, the European Parliament has supported measures to phase out the use of palm oil in certain products, partly due to its perceived contribution to greenhouse gas emissions (Sidik, 2018). However, estimates of emissions from drained peatlands under oil palm cultivation vary widely. Hooijer et al. (2012) reported annual emissions of approximately 95 t CO_2/ha, whereas other studies have reported lower values ranging from 20 to 30 t CO_2/ha per year (Sabiham, 2020), or about 24 ± 5 t CO_2/ha per year in Sumatra (Deshmukh et al., 2021). These discrepancies highlight the need for a more comprehensive understanding of carbon dynamics in peatland oil palm systems.

Beyond soil carbon processes, plant physiological mechanisms play a key role in carbon cycling within oil palm plantations. Through photosynthesis, plants convert atmospheric CO_2 into photoassimilates such as sucrose and starch using solar energy (Sharkey, 2024). Carbon assimilated during photosynthesis contributes to biomass production, including fresh fruit bunches (FFB), fronds, trunks, and roots. Previous studies have shown that oil palm plantations on peatlands contain an average aboveground carbon stock of 47.3 ± 12.8 t C/ha, which is substantially lower than that of secondary forests (116.4 ± 13.4 t C/ha) (Novita et al., 2024). Understanding the interactions among photosynthetic rate, stomatal conductance, and transpiration is therefore essential for evaluating plant responses to environmental conditions in peatland systems.

In addition to oil palm, understory vegetation contributes to ecosystem functioning. Understory plants are often maintained in the inter-row spaces (local term: ‘gawangan’) to protect the soil surface and reduce evaporation. These areas also facilitate plantation management activities and provide a suitable environment for understory growth. At the plantation scale, understory species can influence microclimate, soil moisture, and potentially carbon dynamics. However, physiological studies examining both oil palm and understory vegetation in peatland plantations remain limited.

Previous research has demonstrated that physiological performance in oil palm is influenced by factors such as plant health, environmental stress, and water availability. For example, Susanto et al. (2020) reported that leaf rust reduces photosynthetic efficiency in oil palm. Similarly, Andesmora et al. (2025) showed that oil palm accessions and the duration of water stress significantly affect photosynthetic rate, transpiration, and stomatal conductance. Despite these findings, the combined effects of groundwater level and rainfall on the physiological responses of mature oil palm and understory vegetation in drained peatlands remain incompletely understood.

Therefore, this study aims to evaluate the physiological characteristics of mature oil palm and selected understory species in drained peatland plantations. Key parameters include photosynthetic rate, stomatal conductance, and transpiration rate. The study also examines how these physiological responses are influenced by variations in groundwater levels and rainfall. Understanding these relationships is essential for improving the management and sustainability of peatland-based oil palm systems.

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Materials and Methods

Study Site

The study took place from February 2020 to March 2022 at a private oil palm plantation in Pangkalan Pisang Village, Koto Gasib Subdistrict, Siak Regency, Riau Province, Indonesia. The plantation is located on a drained peatland, a common site for oil palm cultivation.

Plant Materials

The oil palm (*Elaeis guineensis* Jacq.) plants used in this study were 16 years old and of the DxP 'Marihat' variety. They were grown on drained peat soils. This age of palm was selected because it is the mature production phase of oil palm plantations, when canopy structure, leaf physiological activity, and carbon assimilation processes are relatively stable. At this point, the palms have developed a dense canopy that creates a shaded microenvironment in the understory. This facilitated the study of how oil palm and understory plants undergo photosynthetic gas exchange. *Asystasia gangetica* and *Nephrolepis biserrata*, two cover crop species, grew under the oil palm canopy. These were also measured for photosynthesis.

Field Observations and Sampling Design

Field observations were conducted in a deforested tropical peatland oil palm plantation situated in Block D (0°40′ N, 101°45′ E). There were 20 sub-blocks in Block D, each about 30 ha in size. Three sub-blocks were randomly selected (D1, D3, and D6) as observation sites that represented the relatively uniform biophysical conditions in Block D, including similar peat depth (>3 m), drainage management, topography (<3% slope), oil palm age, and planting material.

In each selected sub-block, three healthy, productive oil palm trees were selected as biological replicates. This brought the total number of sampled palms in the study area to nine. The chosen trees were typical of the average stand condition and were located in the middle of each sub-block to avoid edge effects. During each observation period, the same trees were measured repeatedly to study changes in physiological responses over time under different environmental conditions.

Three leaf blades were collected from the same frond of each sampled tree, yielding three leaf replicates per tree. The physiological measurements were taken by observing the same trees and leaves multiple times a day over several months, from February 2020 to March 2022.

Photosynthetic Gas Exchange Measurements

Photosynthetic gas exchange measurements were conducted on frond number 17, which is commonly used as a standard reference leaf in oil palm physiology due to its fully expanded and physiologically active status. Measurements were taken on fully sun-exposed leaflets located at the middle of the frond, approximately halfway along the rachis. To minimize structural variation, the central portion of each leaflet was selected, while the base and tip were excluded.

Leaf orientation and canopy position were standardized by selecting sun-exposed leaflets from the outer canopy layer under comparable light conditions. This approach ensured that differences in gas exchange were not influenced by variation in light exposure between shaded and sunlit leaves.

The measured gas exchange parameters included net photosynthetic rate, stomatal conductance, and transpiration rate. Measurements were taken six times per day at 07:00, 08:00, 09:00, 11:00, 13:00, and 15:00 across six observation periods: February 2020, April 2021, July 2021, November 2021, January 2022, and March 2022.

Understory Cover Crop Measurements

Physiological measurements were also conducted on two dominant understory species, *Asystasia gangetica* and *Nephrolepis biserrata*. Three representative plants of

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

each species were selected per observation block. Measurements were performed on fully expanded, mature leaves exposed to ambient understory light conditions. Gas exchange measurements were taken at 09:00 and 13:00, which represented peak physiological activity in the morning and midday, respectively. The same measurement procedures used for oil palm leaves were applied to the understory species to ensure comparability across plant types.

Leaf Physiological and Structural Assessments

Leaf chlorophyll content was estimated using a SPAD-502 chlorophyll meter, with measurements taken from the middle of leaflets on frond 17. Stomatal density was determined by making epidermal impressions from the abaxial leaf surface. Stomata were counted in three microscopic fields per sample and expressed as stomata per mm^2.

Fresh Fruit Bunch (FFB) Production

Data on fresh fruit bunch (FFB) production were obtained from plantation management records for each observation sub-block (D1, D3, and D6). Harvesting was conducted at 10–14-day intervals, following standard plantation practices. FFB yield was calculated by dividing the total harvested bunch weight by the planted area and expressed in tons per hectare (t/ha). Monthly average yields were computed to align with the physiological observation periods. These data were used to represent overall plantation productivity and to provide context for the relationship between physiological performance and yield.

Environmental Measurements

Groundwater levels were monitored using dip wells installed in each observation block, with measurements recorded weekly throughout the study period. Rainfall data for the years 2018 to 2022 were obtained from the plantation meteorological records.

Data Analysis

All measurements were conducted with three replications. Data were expressed as mean ± standard deviation (SD). Pearson correlation analysis was performed to assess relationships among the measured variables.

Results and Discussion

Photosynthetic Rate, Stomatal Conductance, and Transpiration of Oil Palm

This study evaluated key photosynthetic parameters, including photosynthetic rate, stomatal conductance, and transpiration. The diurnal pattern of photosynthesis varied across the observation months, as presented in Table 1. In February 2020, the photosynthetic rate increased from 15.19 µmol $CO_2/m^2/s$ at 07:00 to 21.02 µmol $CO_2/m^2/s$ at 11:00 and then remained relatively stable until 15:00. A similar trend was observed in March 2022, in which photosynthesis rose from 30.55 µmol $CO_2/m^2/s$ at 07:00 to 33.85 µmol $CO_2/m^2/s$ at 13:00, before declining to 29.59 µmol $CO_2/m^2/s$ at 15:00. However, during other observation periods, variation among measurement times was less pronounced, indicating that diurnal differences were not consistently substantial across months. These findings suggest that the diurnal response of photosynthesis is influenced by environmental factors such as solar radiation and cloud cover during the observation period.

The availability of carbon dioxide (CO_2), the primary substrate for photosynthesis, plays a crucial role in determining oil palm's photosynthetic performance. Ibrahim et al. (2018) reported that elevated CO_2 concentrations enhanced several growth parameters in oil palm seedlings, including plant height, leaf number, stem diameter, root biomass, total dry matter, net assimilation rate, and relative growth rate. Similarly, Scandolera et al. (2024) emphasized that increased atmospheric CO_2 directly influences plant physiological processes, as CO_2 is essential for the synthesis of organic compounds during photosynthesis.

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

The present study indicates that, in addition to CO_2 availability, light intensity during measurement also influenced photosynthetic activity. Several observations were conducted under cloudy or rainy conditions, which likely reduced incoming solar radiation and consequently limited photosynthesis. Dusenge et al. (2019) also reported that lower temperatures and reduced radiation generally decrease plant respiration and net assimilation rates.

Stomatal conductance refers to the rate at which gases, particularly CO_2, enter the leaf and water vapor exits through stomata. Data presented in Table 2 show that stomatal conductance varied across months and measurement times. For instance, in April 2021, stomatal conductance increased from 0.054 mol $H_2O/m^2/s$ at 07:00 to 0.110 mol $H_2O/m^2/s$ at 09:00, then gradually declined in the afternoon. In contrast, in November 2021, stomatal conductance was higher in the afternoon, reaching 0.113 mol $H_2O/m^2/s$ at 15:00. These variations suggest that stomatal conductance did not follow a consistent diurnal pattern across all observation periods.

Environmental factors such as radiation, temperature, and plant water status strongly influence stomatal behavior. Filho et al. (2024) reported that drought stress reduces both photosynthetic activity and stomatal conductance in oil palm. Temperature also plays a critical role, as elevated temperatures can reduce stomatal conductance (Middleby et al., 2024). Because stomata regulate the exchange of CO_2 and water vapor between the leaf and the atmosphere, stomatal conductance is a key determinant of carbon assimilation and plant water use efficiency (Tosens et al., 2025).

Table 1

Photosynthetic Rate of Oil Palm from February 2020 to March 2022 (µmol $CO_2/m^2/s$)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
07:00	15.19	58.75	37.89	26.93	30.38	30.55
08:00	16.70	53.32	38.35	27.51	26.80	30.03
09:00	17.23	50.69	32.57	27.23	28.47	31.42
11:00	21.02	38.65	32.41	32.27	31.68	33.24
13:00	20.03	34.47	34.01	29.14	30.07	33.85
15:00	20.47	24.94	29.21	27.52	29.75	29.59
Average	18.44	43.47	34.07	28.43	29.53	31.45
Standard deviation	2.38	12.89	3.51	2.03	1.69	1.75

Table 2

Stomatal Conductance of Oil Palm from February 2020 to March 2022 (mol $H_2O/m^2/s$)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
07:00	0.115	0.054	0.021	0.048	0.059	0.042
08:00	0.047	0.082	0.034	0.030	0.060	0.034
09:00	0.041	0.110	0.056	0.011	0.040	0.038
11:00	0.033	0.050	0.057	0.100	0.085	0.041
13:00	0.040	0.039	0.078	0.076	0.069	0.121
15:00	0.023	0.022	0.052	0.113	0.090	0.074
Average	0.050	0.060	0.050	0.063	0.067	0.058
Standard deviation	0.033	0.032	0.020	0.040	0.018	0.034

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Plant transpiration is the process by which water is released from plant tissues as water vapor, primarily through stomata on the surfaces of leaves. Table 3 shows that transpiration rates varied over time during the observation period. The transpiration rate increased from 256.47 µmol $H_2O/m^2/s$ at 07:00 to 2,180.33 µmol $H_2O/m^2/s$ at 13:00 in March 2022, and then it dropped to 1,275.27 µmol $H_2O/m^2/s$ at 15:00. However, like photosynthesis and stomatal conductance, the amount of change varied from month to month, showing that the conditions in which transpiration was measured influenced the results.

Wind speed, temperature, air humidity, radiation intensity, and soil water availability are all external factors that can affect transpiration. Shapira et al. (2024) stated that higher wind speeds can enhance the exchange of water vapor between leaves and the air, leading to greater transpiration. Pradiko et al. (2023), using the heat ratio method, also found that the average daily transpiration of 14-year-old oil palms was between 0.82 and 1.66 mm per day. Long periods of drought can lead to water shortages that can greatly lower transpiration and overall plant productivity (Brum et al., 2021).

A correlation analysis was performed among photosynthetic rate, stomatal conductance, and transpiration (Table 4) to further investigate the relationships among physiological parameters. The findings indicate a weak yet positive correlation between photosynthetic rate and stomatal conductance ($r = 0.190$, $p = 0.268$), suggesting that stomatal conductance was not significantly linked to fluctuations in photosynthetic rate during the observation period. Similarly, the relationship between photosynthetic rate and transpiration was weak and not statistically significant ($r = 0.072$, $p = 0.677$). Stomatal conductance, on the other hand, showed a strong, statistically significant positive correlation with transpiration ($r = 0.775$, $p < 0.001$). This finding demonstrates that an increased stomatal aperture enhances the rate of water vapor loss via transpiration. The correlation analysis indicated that transpiration dynamics in oil palm leaves are more strongly influenced by stomatal conductance than by photosynthetic activity.

Photosynthesis, Stomatal Conductance, and Transpiration of *Asystasia gangetica* and *Nephrolepis biserrata*

In addition to assessing photosynthetic characteristics in oil palm, observations were conducted on understory growing beneath the oil palm canopy. The two dominant understory species identified were *Asystasia gangetica* and *Nephrolepis biserrata*. These species play important ecological roles in plantation systems, particularly in enhancing soil quality and supporting overall ecosystem functioning.

Table 5 presents the photosynthetic rates of *A. gangetica* and *N. biserrata* measured at 09:00 and 13:00 over several months of observation.

Table 3

Transpiration Rate of Oil Palm from February 2020 to March 2022 (µmol $H_2O/m^2/s$)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
07:00	537.94	401.56	172.07	398.17	432.72	256.47
08:00	322.67	678.68	284.64	295.32	523.75	259.24
09:00	308.86	1,264.30	516.47	175.65	457.67	433.80
11:00	673.88	882.84	671.48	2,119.50	1,157.89	617.59
13:00	1,115.80	583.03	1,619.85	1,744.01	1,130.86	2,180.33
15:00	507.82	416.32	1,001.17	2,403.20	1,644.55	1,275.27
Average	577.83	704.46	710.95	1,189.31	891.24	837.12
Standard deviation	271.60	298.73	486.80	921.87	452.64	692.60

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

In general, photosynthetic rates increased from morning to midday, although slight declines were observed during certain measurement periods. This trend is consistent with typical diurnal patterns, in which carbon assimilation increases with higher solar radiation and temperature. However, short-term fluctuations in microclimatic conditions—such as cloud cover, shading from the oil palm canopy, and increased vapor pressure deficit—can temporarily reduce photosynthetic activity.

The use of understory has been widely reported to improve agricultural productivity and ecological resilience. Wang et al. (2024) demonstrated that understory enhance soil quality, orchard productivity, and improve the photosynthetic efficiency of main crops by promoting better vegetative growth compared to monoculture systems. In oil palm plantations, selected understory vegetation is often maintained to conserve soil moisture and reduce erosion. Awelewa et al. (2024) found that areas with understory showed significant improvements in soil physical, chemical, and biological properties, leading to increased oil yield. Furthermore, understory vegetation improves soil structure and strengthens ecosystem functioning and resilience (Thoumazeau et al., 2024).

Table 6 shows the stomatal conductance values for *A. gangetica* and *N. biserrata*. In general, stomatal conductance increased from measurements taken at 09:00 to those taken at 13:00. However, there were some months when it decreased. These differences are probably due to changes in light levels, air temperature, and humidity during the measurement period. Stomatal conductance is an important physiological factor that regulates gas exchange between the plant and the atmosphere. It affects both photosynthetic carbon uptake and transpiration.

Table 4

Correlation Value of Photosynthetic Rate, Stomatal Conductance, and Transpiration of Oil Palm

Parameter	Photosynthetic rate	Stomatal conductance	Transpiration
Photosynthetic rate	1		
Stomatal conductance	0.190 (p = 0.268)	1	
Transpiration	0.072 (p = 0.677)	0.775 (p = 0.000)*	1

Note. * = Significant.

Table 5

Photosynthetic Rate of Asystasia gangetica and Nephrolepis biserrata from February 2020 to March 2022 (µmol $CO_2/m^2/s$)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
A. gangetica						
09:00	26.35	41.65	29.34	31.93	29.21	30.42
13:00	20.71	31.09	25.04	28.76	31.96	28.55
Average	23.53	36.37	27.19	30.35	30.59	29.49
Standard deviation	3.99	7.47	3.04	2.24	1.94	1.32
N. biserrata						
09:00	24.43	39.60	26.99	27.56	28.21	30.50
13:00	26.19	23.38	25.43	26.45	30.03	29.45
Average	25.31	31.49	26.21	27.01	29.12	29.98
Standard deviation	1.24	11.47	1.10	0.78	1.29	0.74

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Table 6

Stomatal Conductance of A. gangetica and N. biserrata from February 2020 to March 2022 (mol $H_2O/m^2/s$)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
A. gangetica						
09:00	0.099	0.173	0.048	0.210	0.113	0.184
13:00	0.042	0.098	0.025	0.201	0.231	0.279
Average	0.071	0.136	0.037	0.206	0.172	0.232
Standard deviation	0.040	0.053	0.016	0.006	0.083	0.067
N. biserrata						
09:00	0.101	0.045	0.066	0.010	0.011	0.016
13:00	0.082	0.095	0.141	0.033	0.036	0.013
Average	0.092	0.070	0.104	0.022	0.024	0.015
Standard deviation	0.013	0.035	0.053	0.016	0.018	0.002

Low light intensity, elevated CO_2 concentrations, and moderate temperatures are characteristic conditions under mature plantation canopies. In several leguminous cover crop species, increased light intensity has been shown to significantly enhance net photosynthetic rates and associated physiological parameters, including SPAD index, stomatal conductance, transpiration rate, and vapor pressure deficit (VPD) (Baligar et al., 2020).

In addition to these physiological effects, understory contribute to improvements in soil organic carbon (SOC). Vendig et al. (2022) reported that higher SOC levels are associated with increased crop productivity. Sustainable agricultural practices such as the incorporation of organic matter, the use of understory, and soil conservation measures can enhance soil fertility over time. Qiu et al. (2024) further highlighted that understory improve soil health by reducing erosion, enhancing carbon sequestration, promoting nutrient cycling, increasing biodiversity, and reducing reliance on synthetic fertilizers.

Table 7 presents the transpiration rates of *Asystasia gangetica* and *Nephrolepis biserrata*. Measurements taken at 09:00 and 13:00 showed no statistically significant differences between the species; however, a general increase in transpiration rate from morning to midday was observed. This pattern is commonly associated with rising air temperature and solar radiation, which stimulate stomatal opening and enhance water vapor diffusion from the leaf surface.

Sadok et al. (2021) reported that elevated midday transpiration rates are largely driven by increased stomatal opening under high-temperature conditions. Similarly, Saputri et al. (2021) identified air temperature and solar radiation intensity as key environmental factors regulating plant transpiration. Although both species exhibited similar temporal patterns, no significant differences were detected in their transpiration rates. Transpiration is closely related to plant water use efficiency (WUE), reflecting the balance between carbon assimilation and water loss. Pilloni et al. (2022) noted that genotypes with higher transpiration capacity may allow greater light penetration into the leaves and experience a lower vapor pressure deficit within the leaf microenvironment compared to the surrounding air.

Leaf Greenness Levels

Figure 1 presents the measurements of oil palm leaf greenness in April and November 2021. The results indicate variation in leaf greenness among the observation blocks, with generally higher values recorded in November compared

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

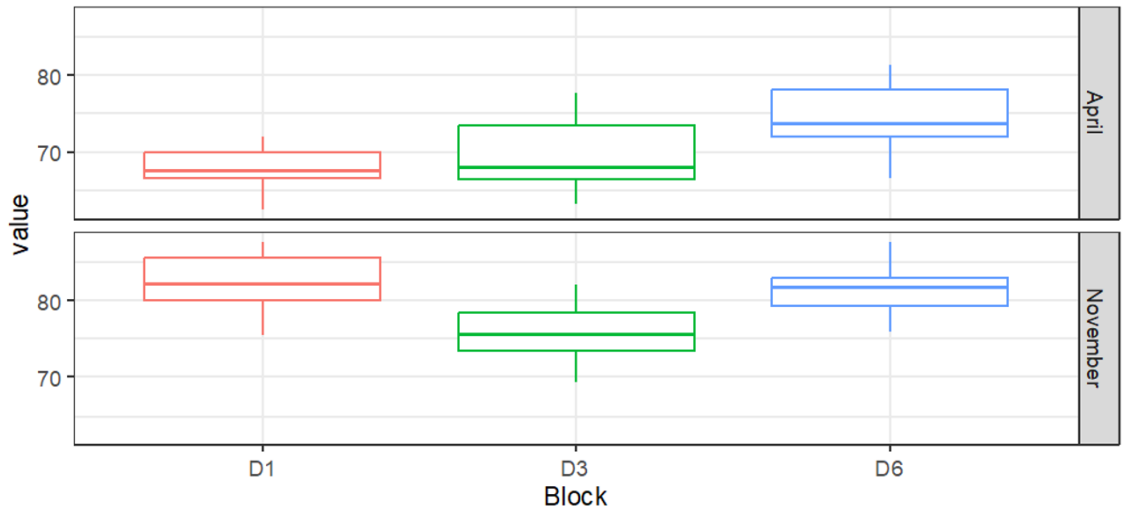
Table 7

Transpiration Rate of A. gangetica and N. biserrata from February 2020 to March 2022 (µmol H_2O/m^2/s)

Observation time	Feb 2020	Apr 2021	Jul 2021	Nov 2021	Jan 2022	Mar 2022
A. gangetica						
09:00	821.90	1,104.22	386.99	1,816.75	843.15	1,374.55
13:00	856.49	1,069.49	433.44	3,053.15	3,121.84	2,926.16
Average	839.20	1,086.85	410.21	2,434.95	1,982.50	2,150.36
Standard deviation	17.30	17.37	23.22	618.20	1,139.34	775.81
N. biserrata						
09:00	1,040.40	371.22	472.80	117.35	93.29	132.93
13:00	1,520.61	1,326.01	1,602.38	612.45	797.76	231.02
Average	1,280.51	848.62	1,037.59	364.90	445.53	181.97
Standard deviation	240.10	477.40	564.79	247.55	352.24	49.05

Figure 1

Greenness Levels of Oil Palm Leaves Recorded between April and November 2021



to April. This difference may be attributed to environmental changes, particularly variations in rainfall during the observation period.

Leaf greenness is commonly used as an indirect indicator of chlorophyll content and plant nutritional status, especially in relation to nitrogen availability. Higher chlorophyll concentrations are closely associated with improved nitrogen uptake and assimilation in plant tissues. The application of potassium nitrate (KNO_3) fertilizer has been reported to enhance leaf area development and chlorophyll content in oil palm seedlings, reflecting improved physiological performance (Usodri & Utoyo, 2021). Furthermore, leaf greenness measurements can serve as an effective diagnostic tool for assessing nitrogen status in oil palm leaves, facilitating early detection of nutrient deficiencies and supporting more efficient nutrient management strategies (Law et al., 2014).

Stomatal Density

Stomatal density was assessed in the three observation blocks, as depicted in Figure

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

2. Stomatal density denotes the number of stomata per unit area of the leaf surface (mm^2) and signifies a crucial anatomical characteristic linked to plant gas exchange, transpiration, and photosynthetic efficiency.

The results indicate that stomatal density did not differ substantially among the observation blocks. This suggests that environmental conditions and management practices across the blocks were relatively uniform and did not significantly influence stomatal development. Nevertheless, previous studies have shown that stomatal density in oil palm can be affected by nutrient availability and cultivation practices. For example, the application of swiftlet manure fertilizer to oil palm seedlings has been reported to increase stomatal density (Kristanto et al., 2022). In addition, stomatal development is closely associated with water availability. Oil palm plants grown under water-limited conditions tend to exhibit higher stomatal density than those in more humid environments (Panggabean et al., 2021). Loso et al. (2021) further reported that the combined application of biopore technology and complete fertilization significantly increased stomatal density in oil palm.

Rainfall Patterns

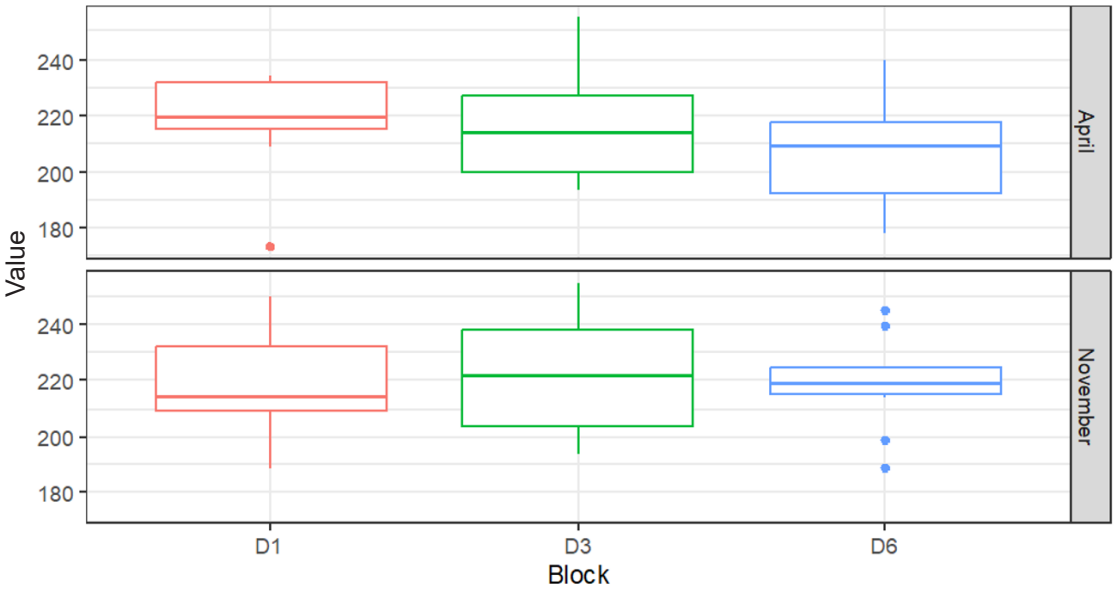
Figure 3 presents rainfall data from 2018 to 2022, showing considerable temporal variability throughout the year. Average rainfall was highest in March and October, while February and July recorded the lowest levels. This seasonal rainfall pattern is typical of tropical regions and can strongly influence hydrological dynamics in peatland ecosystems. Rainfall plays a crucial role in oil palm cultivation on peat soils, as it determines water availability and regulates water table levels. Because of the high water-holding capacity of peat soils, fluctuations in rainfall directly affect soil moisture and groundwater depth, which in turn influence plant growth and physiological processes.

Fresh Fruit Bunch (FFB) Production

The productivity of oil palm in the observation blocks was evaluated using the average fresh fruit bunch (FFB) yield, expressed in tonnes per hectare, as shown in Figure 4. Production data from 2020 to 2022 indicated monthly variations in yield, with the lowest recorded in February. Fluctuations in FFB yield are often associated with environmental and physiological factors,

Figure 2

Stomatal Density of Oil Palm Leaves Recorded between April and November 2021



Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

including rainfall distribution, water table depth, and plant physiological status. Insufficient rainfall or limited water availability can constrain photosynthesis and nutrient uptake, thereby reducing fruit development and overall yield.

Groundwater Levels

Figure 5 illustrates the groundwater levels in the observation blocks. Water table depth is a critical factor for oil palm cultivation on peatlands, as it influences root aeration, nutrient availability, and soil stability. Water table depths between 0 and −30 cm are generally unfavorable for oil palm growth because excessive water can lead to poor root anchorage and oxygen deficiency, resulting in root stress and reduced productivity. In contrast, groundwater levels between −30 and −60 cm are considered optimal for oil palm cultivation on peatlands, as they

Figure 3

Rainfall in 2018-2022 at the Study Location

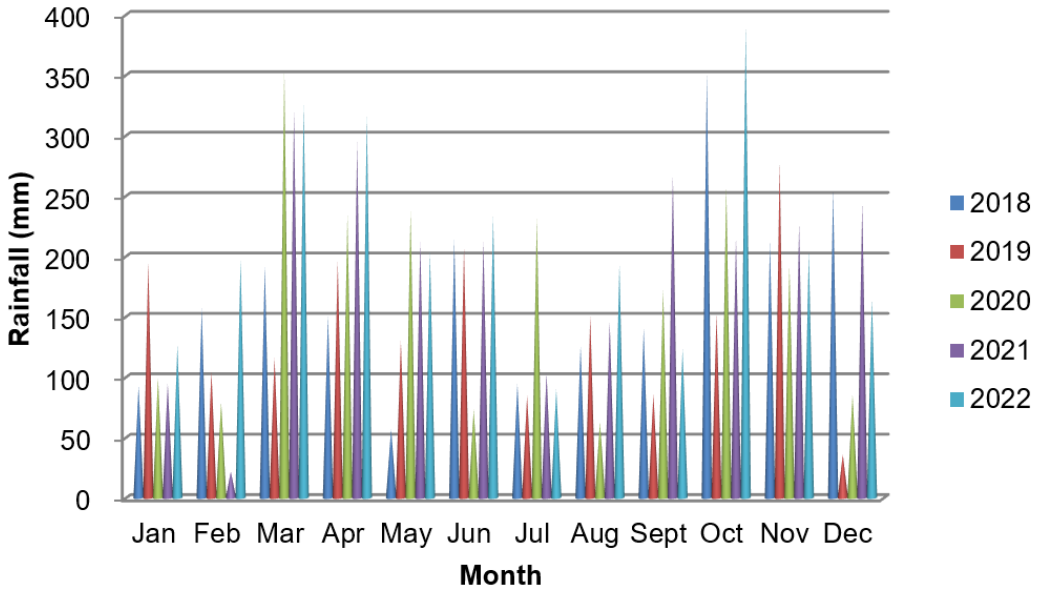
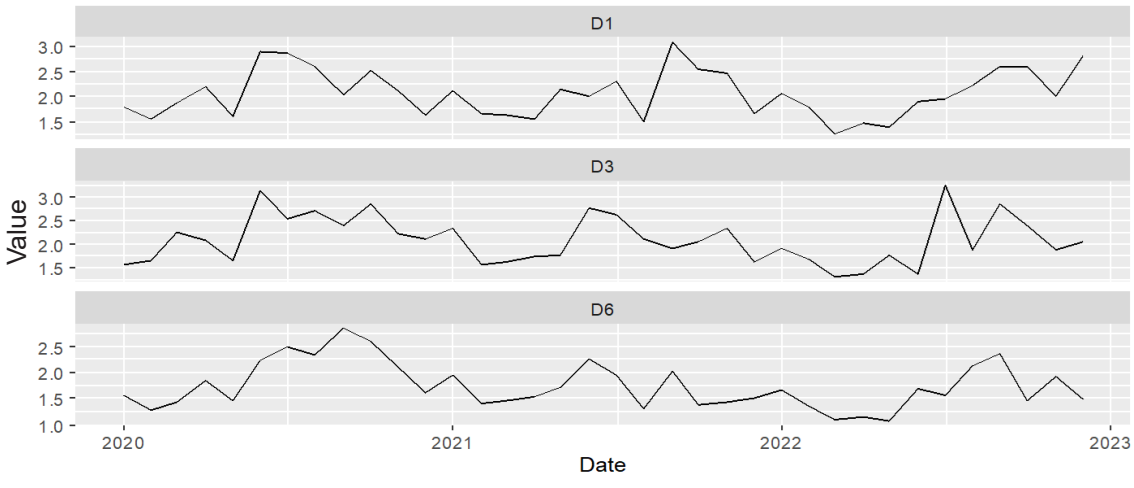


Figure 4

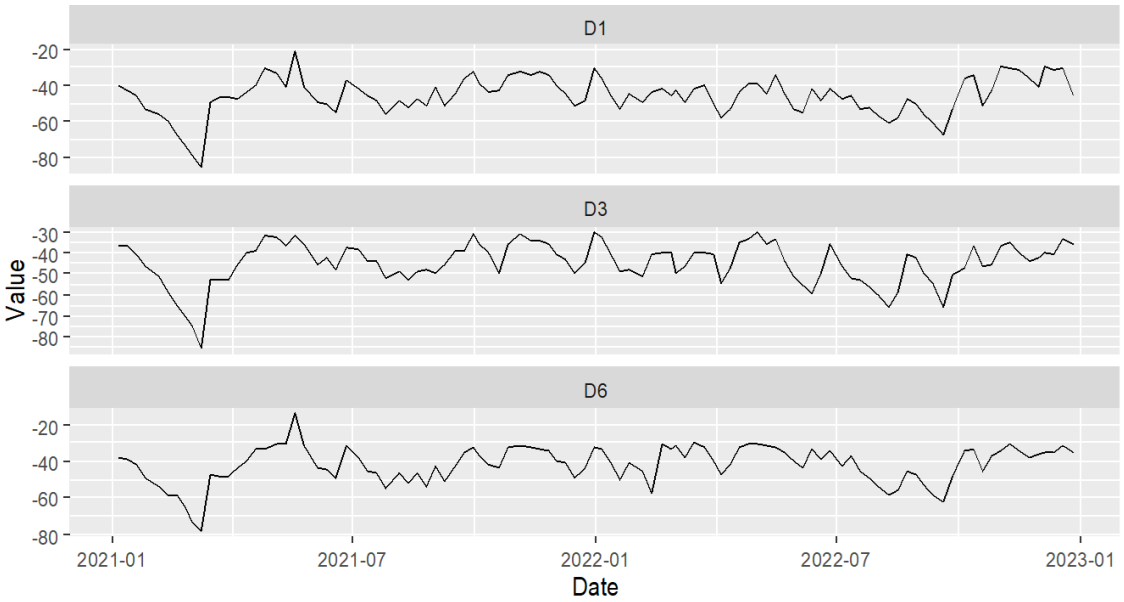
Production of Fresh Fruit Bunch (FFB) in the Observation Block for the Period 2020-2022 (Tons per Hectare)



Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Figure 5

Water Table Level (cm) for Each Observation Block at the Study Site in the Years 2021-2022



maintain adequate soil moisture while ensuring sufficient root aeration. Therefore, maintaining an appropriate groundwater level is essential for effective water management in oil palm plantations on peatlands, as it supports plant growth, maximizes productivity, and reduces the risk of waterlogging.

Conclusions

This research quantified the gas-exchange characteristics of mature oil palm leaves and understory vegetation within a drained tropical peatland plantation. The findings indicated that the average photosynthetic rate of oil palm varied from 18.44 to 43.47 µmol $CO_2/m^2/s$, with corresponding stomatal conductance values ranging from 0.050 to 0.067 mol $H_2O/m^2/s$ and transpiration rates between 577.83 and 1,189.31 µmol $H_2O/m^2/s$ during the observation periods. The correlation analysis showed that stomatal conductance was strongly linked to transpiration ($r = 0.775$, $p < 0.001$). On the other hand, the relationships between photosynthetic rate and the other physiological variables were weak and not statistically significant. The understory species *Asystasia gangetica* and *Nephrolepis biserrata* showed active photosynthesis, with mean photosynthetic rates of 25.31 to 31.49 µmol $CO_2/m^2/s$ and 23.53 to 36.37 µmol $CO_2/m^2/s$, respectively. These findings demonstrate that both oil palm and understory vegetation exhibit quantifiable photosynthetic activity within the canopy environment of mature plantations situated on peat soils. The study provides field-derived physiological data that elucidate the diurnal gas-exchange dynamics of oil palm and understory plants in drained peatland plantations. The study focuses on leaf physiological processes and does not measure peat-derived CO_2 emissions or the ecosystem-level carbon balance.

Acknowledgement

The authors thank the Palm Oil Plantation Fund Management Agency (BPDPKS) for funding this research. We also thank PT Astra Agro Lestari Tbk. for granting permission to conduct research in the plantation.

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

References

Andesmora, E. V., Hamim, H., Sulistijorini, S., & Triadiati, T. (2025). Diversity of oil palm seedlings from Jambi accessions exhibits different physiological responses during waterlogging. *Jurnal Ilmu Pertanian Indonesia, 30*(1), 55–63. https://doi.org/10.18343/jipi.30.1.55

Awelewa, E. A., Umunnakwe, O. C., Effa, E. B., Ebri, B. O., Bisong, O. B., & Ekpenyoung, I. E. (2024). Effect of cover crops on soil properties and oil yield of oil palm (*Elaeis guineensis* L) grown on utisol of Southern Nigeria. Direct Research *Journal of Agriculture and Food Science, 12*(3), 103–109. https://doi.org/10.26765/DRJAFS65733477

Baligar, V. C., Elson, M. K., He, Z., Li, Y., De, A., Almeida, A. A. F., & Ahnert, D. (2020). Light intensity effects on the growth, physiological, and nutritional parameters of tropical perennial legume cover crops. *Agronomy, 10*(10), 1–15. https://doi.org/10.3390/agronomy10101515

Brum, M., Oliveira, R. S., López, J. G., Licata, J., Pypker, T., Chia, G. S., Tinôco, R. S., & Asbjornsen, H. (2021). Effects of irrigation on oil palm transpiration during ENSO-induced drought in the Brazilian Eastern Amazon. *Agricultural Water Management, 245*, 106569. https://doi.org/10.1016/j.agwat.2020.106569

Cook, S., Whelan, M. J., Evans, C. D., Gauci, V., Peacock, M., Garnett, M. H., Kho, L. K., Teh, Y. A., & Page, S. E. (2018). Fluvial organic carbon fluxes from oil palm plantations on tropical peatlands. *Biogeosciences, 15*(24), 7435–7450. https://doi.org/10.5194/bg-15-7435-2018

Deshmukh, C. S., Desai, A. R., Asyhari, A., Page, S. E., Nardi, N., Susanto, A. P., Nurholis, N., Hendrizal, M., Kurnianto, S., Suardiwerianto, Y., Agus, F., Astiani, D., Sabiham, S., Gauci, V., & Evans, C. (2021). Conservation of tropical peatlands provides avoided emissions but may not provide CO_2 sequestration [Conference presentation]. AGU Fall Meeting 2021, New Orleans, LA, United States.

Dusenge, M. E., Duarte, A. G., & Way, D. A. (2019). Plant carbon metabolism and climate change : Elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist, 221*, 32–49. https://doi.org/10.1111/nph.15283

Filho, W. R. L. L., Rodrigues, F. H. S., Chaves, R. P. F., Cunha, R. L., Costa, L. C., & Pinheiro, H. A. (2024). Repeated water deficit events trigger adjustments in the enzymatic antioxidant system in oil palm. *Theoretical and Experimental Plant Physiology, 36*, 235–250. https://doi.org/10.1007/s40626-024-00316-5

Food and Agriculture Organization. (2025). *Crops and livestock products*. https://www.fao.org/faostat/en/#data/QCL

Hooijer, A., Page, S. E., Jauhiainen, J., Lee, W., Lu, X., Idris, A., & Anshari, G. (2012). Subsidence and carbon loss in drained tropical peatlands. *Biogeosciences, 9*, 1053–1071. https://doi.org/10.5194/bg-9-1053-2012

Huang, X., Liu, X., Chen, L., Wang, Y., & Chen, H. (2022). Iron-bound organic carbon dynamics in peatland profiles : The preservation equivalence of deep and surface soil. *Fundamental Research, 3*, 852-860. https://doi.org/10.1016/j.fmre.2022.09.026

Ibrahim, M. H., Nulit, R., Wahab, P. E. M., Najihah, T. S., Razak, A., & Zain, N. A. M. (2018). Impacts of elevated CO_2 on growth, carbohydrate assimilation and nutrient uptake of Elaeis guineensis Jacq seedlings. *Annual Research & Review in Biology, 27*, 1–9. https://doi.org/10.9734/ARRB/2018/42001

Kristanto, A. S., Anggoro, R., Yama, D. I., Fakhrudin, J., & Ali, M. (2022). Respon morfofisiologi tanaman kelapa sawit pre-nursery pada pemberian kompos kotoran walet dan bakteri *Synechococcus* sp. *Jurnal Agroekoteknologi, 14*(2), 182–195. https://doi.org/10.33512/jur.agroekotetek.

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

v14i2.17197

Law, C. C., Zaharah, A. R., Husni, M. H. A., & Akmar, A. S. N. (2014). Leaf nitrogen content in oil palm seedlings and their relationship to SPAD chlorophyll meter readings. *Journal of Oil Palm, Environment & Health, 5*, 8–17. https://doi.org/10.5366/jope.2014.02

Loso, S., Sudradjat, Hariyadi, Yahya, S., & Sutandi, A. (2021). The role of several methods of drainage and fertilization levels on the growth and yield of oil palm plants (*Elaeis guineensis* Jacq.). *Asian Journal of Microbiology, Biotechnology and Environmental Sciences, 23*(1), 51–60.

Lourenco, M., Woodborne, S., & Fitchett, J. M. (2023). Fire regime of peatlands in the Angolan Highlands. *Environmental Monitoring and Assessment, 195*(78). https://doi.org/10.1007/s10661-022-10704-6

Ma, L., Zhu, G., Chen, B., Zhang, K., Niu, S., Wang, J., Ciais, P., & Zuo, H. (2022). A globally robust relationship between water table decline, subsidence rate, and carbon release from peatlands. *Communications Earth & Environment, 3*(254), 1–14. https://doi.org/10.1038/s43247-022-00590-8

Middleby, K. B., Cheesman, A. W., & Cernusak, L. A. (2024). Impacts of elevated temperature and vapor pressure deficit on leaf gas exchange and plant growth across six tropical rainforest tree species. *New Phytologist, 243*(2), 648–661. https://doi.org/10.1111/nph.19822

Miller, M. A., Tonoto, P., & Taylor, D. (2022). Sustainable development of carbon sinks? Lessons from three types of peatland partnerships in Indonesia. *Sustainable Development, 30*(1), 241–255. https://doi.org/10.1002/sd.2241

Novita, N., Asyhari, A., Ritonga, R. P., Gangga, A., Anshari, G. Z., Jupesta, J., Bowen, J. C., Lestari, N. S., Kauffman, J. B., Hoyt, A. M., Perryman, C. R., Albar, I., Putra, C. A. S., Adinugroho, W. C., Winarno, B., Castro, M., Yeo, S., Budiarna, T., Yuono, E., & Sianipar, V. C. (2024). Strong climate mitigation potential of rewetting oil palm plantations on tropical peatlands. *Science of The Total Environment, 952*, 175829. https://doi.org/10.1016/j.scitotenv.2024.175829

Panggabean, N. H., Nurwahyuni, I., & Djamaan, E. (2021). Response of oil palm plant growth (*Elaeis guineensis* Jacq.) to aluminium stress. *IOP Conference Series: Materials Science and Engineering, 1156*(1), 12017. https://doi.org/10.1088/1757-899X/1156/1/012017

Pilloni, R., Aparna, K., El Ghazzal, Z., Kar, S., Kumar, A. A., Hajjarpoor, A., Affortit, P., Kholova, J., Ribière, W., Tardieu, F., & Vadez, V. (2022). Transpiration and water use efficiency of sorghum canopies have a large genetic variability and are positively related under naturally high evaporative demand. *bioRxiv, 50884*, 1–29. https://doi.org/10.1101/2022.09.21.508841

Pradiko, I., Rahutomo, S., Farrasati, R., Ginting, E. N., Hidayat, F., & Syarovy, M. (2023). Transpiration of oil palm (*Elaeis guineensis* Jacq.) based on sap flow measurement: the relation to soil and climate variables. *Journal of Oil Palm Research, 35*(1), 168–184. https://doi.org/10.21894/jopr.2022.0035

Qiu, T., Shi, Y., Peñuelas, J., Liu, J., Cui, Q., Sardans, J., Zhou, F., Xia, L., Yan, W., Zhao, S., Peng, S., Jian, J., He, Q., Zhang, W., Huang, M., Tan, W., & Fang, L. (2024). Optimizing cover crop practices as a sustainable solution for global agroecosystem services. *Nature Communications, 15*(10617), 1-14. https://doi.org/10.1038/s41467-024-54536-z

Sabiham, S. (2020). Faktor emisi lahan gambut Indonesia yang didrainase untuk budidaya kelapa sawit. In *Grant riset sawit* 2020 (pp. 35–36). Badan Pengelola Dana Perkebunan Kelapa Sawit.

Sadok, W., Lopez, J. R., & Smith, K. P. (2021). Transpiration increases under high-temperature stress: Potential mechanisms, trade-offs and prospects for crop resilience in a warming world. *Plant Cell and*

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

Environment, 44(7), 2102–2116. https://doi.org/10.1111/pce.13970

Saputri, J. Y., Prijono, S., & Prasetya, B. (2021). Robusta coffee transpiration rate in smallholder coffee plantations on Inceptisols of Malang, East Java. *Journal of Degraded and Mining Lands Management, 9*(1), 3165–3173. https://doi.org/10.15243/jdmlm.2021.091.3165

Scandolera, T., Teano, G., Naderpour, M., Geffroy, V., & Pflieger, S. (2024). Insights into the effects of elevated atmospheric carbon dioxide on plant-virus interactions: A literature review. *Environmental and Experimental Botany, 221*,105737. https://doi.org/10.1016/j.envexpbot.2024.105737

Shapira, O., Hochberg, U., Joseph, A., McAdam, S., Azoulay-Shemer, T., Brodersen, C. R., Holbrook, N. M., & Zait, Y. (2024). Wind speed affects the rate and kinetics of stomatal conductance. *Plant Journal, 120*(4), 1552–1562. https://doi.org/10.1111/tpj.17066

Sharkey, T. D. (2024). The end game(s) of photosynthetic carbon metabolism. *Plant Physiology, 195*(1), 67–78. https://doi.org/10.1093/plphys/kiad601

Sidik, R. M. (2018). *CPO Indonesia ditolak Uni Eropa, Kenapa?* https://igj.or.id/wp-content/uploads/2018/04/CPO-Indonesia-ditolak-Uni-Eropa_Palm-Oil-Issues.pdf

Stuart, J. E. M., Tucker, C. L., Lilleskov, E. A., Kolka, R. K., Chimner, R. A., Heckman, K. A., & Kane, E. S. (2022). Evidence for older carbon loss with lowered water tables and changing plant functional groups in peatlands. *Global Change Biology, 29*(3), 780–793. https://doi.org/10.1111/gcb.16508

Sulaiman, A., Arriyadi, D., Darusman, T., Irfan, M., Ajie, G. S., Anggono, T., Witono, A., Yan, S., Febriani, F., Dewi, C. N., & Prasetio, A. D. (2022). Analytical modeling of groundwater level dynamics of tropical peatland drainage (Katingan Mentaya project area). *AIP Conference Proceedings, 2652*(030007). https://doi.org/10.1063/5.0106453

Susanto, A., Prasetyo, A. E., Priwiratama, H., & Syarovi, M. (2020). Laju fotosintesis pada tanaman kelapa sawit terinfeksi karat daun *Cephaleuros virescens*. *Jurnal Fitopatologi Indonesia, 16*(1), 21–29. https://doi.org/10.14692/jfi.16.1.21-29

Swails, E., Hertanti, D., Hergoualc'h, K., Verchot, L., & Lawrence, D. (2018). The response of soil respiration to climatic drivers in undrained forest and drained oil palm plantations in an Indonesian peatland. *Biogeochemistry, October 2018*. https://doi.org/10.1007/s10533-018-0519-x

Thoumazeau, A., Mettauer, R., Turinah, Junedi, H., Baron, V., Chéron-Bessou, C., & Ollivier, J. (2024). Effects of fertilization practices and understory on soil health and oil palm performances in smallholdings: An Indonesian case study. *Agricultural Systems, 213*, 103802. https://doi.org/10.1016/j.agsy.2023.103802

Tosens, T., Alboresi, A., van Amerongen, H., Bassi, R., Busch, F. A., Consoli, G., Ebenhöh, O., Flexas, J., Harbinson, J., Jahns, P., Kamennaya, N., Kramer, D. M., Kromdijk, J., Lawson, T., Murchie, E. H., Niinemets, Ü., Natale, S., Nürnberg, D. J., Persello, A., … Weber, A. P. M. (2025). New avenues in photosynthesis: From light harvesting to global modeling. *Physiologia Plantarum, 177*(2). https://doi.org/10.1111/ppl.70198

Uning, R., Latif, M. T., Othman, M., & Juneng, L. (2020). A review of Southeast Asian oil palm and its CO_2 fluxes. *Sustainability, 12*, 5077, 1–15. https://doi.org/10.3390/su12125077

Urzainki, I., Palviainen, M., Hökkä, H., Persch, S., Chatellier, J., Wang, O., Mahardhitama, P., Yudhista, R., & Laurén, A. A. (2022). A process-based model for quantifying the effects of canal blocking on water table and CO_2 emissions in restored tropical peatlands. *Biogeosciences Discussions, 20*, 1–30. https://doi.org/10.5194/bg-2022-218

Usodri, K. S., & Utoyo, B. (2021). Pengaruh penggunaan KNO_3 pada pertumbuhan

Received 8/27/2025; Revised 7/13/2026; Accepted 10/26/2026
https://doi.org/10.29244/jtcs.13.03.757-772

bibit kelapa sawit (*Elaeis guineensis* Jacq.) fase pre-nursery. *Jurnal Agrinika, 5*(1), 1–9. https://doi.org/10.30737/agrinika.v5i1.1521

Vendig, I., Guzman, A., Cerda, G. D. La, Esquivel, K., Mayer, A., Ponisio, L., & Bowles, T. M. (2022). Direct yield benefits of soil carbon increases in low-carbon soils: A global meta-analysis of cover cropping co-benefits. *Nature Sustainability, December 1, 1-20*. https://doi.org/10.21203/rs.3.rs-1848483/v1

Wang, F., Zhu, L., He, J., Nan, X., Chen, H., Yang, L., Jia, Q., Yu, Z., Wang, H., Zhao, Y., & Yan, H. (2024). Selecting appropriate forage cover crops to improve growth, yield, and fruit quality of wolfberry by regulating photosynthesis and biotic stress resistance. *Scientia Horticulturae, 337*, 113470. https://doi.org/10.1016/j.scienta.2024.113470