



Water Use Efficiency and Adaptive Responses of Oil Palm under El Niño-Induced Drought and Haze

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ABSTRACT

Oil palm plays an important role in the tropical carbon cycle but is highly sensitive to climatic variability. Understanding the coupled dynamics of carbon and water fluxes in such ecosystems essential for sustainable management under variable climatic conditions. This study analyses the Water Use Efficiency (WUE) and coupled carbon–water fluxes of an 18-year-old oil palm plantation in Jambi, Indonesia, during the 2015 El Niño event using data from an eddy covariance flux tower. The analysis focused on the diurnal variations of Net Ecosystem Production (NEP), evapotranspiration (ET), and water use efficiency (WUE) during wet, dry, and dry with haze periods, which were determined based on rainfall data. Our results show that WUE reached its highest value during the dry-with-haze period (7,484 g CO₂ kg⁻¹ H₂O), more than double that of the wet (3,440) and dry (3,347) periods. This increase resulted from reduced evapotranspiration (ET) due to stomatal regulation, despite lower Net Ecosystem Production (NEP) caused by light limitation from haze. Diurnal analyses showed WUE peaking in the morning and declining at midday as the Vapor Pressure Deficit (VPD) increased (up to 0.88 kPa under haze). These findings highlight oil palm's adaptive strategy to conserve water under stress while maintaining productivity. However, severe haze markedly weakens carbon sequestration. The results provide critical insights for optimizing irrigation and water management in the face of increasing climate variability.

KEYWORDS

evapotranspiration, net ecosystem production, oil palm, vapor pressure deficit, water use efficiency

1. INTRODUCTION

Water Use Efficiency (WUE) is a critical indicator of ecosystem productivity that links the carbon and water cycles, reflecting how efficiently plants utilize water to produce biomass (Zhou et al., 2020). This metric is particularly crucial for economically important crops like oil palm (*Elaeis guensis*), which are cultivated extensively in tropical regions often subject to significant climatic variability. Under conditions of water scarcity, plant growth and development can be disrupted as a result of an imbalance in the water balance (June et al., 2018a). As rainfall decreases, WUE typically declines due to a reduction in stomatal conductance, which limits transpiration more effectively than it limits CO₂

assimilation (Niu et al., 2011). At the physiological level, plants employ several strategies to cope with water stress, with a key mechanism being stomatal regulation to reduce water loss through transpiration (Osakabe et al., 2014). While this strategy conserves water, it also restricts CO₂ uptake, thereby affecting photosynthesis. Despite this trade-off, plants with more efficient water use can often maintain growth by optimizing their photosynthetic capacity relative to water availability (Lawson and Blatt, 2014).

At the ecosystem level, this relationship is often quantified by the ratio of Net Ecosystem Production (NEP) to evapotranspiration (ET). During periods of water stress, NEP often decreases due to the combined

effects of reduced photosynthesis and increased respiration (Cui et al., 2020). However, ecosystems with high WUE may sustain positive NEP by efficiently utilizing available water (El Masri et al., 2019). Despite the fundamental importance of these processes, a significant research gap exists concerning the in-situ WUE mechanisms of mature oil palm plantations, especially under the dual stress of drought and atmospheric haze, a recurring phenomenon in Southeast Asia. While the influence of various environmental drivers, such as vapor pressure deficit (VPD), photosynthetically active radiation (PAR), and soil moisture on WUE is known (Hinojo-Hinojo et al., 2016; Zhang et al., 2017), their integrated effect on oil palm remains less understood. The continuous, high-frequency measurements provided by the Eddy Covariance (EC) method offer a powerful tool to investigate these complex interactions and their variations at the ecosystem level (June et al., 2018b; Lin et al., 2019; Ma et al., 2019).

Therefore, this study aims to fill this knowledge gap by investigating the diurnal and seasonal dynamics of WUE in a mature oil palm plantation in Jambi, Indonesia. The primary objective is to analyze the response mechanisms of oil palm to water scarcity and atmospheric haze by quantifying and comparing Net Ecosystem Production (NEP), evapotranspiration (ET), and Water Use Efficiency (WUE) across distinct wet, dry, and dry with haze periods during the year 2015. By examining these coupled fluxes in relation to key environmental drivers, this research seeks to elucidate the adaptive strategies of oil palm to environmental stress and provide critical insights for improving water management and productivity in the face of future climate variability.

2. MATERIALS AND METHODS

2.1 Study Area

This study utilized data from the year 2015 as a representative of El-Nino period. The research site was conducted in oil palm plantation managed by PT Perkebunan Nusantara (PTPN) VI in Batanghari, Jambi, located between 01°40'30"–01°45'00" S and 103°22'30"–103°25'30" E, covering a total area of 2,186 hectares (Figure 1). The land cover is dominated by an 18-year-old oil palm stand with an average canopy height of approximately 14.8 meters (Meijide et al., 2017). A micrometeorological flux tower, used for data recording, is situated within plot 23 at coordinates 1°41'35" S and 103°23'29" E. This site located in lowland region with average elevation below 500 meter above sea level (asl) and annual rainfall approximately 2500 mm (Lisnawati et al., 2022), which is ~20% lower than annual rainfall of Sumatra (Hidayat et al., 2025).

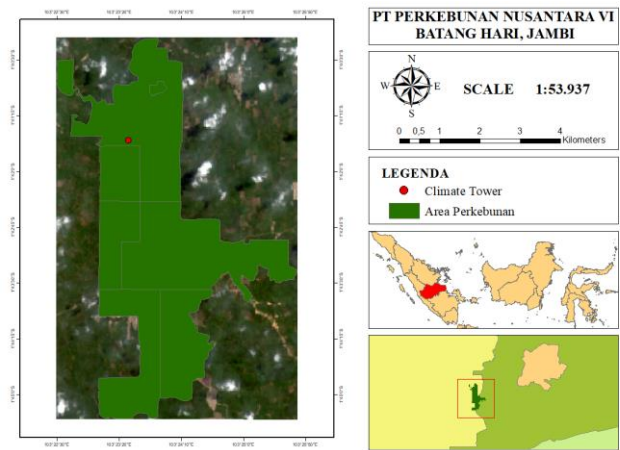


Figure 1 Map of the study area

2.2 Tools and Data Collection

We performed our analysis using Microsoft Office 2019, OriginPro 2024, and MiniTab 19 software for statistical data processing. The data utilized in the study comprised CO₂ flux data, evapotranspiration (ET) data, and climate data obtained from a climate tower equipped with an Eddy Covariance System (CRC990-EFForTS Project) located at PTPN VI, Batanghari, Jambi. A detailed summary of climate data variables is presented in Table 1.

Table 1 Summary of climatic and flux variables used

Data	Unit of Measurement	Data Source
Rainfall	mm	Climate tower PTPN VI Batanghari, Jambi
Solar Radiation	Watt/m ²	
Photosynthetically Active Radiation (PAR)	μmol/m ² /s	
Air Temperature	°C	
Air Humidity	%	
CO ₂ Flux	μmol/m ² /s	
Evapotranspiration data using the Eddy Covariance method	μmol/m ² /s	

2.3 Data Analysis

The data analysis procedure was divided into five main stages: (1) determination of wet and dry periods based on rainfall data and other climatic parameters, (2) CO₂ flux data analysis, (3) evapotranspiration (ET) data analysis, (4) water use efficiency (WUE) calculations and (5) estimation of Vapor Pressure Deficit (VPD). Also, climate variables, including solar radiation, air temperature, and relative humidity, were also utilized to determine seasonal periods. WUE was calculated using NEE and ET data, while VPD was derived from air temperature and relative humidity data.

2.3.1 Determination of Wet and Dry Periods

The wet and dry periods for the year 2015 were delineated based on the Schmidt-Ferguson climate classification method, using monthly rainfall data (Schmidt & Ferguson, 1951). A month was classified as a wet period if rainfall exceeded 100 mm and as a dry period if rainfall was below 60 mm. Months with rainfall between 60 and 100 mm were categorized as 'moist' periods and were excluded from the primary comparative analysis to ensure a distinct contrast between the selected conditions. To validate this classification and further characterize the contrasting environmental conditions-other meteorological parameters including solar radiation, air temperature, and air humidity-were graphically analyzed. This approach confirmed that the identified wet and dry periods were not only distinct in terms of precipitation but also exhibited consistent differences in other key climatic drivers.

2.3.2 CO₂ Flux Data Analysis

CO₂ flux was calculated using the Eddy Covariance System, which involves a sonic anemometer and infrared gas analyzers to simultaneously measure water vapor and CO₂ fluxes. Therefore, the CO₂ flux value calculated using the Eddy Covariance method can be determined using the Equation 1 below (Burba and Anderson, 2010).

$$F_c = \overline{\rho w'c'} \quad (1)$$

Where, F_c is carbon flux representing the NEP value (mg m⁻¹), $\overline{w'}$ is mean deviation of the vertical wind component (m s⁻¹), $\overline{\rho'}$ is mean deviation of carbon density (mg m⁻³).

2.3.3 Evapotranspiration (ET)

ET was derived from the latent heat flux (LE) measured by the eddy covariance system. ET was calculated using the idem equation (Wang et al., 2021).

$$ET = \lambda \rho \alpha \overline{w'q'} \quad (2)$$

Where, λ is latent heat of water vaporization (J kg⁻¹), ρ is air density (kg m⁻³), $\overline{w'q'}$ is covariance between turbulent fluctuations of vertical wind speed (m s⁻¹).

2.3.4 Water Use Efficiency (WUE)

The analysis was restricted to daytime hours, as this is the period when CO₂ uptake and transpiration are the dominant and tightly linked physiological processes. WUE can be calculated as the ratio between NEP and ET, or as the ratio between biomass growth and water consumption by plants (Wang et al., 2021).

$$WUE = \frac{NEP}{ET} \text{ (g CO}_2 \text{ kg}^{-1} \text{ H}_2\text{O)} \quad (3)$$

Where, NEP is Net Ecosystem Production (μmol/m²/s), ET is Evapotranspiration (mmol/m²/s)

2.3.5 Vapor Pressure Deficit (VPD) Calculation

The VPD was calculated using the standard methodology outlined by (Allen et al., 1998), which requires air temperature and relative humidity data. The governing equations are idem, as shown below:

$$VPD = e_s - e_a \quad (4)$$

$$e_s = 0,61078 \exp ((17,27 T)/(T+237,3)) \quad (5)$$

$$e_a = \frac{RH e_s}{100} \quad (6)$$

Where, VPD is vapor pressure deficit in the atmosphere (kPa), e_s is saturated vapor pressure in the atmosphere (kPa), e_a is actual vapor pressure in the atmosphere (kPa), RH is relative humidity (%), T is air temperature (°C).

3. RESULTS AND DISCUSSION

The classification of distinct climatic periods for the year 2015 was based on the monthly rainfall data recorded at PTPN VI Batanghari, Jambi. According to the Schmidt-Ferguson classification, a wet month is defined by rainfall exceeding 100 mm, and a dry month by rainfall below 60 mm. The year 2015 was marked by a strong El Niño event which intensified by positive IOD (Hidayat et al., 2025), resulting in a relatively low total annual rainfall of 1853.3 mm and a severe drought that led to widespread land fires and thick smoke haze from mid-September to early November (Stiegler et al., 2019). This haze significantly reduced incoming solar radiation, thereby affecting CO₂ uptake, photosynthesis and evapotranspiration (Kii et al., 2020; Stiegler et al., 2019). For a detailed comparative analysis based on these conditions, three representative months were selected: April was chosen to represent the wet period due to its very high rainfall (299.1 mm) following a sustained period of high precipitation; August was selected for the dry period, characterized by very low rainfall (25.1 mm) within a prolonged dry spell; and October was selected to represent the dry period with haze, as it fell squarely within the severe smoke haze event and experienced low rainfall (95.3 mm).

Analysis of the diurnal data revealed a remarkably strong and statistically significant linear correlation between Net Ecosystem Production (NEP) and Evapotranspiration (ET) across all observed periods (Figure 3), which encompassed wet (April 2015), dry (August 2015), and transitional (October 2015) seasonal conditions. Generally, a close coupling between NEP and ET is expected, as stomatal conductance simultaneously regulates both water vapor release and CO₂ uptake.

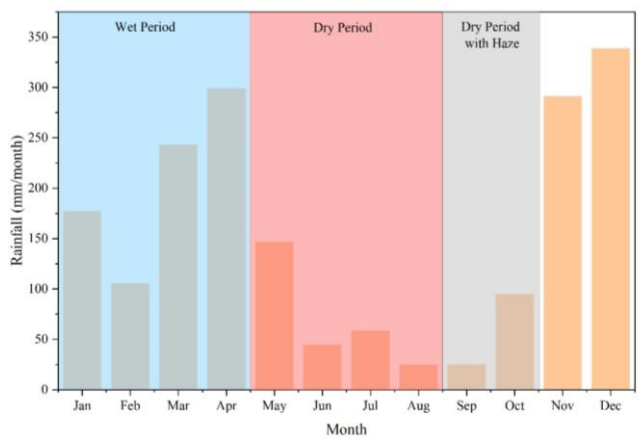


Figure 2 Monthly rainfall pattern at PTPN VI Batanghari, Jambi in 2015

However, the strength of this coupling is highly dependent on environmental conditions, particularly water availability.

The strength of this relationship is evidenced by the high coefficients of determination (R^2). In April 2015, representing the wet season, the R^2 value was 0.935. This value slightly decreased to 0.909 during the dry season in August 2015. Interestingly, the relationship strengthened significantly in October 2015, with an R^2 value of 0.960. This fluctuation in the R^2 value provides insight into the ecosystem's response to varying levels of stress. The slight decrease during the dry period (August) might suggest that under moderate water stress, the relationship could be influenced by other factors, such as changes in the contribution of soil evaporation to the total ET (Aulia et al., 2022). Conversely, the very tight correlation during the dry with haze period (October) likely reflects a condition where stomatal control becomes the overwhelmingly

dominant factor regulating both fluxes. This tight coupling is fundamentally governed by plant physiological mechanisms, primarily stomatal conductance (Meijide et al., 2017). Under such extreme stress, the plant's response becomes highly constrained, forcing a nearly perfectly proportional decline in both carbon gain and water loss, thereby strengthening their statistical relationship (Meza et al., 2018). The strength of this linear relationship is further affirmed by the Pearson correlation coefficients (r), which were proximate to 1.0 in each period: 0.967 in April, 0.953 in August, and 0.980 in October.

Although the correlation between ET and NEP remained strong across all seasons, the data show a clear reduction in the absolute values of both variables during the transition from wet to drier conditions. During the wet season, the ranges of ET and NEP were at their maximum, with ET values reaching approximately 6 mmol/m²/s and NEP peaking above 25 μmol/m²/s. In the dry period, a contraction in these ranges was observed. This reduction was even more pronounced in October, where ET values only reached approximately 2 mmol/m²/s and NEP remained below 15 μmol/m²/s. This reduction is an ecosystem-level response to decreasing water availability. During drier periods, plants typically reduce stomatal aperture to conserve water and mitigate drought stress (Stiegler et al., 2019). This water-conservation strategy directly limits the rate of transpiration (a major component of ET) and, as a consequence, concurrently reduces the rate of CO₂ uptake for photosynthesis (Kiew et al., 2020). Therefore, while the ratio between carbon gain and water loss remains largely proportional, the total magnitude of both fluxes diminishes significantly as water becomes less available.

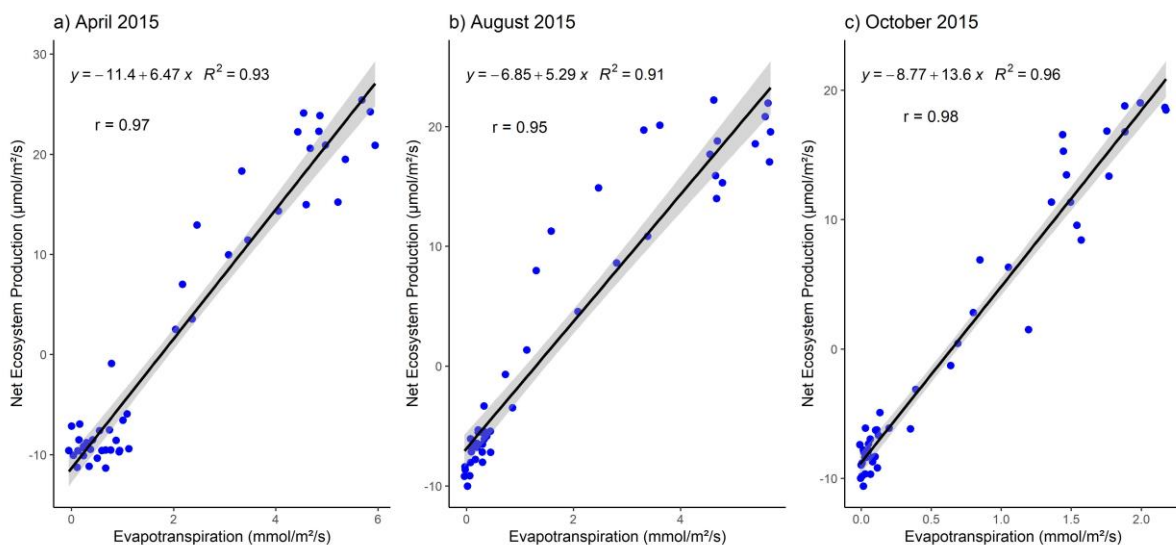


Figure 3 Diurnal relationship between Net Ecosystem Production (NEP) and Evapotranspiration (ET) during the (a) wet, (b) dry, and (c) dry with haze periods

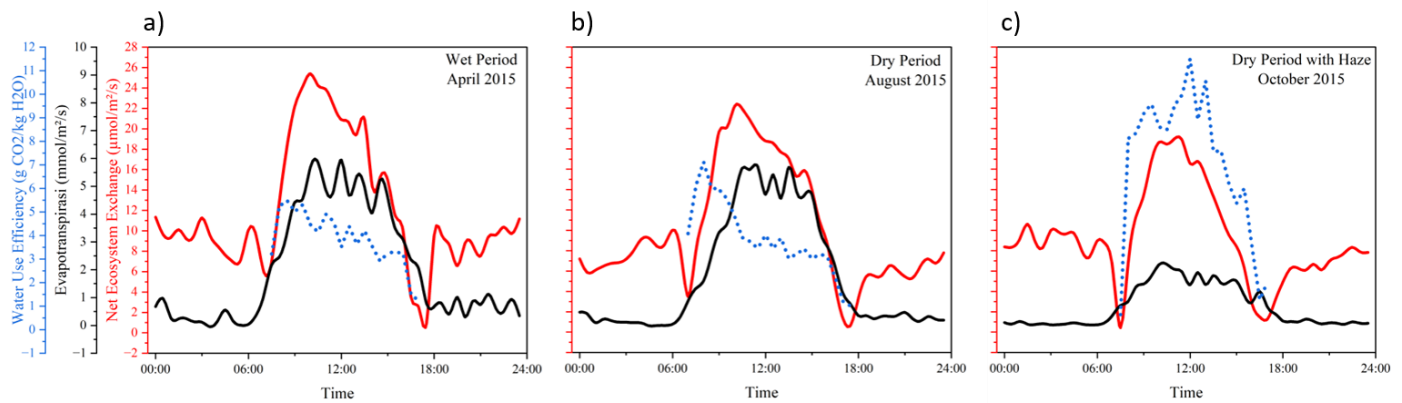


Figure 4 Diurnal variations in Net Ecosystem Production (NEP), Evapotranspiration (ET), and Water Use Efficiency (WUE) during the (a) wet, (b) dry, and (c) dry with haze periods

In this study, WUE showed a clear diurnal pattern, with higher values observed in the morning and a decline during midday under elevated vapor pressure deficit (VPD). This indicates that stomatal regulation played a key role in balancing carbon assimilation and water loss. Similar diurnal dynamics of WUE were also reported by (Meijide et al., 2017). As highlighted by (Lin et al., 2019), understanding such diurnal variability is essential for optimizing irrigation strategies and improving predictions of plant water consumption under future climate warming scenarios.

The diurnal variations in NEP, ET, and WUE were observed during three different periods in 2015 (Figure 4). The WUE represents daytime data reflecting plant adaptation to the conditions of these months. This indicates that the peak NEP occurs earlier in the morning compared to ET, consistent with the diurnal pattern of plant activity reflecting high photosynthesis in the morning, followed by increased ET throughout the day (Meijide et al., 2017). Maximum WUE is also recorded in the morning but shows a decreasing trend throughout the day (Mendes et al., 2020). Additionally, the increase in ET suggests that excessive ET at midday can reduce WUE. The relationship between NEP and ET, along with the decrease in WUE at midday, can be associated with the phenomenon of “midday depression” (Wang et al., 2021). During the daytime in the three periods, the average WUE values are 3,440 g CO₂/kg H₂O; 3,347 g CO₂/kg H₂O; and 7,484 g CO₂/kg H₂O for each respective period.

The average WUE during the dry with haze period was the highest. Under this condition, NEP was significantly greater relative to ET, leading to the highest NEP/ET ratio or WUE where both NEP and ET decreased compared with the wet and dry periods. This reduction was attributed to the smoke haze phenomenon that occurred in October 2015 in the study area. The haze negatively affected the capacity of oil palm to absorb CO₂, as the high concentration of gases and aerosol particles in the atmosphere reduced the

intensity of direct solar radiation reaching the earth’s surface (Stiegler et al., 2019). The decline in direct radiation limited optimal photosynthesis in oil palm, thereby reducing CO₂ uptake and resulting in lower NEP and ET. According to June (2002), atmospheric turbidity caused by aerosols can have a positive effect by increasing diffuse radiation, which is evenly scattered across leaf layers and enhances photosynthesis. However, when atmospheric turbidity exceeds a certain threshold, CO₂ absorption declines due to the substantial reduction of solar radiation reaching the surface.

During the wet, dry, and dry with haze periods, Water Use Efficiency (WUE) exhibited distinct diurnal patterns (Figure 5), characterized by higher values in the morning followed by a decline in the afternoon (Figure 5a). This decline was strongly associated with increasing Vapor Pressure Deficit (VPD), which rose markedly in the afternoon due to higher temperatures and reduced relative humidity (Figure 5b). The relationship between WUE and VPD is crucial for understanding how plants adapt to varying water availability, as higher VPD increases evaporative demand, accelerating water loss through transpiration (Zhang et al., 2021).

In wet period, WUE remained relatively stable due to the ample availability of soil moisture, which enabled plants to maintain stomatal conductance without experiencing significant water stress (López et al., 2021). The average WUE during the wet period was 3,440 g CO₂/kg H₂O, with a VPD of 0.454 kPa. Although WUE declined in the late morning in response to rising VPD, the reduction was relatively moderate due to favorable environmental conditions, which allowed plants to sustain productivity and carbon assimilation without major losses in transpiration efficiency. The decline in WUE during the afternoon hours, around 09:00 a.m., corresponded to the rise in VPD but was relatively moderate due to the favorable environmental conditions.

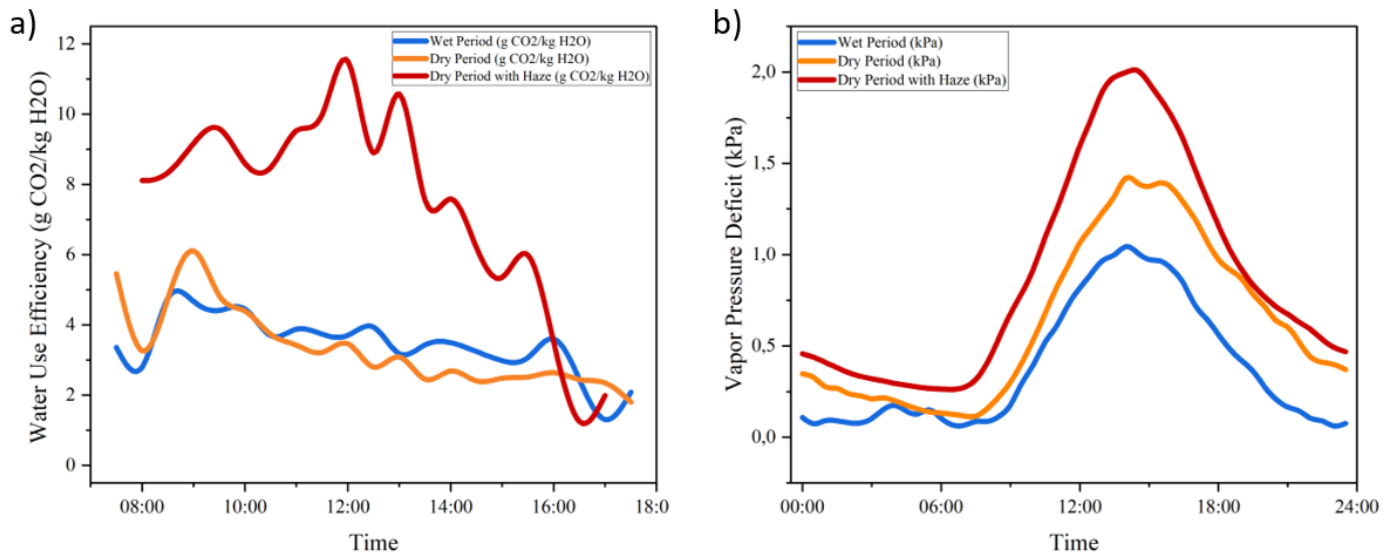


Figure 5 Mean diurnal profiles of (a) Water Use Efficiency (WUE) and (b) Vapor Pressure Deficit (VPD) during wet, dry, and dry with haze periods.

During the dry period, however, a marked shift in plant response was observed. The average WUE decreased slightly to 3,347 g CO₂/kg H₂O, while VPD increased to 0.706 kPa. Elevated VPD accelerated soil moisture depletion and increased transpiration, prompting earlier stomatal closure to reduce water loss (Thienelt and Anderson, 2021). This response directly impacted WUE, as restricting transpiration also limited CO₂ assimilation, creating a trade-off where plants prioritized water conservation over carbon gain. The more rapid decline in WUE reflects the plant's adaptation to water stress, where maintaining water balance becomes a critical priority (Zhang et al., 2021). In contrast, during the dry with haze period, WUE reached the highest values, averaging 7,484 g CO₂/kg H₂O, despite experiencing the highest VPD of 0.882 kPa. This phenomenon may be attributed to the complex interaction between reduced incoming solar radiation due to haze and plant physiological adjustments under extreme water limitations. The smoke haze likely decreased direct radiation and slightly reduced evapotranspiration demands, while still allowing sufficient diffuse radiation to enhance photosynthesis. At the same time, rising atmospheric CO₂ concentrations can improve water use efficiency by enabling plants to maximize carbon gain per unit of water loss (Sinclair et al., 2017). Under these stressful conditions, oil palm trees may have relied on stem water reserves to sustain higher WUE early in the day before stomatal closure restricted further transpiration.

The contrasting WUE responses across the three periods highlight the adaptive strategies of plants in managing water resources under different environmental conditions. Under wet conditions, plants maintained high transpiration rates with minimal trade-offs

in carbon gain. In dry and haze periods, however, plants adopted conservative water-use strategies, closing stomata earlier to minimize water loss (Stiegler et al., 2019). The early morning peak in WUE, followed by its afternoon decline, reflects the plant's effort to balance water conservation with carbon assimilation. During the dry and haze periods, this pattern suggests that internal water reserves were used in the morning, after which stomatal closure limited further water use, reducing WUE (Röll et al., 2015). These findings underscore the role of VPD as a key environmental driver influencing WUE under different water availability conditions. Under severe water limitations, such as in the dry with haze period, plants demonstrated greater efficiency in water management, supported by physiological adjustments and the fertilization effect of elevated atmospheric CO₂ (Zhang et al., 2018). This adaptive response enables oil palm to sustain productivity despite challenging conditions, emphasizing the resilience of ecosystems under fluctuating environmental stressors.

Overall, these findings reveal two significant implications. First, the adaptive plasticity of oil palm—shifting from liberal to conservative water use, but this comes at the cost of carbon uptake. The existence of a morning "optimal window" for productivity could inform precision irrigation strategies. Second, the exceptionally high WUE during the haze period, while a remarkable defense mechanism, signifies a decline in the plantation's function as a carbon sink. This highlights a crucial trade-off between the ecosystem's resilience to climatic stress and its mitigation potential, a critical consideration for future sustainable plantation management.

However, this study has several limitations that should be acknowledged. This study is constrained by its single-year temporal scope and the absence of detailed physiological measurements in represent various water conditions which may influence the accuracy of long-term of water use efficiency dynamics. Future research should therefore examine long-term and multi-site responses to recurrent drought and haze to better understand ecosystem resilience and sustainability.

4. CONCLUSION

This study demonstrates a consistently strong coupling between Net Ecosystem Production (NEP) and Evapotranspiration (ET) ($R^2 > 0.90$) across all climatic conditions and reveals significant adaptive adjustments in Water Use Efficiency (WUE) in response to drought and haze stress. The main adaptive response observed was a sharp increase in WUE during the dry-with-haze period ($7,484 \text{ g CO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$), more than double that of the wet and dry seasons. This rise was primarily driven by a reduction in ET that outweighed the decline in NEP caused by limited photosynthetic radiation under haze conditions. Diurnal analyses further show WUE consistently peaking in the morning and decreasing with increasing Vapor Pressure Deficit (VPD) through midday, most notably under haze when VPD reached 0.88 kPa.

These findings highlight a crucial trade-off: oil palms can conserve water effectively under stress, but their carbon sequestration capacity declines substantially, reducing their role as reliable carbon sinks during extreme climate events. The study underscores the need for adaptive management strategies, such as targeted irrigation scheduling during morning high-efficiency windows, to maintain productivity while mitigating drought impacts. Future work should incorporate multi-year, multi-site datasets and direct physiological measurements (e.g., stomatal conductance and plant water potential) to deepen understanding of oil palm resilience under compounded drought and haze conditions.

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