INTRODUCTION

Water is the basic requirement for crop growth and development. Water promotes seed germination, mediates nutrition uptake from the soil, circulates minerals and organic nutrients throughout the plant, controls turgor pressure, generates plant cell expansion, supports plant form and function, and controls stomatal movements (Blatt et al., 2014). Hence, adequate water is needed to support plant development and maximise the crop’s yield (Nascimento et al., 2018).

Amounts of water required by a specific crop vary from one site to another due to the crop growth stages, environmental conditions, and agricultural practices (Pereira and Alves, 2005). There are various methods to estimate crop water requirements, i.e., evapotranspiration based-methods (Doorenbos and Pruitt, 1977), lysimeter method (Ruiz-Penalver et al., 2015), and transpiration based-methods. The transpiration based-methods consist of the Penman-Monteith combination equation (Milne et al., 1985), energy balance method (Milne et al., 1985), water potential based-method (Garnier et al., 1988), gravimetric (Ferrara and Flore, 2003), allometric based-method (Legros et al., 2009) and gas exchange measurements (Ferrara and Flore, 2003; Suresh et al., 2012a). Bayona-Rodríguez and Romero (2016) stated that all methods generally provided information...
about the actual water demand of a specific crop under partially controlled conditions. Thus, direct measurement is needed to determine water use under field conditions.

Not all of the methods stated can be used to estimate water use on perennial crops under field conditions, particularly for oil palm. Unfortunately, measurement of actual water requirements on oil palm is not easy due to the unique vegetative structures, long duration of generative stages (almost three years) (Carr, 2011), monocot vascular tissue (Madurarpperuma et al., 2009), and morphological structures of oil palm. Heat Ratio Method (HRM) is one of the methods that has been successfully used to measure sap flow (SF) on monocots plants, i.e., oil palm (Madurarpperuma et al., 2009). The HRM is a heat pulse method that can do direct measurements of SF in situ, it is relatively cheap and easily automated for continuous, high-resolution monitoring of plant water demand (Smith and Allen, 1996). HRM gauges SF rates and volumetric flow of water in xylem tissue uses a short heat pulse principle (Bleby et al., 2004; Burgess et al., 2001).

SF is defined as the flow of water in the xylem tissue. SF is also described as a flow of water or assimilates generated by soil water resistance and hydraulic conductance of the plant (Kirkham, 2014). The SF maintains the hydraulic connection between soil and atmosphere (Steppe et al., 2015), therefore investigations of SF characteristics can be used to estimate actual water transpiration as well as crop water requirements (Hajjun et al., 2015; Ismakov et al., 2019). Several studies have shown that transpiration response to environmental variables is specific to the climate and ecosystem where plants grow (Xu and Yu, 2020). This information is crucial because it can be used to determine transpiration heterogeneity between stands (Oteino et al., 2017) and calculate the ecosystem water budget (Zhao et al., 2016).

Moreover, Zhang et al. (1999) stated that the effects of the environment on plant water relations could be examined by measurements of SF in conjunction with the component of water potentials (Ψ). Water potentials are fundamental for the movement of water to the leaves in the process of photosynthesis. The gradient between Ψ\textsubscript{soil} and Ψ\textsubscript{plant} is the driving force for soil water uptake by the plant, while the gradient between Ψ\textsubscript{plant} and Ψ\textsubscript{atmosphere} drives the water movement from the plant to the atmosphere (Fricke, 2017; Zhang et al., 2017). On oil palm, water potential can be measured using a psychrometer (Yono et al., 2019).

Recent studies on oil palm SF using HRM to estimate transpiration have been carried out by Bayona-Rodríguez and Romero (2016); Brum et al. (2020); Ellsäßer et al. (2020); Hardanto et al. (2017); Merten et al. (2016); Niu et al. (2015); Röll et al. (2015); Santi et al. (2021). On the contrary, not many have observed the Ψ\textsubscript{plant} of oil palm under field conditions, one of which was Suresh et al. (2012b). Moreover, measurement of SF and oil palm water potential was still partially done. Hence, the characteristics of oil palm water flux as a response to environment factors are still unclear.

This research employed direct-integrated measurements of SF, Ψ\textsubscript{plant}, climate, and soil variables in oil palm under field conditions. In addition, this study estimated the actual daily stand transpiration and quantified environmental variables’ contribution to oil palm water flux dynamics. Thus, this study was expected to provide more detailed information about primary ecological factors that control oil palm water flux.

**MATERIALS AND METHODS**

**Study Site**

The study was conducted from 21 August to 18 September 2018 in Medan, North Sumatera. The study site had a flat topography (slope of 0%-3%) and a dominant soil type of Typic Dystrudepts. Two oil palm trees (Elaeis guineensis Jacq.) arranged in a 9 m wide triangle were selected. Both palms were 14 years old and well maintained. The trunk height of palm No. 1 was 6.87 m, while palm No. 2 was 7.35 m. Soil texture around oil palm sample No. 1 was sandy loam with sand, silt, and clay portions of 60%, 32% and 8%, respectively. Oil palm sample No. 2 also had a similar soil texture with the proportion of sand, silt, and clay at 55%, 36% and 9%, respectively. The rainfall (RF) pattern in the study site was equatorially marked by two peaks of the rainy season in May and September (Pradiko et al., 2016a). The average annual RF during the period of 2013-2018 was 2164 mm yr\textsuperscript{-1}. Mean air temperature ranged between 27°C to 28°C, while maximum and minimum air temperatures were 38°C and 22°C, respectively. Average relative air humidity was 80%, where lower humidity was in the middle of the year (June-August). Average solar radiation (Qs) fluctuated from 13.69 to 20.07 MJ m\textsuperscript{-2}.

Oil palm is a monocot, and it has a non-wood lignocellulosic material (Hashim et al., 2011). In contrast to dicot plants, the xylem and phloem vessels of oil palm are located within a complex structure known as vascular bundle. In the trunk, vascular bundles are scattered with various densities depending on the depth and height (Darwis et al., 2013). Niu et al. (2015) stated that the vascular bundle density in palm leaf petioles was higher compared with the trunk. It is confirmed in this study (Figure 5). Thus, SF and water potential can be measured at the petiole.
**Sap flow (SF) measurement.** SF velocity measurement was calculated using the following Equations (1) and (2):

\[
V_z = \frac{V \rho_h (c_w + m c_c)}{\rho_p c_w} \tag{1}
\]

where,

\[
V_c = bV_h + cV_h^2 + dV_h^3 \tag{2}
\]

where \( V_z \) is sap velocity (cm hr\(^{-1}\)), \( V_c \) is corrected heat pulse velocity (cm hr\(^{-1}\)), \( \rho_h \) is basic density of wood (dry weight/fresh volume), \( \rho_p \) is density of water, \( c_w \) is the specific heat capacity of wood at an average air temperature of 30°C, 1260 J kg\(^{-1}\)°C\(^{-1}\) (Becker and Edwards, 1999), \( c_c \) is the specific heat capacity of the water, 4182 J kg\(^{-1}\)°C\(^{-1}\) (Lide, 1992), then \( m_c \) is the water content of sapwood. Sapwood properties with installed Sap Flow Meter (SFM1) were taken to estimate \( \rho_h \) and \( m_c \). Fresh and dry weights of sapwood were gauged before and after oven drying at 60°C for 72 hr. Fresh volume was estimated by immersing the samples in distilled water following Archimedes’ principle [modified from Madurapperuma in distilled water following Archimedes’ principle before and after oven drying at 60°C for 72 hr. Fresh was estimated from \( V_h \) by using b-d as the correction coefficient (Burgess et al., 2001)]. In this study, it was assumed that \( V_h = V_c \) because the wound diameter was very small [<0.17 cm; minimum wound width listed in Burgess et al. (2001)].

\( V_h \) was measured using SFM1 produced by ICT International Australia. SFM1 employed the HRM, which gauged the ratio of temperature increment, following the release of a pulse of heat at points equidistant downstream and upstream from a line heater (Bayona-Rodríguez and Romero, 2016). SFM1 sensors consisted of three probes where one probe located in the middle generated a heat pulse, and the other two were positioned above and below the heater probe equipped with thermocouples. SFM sensors were installed according to standard practice provided by ICT International, including the use of a steel drill guide to ensure that holes were drilled parallel and correctly. Also, including the use of aluminium foil and plastic shield to avoid external disturbances such as Qs, air temperature, etc., SFM1 was attached in the petiole where higher vessel density and homogeneity were located (Madurapperuma et al., 2009). One sensor was installed at frond No. 17 of each palm (Figure 1). Frond No. 17 was selected to represent the intermediate value between the upper (frond No. 9) and lower frond (frond No. 25) (Bayona-Rodríguez and Romero, 2016). Frond addition of sampled palms was just at only one frond per month (data not shown); thus, it was assumed that there was no change in fronds number. The heat pulse used was 30 J. The selection of heat pulse levels depends on environmental conditions and the plant’s transpiration rate. If during the measurement there is a diagnostic comment, such as ‘temperature rises insufficient’ then the heat pulse must be increased.

Volumetric SF (Q) was calculated by multiplying \( V_c \) with the total area that actively transpires (A). The sap of each petiole near SFM1 attached. A was estimated by multiplying the area and the total number of active vascular bundles. The images of the petiole were processed using ArcGIS 10 to measure the total petiole area, as well as the number and total area of the active vascular bundles. The calculation of the active vascular bundles only addressed the vascular bundles that transpired a safranin solution (Figure 5).

**Measurement of Frond Water Potential**

The frond water potential of the sample palms was measured using a psychrometer (PSY1) produced by ICT International Australia. PSY1 can log changes in plant water status/potential continuously; thus, the data logged by PSY1 directly reflect the energy required to access water (Dixon and Downey, 2013). PSY1 was attached to the petiole of frond No. 17 and maintained using the procedures by Tran et al. (2015). PSY1 was placed in the front part of the petiole, while the SFM1 was installed in the back part of the petiole. PSY1 was installed 20 cm away from SFM1, as illustrated in Figure 1. Heat pulse velocity (cm hr\(^{-1}\)) and frond water potential/\( \Psi_{frond} \) (MPa) data were logged every 15 min during 29 days of observation.

**Measurement of soil and climate variables.** Observation of soil physical properties included bulk density (g cm\(^{-3}\)), porosity (%), permeability (cm hr\(^{-1}\)), and soil moisture (SM) (%). For these properties, undisturbed soil samples were collected using a core/ring sampler at the radius of 50 cm, 100 cm, 150 cm and 200 cm from the basal stem. Bulk density was calculated based on the dry weight of the soil and the volume of the ring sampler. Then, porosity was determined from the bulk and particle densities. The particle density was obtained from the ratio of the soil dry weight to soil volume. A pycnometer was employed to calculate soil volume. Meanwhile, the permeameter calculated the permeability. Furthermore, Soil Moisture Meter (SMM) MP 306 was installed at the same radius of soil sampling (Figure 1).

RF (mm), air temperature (°C), relative humidity...
and Qs (W m\(^{-2}\)) were gauged by AWS Davis Vantage Pro-II Plus. The data logging interval of AWS was formatted every 15 min and the same for SFM1, PSY1, and SMM. Vapour pressure deficit (VPD) was estimated from air temperature and relative humidity using an equation postulated by Murray (1967). Daily Qs (MJ m\(^{-2}\) d\(^{-1}\)) was calculated from the quarter-hourly of Qs (W m\(^{-2}\)) based on the following Equation (3):

\[
Q_{s, d} = \frac{\sum (Q_{s, 15} \times \text{logging periods})}{1,000,000} \tag{3}
\]

where, \(Q_{s, d}\) is daily Qs (MJ m\(^{-2}\)), \(Q_{s, 15}\) is Qs per 15 min (W m\(^{-2}\)), logging periods is 15 min or 900 s.

**Data analysis.** The daily volumetric SF was cumulated to estimate the total daily transpiration. The multiple linear regression method was employed to determine the effects of \(\Psi_{\text{frond}}\), SM, RF, Qs, and VPD on SF dynamic. A similar method was also used to quantify the effects of climate (RF, Qs, and VPD) and SM on \(\Psi_{\text{frond}}\). According to Ismanov et al. (2019) and Cai et al. (2020), gradients of water potential on the soil-plant-atmosphere continuum (SPAC) are a driving force for SF and transpiration.

Data analysis also included quantification of the contribution of \(\Psi_{\text{frond}}\) SM, RF, Qs, and VPD to the dynamic of SF. Furthermore, the contribution of SM, RF, Qs, and VPD to \(\Psi_{\text{frond}}\) fluctuations was also quantified. Quantification of the contribution of each variable to SF and \(\Psi_{\text{frond}}\) was estimated using a computer-intensive relative importance metric developed by Lindemann, Merenda, and Gold (known as metric LMG) (Grömping, 2006; 2015; Lindemann et al., 1980). The metric LMG was calculated using R-software version 4.0.4 and RStudio version 1.4.1106, where its calculation package or the package relaimpo was obtained from the following website: http://prof.beuth-hochschule.de/groemping/software/relaimpo/.

Moreover, the effects of environment variables that have a major contribution to the SF rate (cm\(^3\) hr\(^{-1}\)) and \(\Psi_{\text{frond}}\) were analysed diurnally using a hysteresis curve. The hysteresis curve is commonly used to identify the responses of SF and \(\Psi_{\text{frond}}\) to environment variables. Analysis using the hysteresis curve was employed in this study because, in a diurnal pattern, changes in environment variables in the morning will result in a different pattern compared to that in the mid-day (Roddy et al., 2013). In this study, plot points in the hysteresis curve were divided into three time zones, they were before dusk (24.00-06.15), daytime (06.30-18.45), and after dawn (19.00-23.45). In this study, the hysteresis of SF and frond was expressed by the area inside the curve or loops.

**RESULTS AND DISCUSSION**

**Soil and Climate Variables Condition**

Soil physical properties around sampled palms are shown in Table 1. It indicates that soil bulk density increased from the most outer radius to the most inner radius. On the contrary, soil porosity and soil permeability decreased from the most outer radius to the most inner radius.
Note: Soil samples were collected twice in weeding circle of each palm. SE is the standard error.

Figure 2 shows SM (%vwc), RF (mm), Qs (W m\(^{-2}\)), and VPD (kPa) during the study. SM at a radius of 200 cm is the highest compared to another radius. The SM pattern followed the pattern of other soil physical properties. The highest SM is found in the soil with lower bulk density, higher porosity, and higher permeability. A previous study showed that soil physical properties in the weeding circle affected SM, where the highest value of average SM was found in the radius of 200 cm (Pradiko et al., 2020).

Furthermore, it has been raining more for the last 15 days of the study. Most of the RF occurred in the afternoon to evening. Therefore, it implied a lower VPD value while Qs was relatively unaffected.

**SF Characteristics**

SF measurement during the study is shown in Figure 2. Overall, SF in both sample plants did not exceed 800 cm\(^3\) hr\(^{-1}\). The SF is similar to Qs and VPD, which is low at night and then peaks during the day. Meanwhile, there is no clear pattern between SF and other environmental variables.

Based on the multiple linear regression analysis, \(\Psi_{\text{sd}}\) and environmental factors (RF, Qs, VPD, and SM) explained 80.02% and 76.59% of the SF on plant samples No. 1 and 2, respectively. The results are similar to the research conducted by Xu and Yu (2020) on arid and semi-arid ecosystems showing that Qs and VPD are two of three climatic factors besides air temperature that can explain SF. Qs and VPD had a major contribution to the SF, which can be seen from the higher value of contribution (%) and correlation coefficient (r) in Table 2. VPD explains 33.73% and 25.72% palm 1 and 2 SF dynamics, respectively. The correlation between Qs and SF, as well as VPD and SF, is more than 0.60. Therefore according to Obilor and Amadi (2018), it is classified as significantly strong. Moreover, Qs explain SF dynamic is higher than VPD. Qs also has a considerably stronger correlation to SF than VPD. It means Qs is more dominant in affecting the SF than VPD. Therefore, Qs is more prevalent in affecting the transpiration of oil palm. It is related to research conducted by Xu and Yu (2020) which shows Qs is an environmental factor that acts as the primary driving force for SF.

The findings in this study were different from the research by Bayona-Rodríguez and Romero (2016), which stated that the daily fluctuation of SF depended on weather variations, especially VPD. Brum et al. (2020) also noted that VPD assigned more influences on transpiration than PAR (Photosynthetic Active Qsiation). Meanwhile, in another study, Röll et al. (2015) stated that transpiration was related to VPD and Qs, though it was unclear which one was more dominant in affecting SF.

Figure 3a shows that the SF rate started to increase at 06:30 am and reached the peak at 00:45-1:00 pm. Average SF at the peak was 386.77 cm\(^3\) hr\(^{-1}\) and 457.79 cm\(^3\) hr\(^{-1}\) on palm samples No. 1 and 2, respectively. Furthermore, SF tended to plateau and then started to decrease after 3:00 pm. Results of this study were different from the other studies, which described that daily transpiration of oil palm reached the peak at 10:00-11:00 am, it was before maximum Qs (12:00 am-1:00 pm), and when VPD reached the peak (2:00-3:00 pm) (Röll et al., 2015).

Meanwhile, a previous study reported a relatively similar pattern of SF fluctuation using a five-year-old oil palm in Colombia. In that study, the SF rate on oil palm started to increase at 07.30 am, peaked by mid-day, and decreased after 3:50 pm (Bayona-Rodríguez and Romero, 2016). However, the pattern of SF in this study was relatively similar to those in other studies using different plants, i.e., poplar (Zhang et al., 1999), banana (Haijun et al., 2015), and black locust (Zhang et al., 2018).

The plot between quarter-hourly stand SF against Qs and VPD shows clockwise hysteresis loops (Figure 3b). The same pattern was observed in hardwood forests (Matheny et al., 2014) and plants in arid and semi-arid ecosystems (Xu and Yu, 2020). The difference in response of SF to the environment before dusk, during the daytime, and after dawn can be seen in the hysteresis loops. During the daytime, the SF rate tended to increase along with the increment of VPD. However, when VPD was higher than 1 kPa, there was no further dramatic increase in transpiration rate; even the SF decreased when VPD was 2.1 kPa. These findings were similar to the previous studies that described a decrease in transpiration of oil palm when VPD was 1.7-2.0 kPa (Carr, 2011; Meijide et al., 2017; Waite et al., 2019). A decrease in transpiration rate is closely associated with stomatal conductance (g\(_s\)), where the high value of VPD (Hernandez et al., 2016; Ocheltree et al., 2014; Su et al., 2019) or Qs (Francesconi et al., 1997; Massonnet et al., 2007) cause a depression in the stomatal conductance. Li et al. (2019a) added that the concentration of phytohormones, i.e., abscisic acid (ABA), in leaf was correlated positively with the sensitivity of stomata conductances to VPD. It

### Table 1. Soil’s Physical Properties at Different Radius of 50, 100, 150, and 200 cm from the Basal Stem

| Radius (cm) | Bulk density (g cm\(^{-3}\)) | Porosity (%) | Permeability (cm hr\(^{-1}\)) |
|------------|-----------------------------|--------------|------------------------------|
| 50         | 1.53 ± 0.02                 | 44.05 ± 0.73 | 0.22 ± 0.09                  |
| 100        | 1.40 ± 0.04                 | 49.05 ± 1.75 | 0.27 ± 0.03                  |
| 150        | 1.32 ± 0.04                 | 52.04 ± 1.98 | 0.52 ± 0.07                  |
| 200        | 1.25 ± 0.07                 | 55.04 ± 1.30 | 0.55 ± 0.03                  |

The SM pattern followed the pattern of other soil physical properties. The highest SM is found in the soil with lower bulk density, higher porosity, and higher permeability.
is unclear whether stomata conductance is a direct response of oil palm to environmental stress or is mediated by a chemical reaction or another signal stress (Waite et al., 2019). In another study, it stated that the stomatal aperture could be regulated by sugars and sugar-derived molecules (Figueroa and Lunn, 2016); water status, turgor, and ABA concentration (Brodribb and McAdam, 2017); CO₂ concentration in ambient air and intercellular air spaces (Engineer et al., 2016).

The SF-hysteresis curve as a function of Qs showed a similar clockwise pattern (Figure 3c) to that in Figure 3b. An identical pattern was obtained in hysteresis loops between sap flux...
TABLE 2. THE CONTRIBUTION AND PARTIAL PEARSON CORRELATION OF VARIABLES TO SAP FLOW (SF)

| Variables      | Palm 1 Contribution (%) | r    | Palm 2 Contribution (%) | R   |
|----------------|-------------------------|------|-------------------------|-----|
| $\Psi_{frond}$ | 7.90                    | -0.46** | 8.05                    | -0.45** |
| VPD            | 33.73                   | 0.83** | 25.72                   | 0.75** |
| RF             | 0.17                    | -0.08** | 0.22                    | -0.08** |
| Qs             | 35.63                   | 0.84** | 40.43                   | 0.85** |
| SM$_{50}$      | 0.49                    | -0.12** | 0.37                    | -0.10** |
| SM$_{100}$     | 0.58                    | -0.15** | 0.55                    | -0.15** |
| SM$_{150}$     | 0.56                    | -0.16** | 0.63                    | -0.15** |
| SM$_{200}$     | 0.96                    | -0.18** | 0.60                    | -0.14** |
| Total          | 80.02                   |       | 76.59                   |      |

Note: The contribution (%) was calculated using the metrics LMG (Grömping 2006; 2015).
The total contribution is equal with $R^2$ of variables to SF.$\Psi_{frond}$ - frond water potential; VPD - vapour pressure deficit; RF - rainfall; Qs - solar radiation; SM$_{50,100,150,200}$ - soil moisture at radius 50 cm, 100, 150 and 200 from basal stem.

**correlation is significant at the 0.01 level (1-tailed).

Figure 3. Fluctuation of SF, Qs, and VPD in every 15 min (a) Hysteresis curve of SF as a function of Qs and VPD (b and c). SF (cm$^3$ hr$^{-1}$), Qs (W m$^{-2}$), VPD- vapour pressure deficit (kPa). Arrows in Figures 3b and 3c indicated the progression of the diurnal cycle from sunrise to sunset. The data in the yellow box shows the conditions after dawn, while the data in the blue box shows the conditions before dusk. Box in the black dashed vertical line is a point where the increment of SF rate starts to be a plateau. The detail of average and standard deviation SF, Qs, and VPD data from Figure 3a came from the average of all-day data.
and Qs by Xu and Yu (2020). The data of sap flux response to Qs at night, where there is no light, are low and concentrated in the bottom-left of the curve. During the daytime, the SF rate drastically increased until solar was 267 W m\(^{-2}\); then the SF tended to be stagnant. SF then decreased after Qs was 622 W m\(^{-2}\). These findings were different from the study by Brum et al. (2020), which described that decrease in the rate of sap flux density on oil palm occurred when the value of PAR was 600 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) or 130 W m\(^{-2}\) (assumed 1 W m\(^{-2}\) = 4.6 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) and VPD was more than 1 kPa. Meijide et al. (2017) also stated that mature oil palm reached maximum transpiration when PAR was 600 \(\mu\)mol m\(^{-2}\) s\(^{-1}\).

Figures 3b and 3c show that the SF rate is lower in the period after sunset to the time before sunrise. Another interesting fact from the hysteresis curves is that the SF after dawn is slightly higher than before dusk. These conditions indicate that plants are trying to replenish water loss in plants during daytime transpiration (Xu and Yu, 2020). The SF at night reveals the presence of night-time transpiration. The respiration causes night-time transpirational water loss at night. This process can provide more efficiency in using water for leaf expansion (Fricke, 2019). A gradual decrease of the hysteresis curve between SF and VPD before dusk and after dawn indicates that the VPD is involved in regulating night-time transpiration. A previous study on Eucalyptus plants showed that VPD and wind speed were factors that drive nocturnal transpiration (Phillips et al., 2010).

Based on the response of the SF rate to VPD and Qs conditions, this study concludes that the SF rate reached the plateau point at VPD of 1 kPa and Qs of 267 W m\(^{-2}\). Dufrene and Saugier (1993) explained that there was no significant change in stomatal conductance and net rate of CO\(_2\) uptake after PAR exceeded 1100 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) (equal to 239 W m\(^{-2}\)) at VPD of 1 kPa. Cheah and Teh (2020) obtained the light saturation for stomatal conductance at about 1500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) (equal to 326 W m\(^{-2}\)). The plateau point here was defined as a point where the increment in VPD and Qs did not drastically increase the SF rate.

Although this research shows that Qs affect SF more, different combinations of Qs and VPD conditions will affect the SF differently. There is a complex relationship between Qs and VPD in influencing SF dynamics. Qs and VPD had a significant combined effect on SF (Matheny et al., 2014). Thus, further study is needed to understand how these factors affect the SF of oil palm. According to Apichatmeta et al. (2017), a mature oil palm would reach optimum photosynthesis at a PAR value of 600 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) without describing its association with VPD. Meanwhile, Meijide et al. (2017) reported that transpiration of oil palm started decreasing when the PAR had not reached the maximum point. At this point, stomata had partially closed due to leaf-level water stress initiated by VPD and PAR (Waite et al., 2019). Brum et al. (2020) described sap flux which reached the highest point before the maximum value of PAR, showing that the physiological condition of oil palm was more affected by atmospheric water stress than light availability.

**Factors Affecting Frond Water Potential**

The frond was negatively correlated to the SF (Figure 2), with the value of partial Pearson correlation being negatively moderate (Table 2). \(\Psi_{frond}\) reached the minimum at mid-day (Figure 5a), it agreed with the previous study by Suresh et al. (2012b). In detail, \(\Psi_{frond}\) has the minimum values at about 30-45 min after SF reached the maximum value. The minimum value of \(\Psi_{frond}\) on palm samples No. 1 and 2 was -0.84 and -0.78 MPa, respectively. The leaf water potential decreased in the mid-day while the SF increased (Beyer et al., 2018; Zhang et al., 1999). Thus, when the \(\Psi_{frond}\) was more negative, the potential gradient between plant and environment would be more significant, and then the SF rate would be higher (Cai et al., 2020).

Analysis of the determination coefficient showed that \(\Psi_{frond}\) fluctuation was only able to explain 7.90% of SF fluctuation on palm No. 1 and 8.05% on palm No. 2. It indicates that measurement of \(\Psi_{frond}\) solely is insufficient to explain SF dynamic because SF movement is a function of water potential gradients between the SPAC, as stated in the previous study by Steppe et al. (2015). A more complete water potential observation (not only in the frond) will determine the relationship between water potential and transpiration. For example, Wang et al. (2013) research showed that the potential difference between root and leaf showed a significant relation with transpiration. Furthermore, a study conducted by Zhang et al. (2014) showed that the condition of the leaf-root-soil water potential would significantly affect the plant’s evapotranspiration.

Plant water potential (represented by \(\Psi_{frond}\)) was affected by variables of climate, soil, and condition of the plant (Wang et al., 2013). Quantification of \(\Psi_{frond}\) response to climate and soil variables is listed in Table 3. The analysis using the LMG Method showed that the effects of climate and soil variables on \(\Psi_{frond}\) were not higher than 24%. Climate variables consistently had more impacts on \(\Psi_{frond}\) than SM. A similar condition was found in Robinia pseudoacacia, where leaf water potential values were more affected by air temperature, air humidity, and Qs than soil temperature (Wang et al., 2013).

Qs and VPD are two variables with the highest...
values of partial Pearson correlation to $\Psi_{frond}$. Coolong et al. (2012) stated that $\Psi_{frond}$ was well correlated with air temperature, humidity, dew point, and Qs. Nevertheless, VPD only represented 8.53% and 8.39% of $\Psi_{frond}$ fluctuation on palms No. 1 and 2, respectively. Meanwhile, Qs only explained 9.21% and 7.57% of $\Psi_{frond}$ flux on palm samples No. 1 and 2, respectively. There was no consistent contribution of Qs and VPD to the dynamics of $\Psi_{frond}$ on the two plant samples. Therefore the contribution pattern of the two variables on $\Psi_{frond}$ remained unclear.

The less contribution of the environment to the $\Psi_{frond}$ dynamics in this study is related to the complexity of SPAC. Changes in environmental conditions will affect the plant, soil and atmospheric water potential. Therefore, to improve understanding of the water potential dynamic, it is better to simultaneously measure the soil-plant-atmosphere water potential. In addition, the oil palm stem plays a significant role in diurnal water flux by storing water (Waite et al., 2019) and large amounts of carbohydrates to buffer environmental influences (Legros et al., 2009; Suresh et al., 2012b). Therefore, not all ecological changes will immediately affect the dynamics of $\Psi_{frond}$.

Figures 4a and 4b reveal that $\Psi_{frond}$ were more negative as Qs and VPD increased. Then, $\Psi_{frond}$ tended to increase drastically to about -0.1 MPa after dawn until dusk. Figures 4c and 4d show the clockwise hysteresis loops. Both figures show that $\Psi_{frond}$ after dawn is lower (more negative) than before dusk. This condition is in line with the pattern of SF response to Qs and VPD. Moreover, $\Psi_{frond}$ reached the minimum value at the mid-day when the VPD value was 2.1 kPa and Qs reached the value of 622 W m$^{-2}$.

Oil palm is an isohydric plant. It can maintain a more or less constant midday leaf water potential regardless of variations in atmospheric conditions and predawn soil water potential (Hochberg et al., 2018; Martínez-Vilalta and García-Forner, 2017). Isohydric plants are characterised by flatter slopes between predawn and midday water potential (Charrier, 2020; Villalobos-González et al., 2019). The slope between predawn and midday water potential in this study is 0.915 (less than 1 - data not shown), indicating that oil palm is an isohydric species. Consequently, to avoid hydraulic failure, oil palm plants develop considerable plasticity in the hydraulic system, develop embolism resistance from environmental conditions, and take advantage of the large stem capacitance (Waite et al., 2019).

**Effects of RF and SM on SF and $\Psi_{frond}$**

In comparison to other variables, RF and SM were not dominant in affecting SF and $\Psi_{frond}$. A similar result was found in the previous research on black locusts by Zhang et al. (2018), where RF and SM were not correlated to the daily stand transpiration. The less contribution of RF was because it did not directly affect SF and $\Psi_{frond}$. However, it affected Qs, VPD, and SM. RF might decrease Qs and VPD as well as increase SM (Li et al., 2019b). More detailed studies on the effects of RF and SM at several radius in an oil palm weeding circle had been reported by Pradiko et al. (2020), where there was a strong and positive correlation between RF and SM.

The results are different from previous studies, which showed a significant SF response to SM as in the study of Ismanov et al. (2019); Sitková et al. (2014); Zha et al. (2017). SM also did not contribute much to $\Psi_{frond}$. In contrast, other studies explain that SM also plays a vital role in the dynamics of leaf water potential (Rivera-Méndez et al., 2012). Figure 3 shows that SF and $\Psi_{frond}$ fluctuations do not follow SM changes. For example, SF and $\Psi_{frond}$ tend to be constant even though there was a decrease in SM from 27 August to 4 September. The day after, midday $\Psi_{frond}$ was observed to reach its lowest value on palm samples No. 1 and 2, i.e., -3.58 MPa and -4.13 MPa, respectively. The

| Variables | Palm No. 1 | r         | Palm No. 2 | r         |
|-----------|------------|-----------|------------|-----------|
| VPD       | 8.53       | -0.37**   | 8.39       | -0.37**   |
| RF        | 0.03       | -0.03     | 0.05       | -0.10     |
| Qs        | 9.21       | -0.40**   | 7.57       | -0.37**   |
| SM$_{50}$ | 1.37       | -0.10**   | 5.02       | -0.12**   |
| SM$_{100}$| 0.86       | -0.07     | 1.03       | -0.04**   |
| SM$_{150}$| 1.35       | -0.03     | 1.12       | -0.03     |
| SM$_{200}$| 0.29       | -0.02     | 0.65       | -0.05     |

Total 21.65 23.83

Note: The contribution (%) was calculated using the metrics LMG (Grömping 2006; 2015). The total contribution is equal with $R^2$ of variables to $\Psi_{frond}$. VPD - vapour pressure deficit; RF - rainfall; Qs - solar radiation; SM$_{50-200}$ - soil moisture at radius 50 cm, 100, 150, and 200 from basal stem. **Correlation is significant at the 0.01 level (1-tailed).
SF value during the plateau phase also tends to be lower than the previous days. The same thing also happened in the period 5-9 September, where $\Psi_{frond}$ did not immediately respond to the decline in SM. Instead, the $\Psi_{frond}$ reduction was observed on 10-11 September. The lag, especially between the decrease in SM and $\Psi_{frond}$, ensures that oil palm has a specific capacitance in buffering environmental changes.

SM contribution to SF fluctuation was different when compared to $\Psi_{frond}$. The contribution of SM to SF followed the order of SM$_{200}$ > SM$_{100}$ > SM$_{150}$ > SM$_{50}$ (Table 2), and the order was SM$_{50}$ > SM$_{150}$ > SM$_{100}$ > SM$_{200}$ for the contribution of SM to $\Psi_{frond}$ (Table 3). This study indicated that SM at the edge of the weeding circle tended to have more influence on SF than those at the other radius. The pattern of SF response to SM was regulated by roots distribution because tertiary and quaternary roots, which have a significant role in water and nutrient uptake, were dominantly found at >150 cm from the basal stem (Pradiko et al., 2016b). However, the contribution pattern of SM to the $\Psi_{frond}$ is difficult to explain. Aside from buffer effects, the absence of drought and drastic changes in SM during the study allegedly caused the contribution of SM to water flux (especially $\Psi_{frond}$) to be minimal. Waite et al. (2019) stated that oil palm growing in riparian areas has lower xylem water potential than in well-drained areas. Therefore, it is necessary to conduct further research in drier areas to ascertain the role of SM in $\Psi_{frond}$.

**Oil Palm Transpiration**

As explained before, the SF needs to be multiplied by the area of the active vascular bundles to obtain the oil palm stand transpiration. The density of vascular bundles in the petiole of the two palms is shown in Figure 5. It shows that the vascular bundles spread across the entire cross-section, where more vascular bundles are
located near the bark of the petiole. The total area of active vascular bundles for palm samples No. 1 and 2 are 31,890 cm² (78.49% of total petiole area) and 34,350 cm² (83.36% of total petiole area), respectively. It should be understood that the calculation of vascular bundles is critical so that the estimation of oil palm stand transpiration is not overestimated.

Stand transpiration of the oil palm in this study is shown in Figure 6. The daily stand transpiration ranged between 0.83-1.53 mm day⁻¹ and 0.82-1.66 mm day⁻¹ on the oil palm samples No. 1 and 2, respectively. Furthermore, average transpiration was 1.28 dan 1.39 mm day⁻¹ on palm trees No. 1 and 2, respectively. The pattern of daily transpiration of the two palms nearly followed the daily fluctuation of Qs and VPD. The low daily transpiration occurred when the daily Qs were less than 10 MJ m⁻² day⁻¹ and the average VPD was less than 0.5 kPa. Though the daily transpiration increased along with the increment of Qs and VPD, it tended to be stagnant when the Qs were higher than 15 MJ m⁻² day⁻¹, and the average VPD was higher than 1.0 kPa.

At least for four days, stand daily transpiration was lower than on any other day (Figure 6). The combination of Qs and VPD is a significant contributor to this situation. However, there is also an indication that decreasing \( \Psi_{\text{frond}} \) due to the drop in SM at 1-2 days earlier has a role in lowering stand daily water loss (Figure 3). SM may have a more significant contribution in determining daily transpiration in drier areas, such as the southern part of Indonesia (Darlan et al., 2016). Research conducted by Sitková et al. (2014) on European beech showed that sap flux would decrease by up to 30% compared to well-irrigated areas under drought stress conditions.

Compared to other previous studies, the transpiration of the 14 years old oil palm in this study was higher than the younger palm. Bayona-Rodríguez and Romero (2016) estimated that transpiration of five years old oil palm was 1.15 mm day⁻¹. Moreover, transpiration of 12 years old oil palm was 1.1 mm day⁻¹ by Niu et al. (2015) and 2.5 mm day⁻¹ by Röll et al. (2015). In this study, the stand transpiration of oil palm was relatively similar to the other crops. In comparison, transpiration of rubber was 2.44 mm on day⁻¹ (Kobayashi et al., 2014), cacao under different shade tree shelters was about 0.5-2.2 mm on day⁻¹ (Kohler et al., 2014), reforestation and agroforestry stands were about 0.6-2.5 mm day⁻¹ (Dierick et al., 2010), and the tropical forest was about 1.0-1.7 mm day⁻¹ (McJanet et al., 2007).

Assumed that evapotranspiration of oil palm was about 4.7 mm day⁻¹, it was estimated that transpiration of oil palm in this study comprised about 30% of the stand evapotranspiration. A previous study stated that the transpiration of oil palm included about 8%-53% of total evapotranspiration. The remaining 70% component of the evapotranspiration was the evaporation of the soils and other vegetations on the soil surface. In addition, the trapped water on the leaves petioles might have contributed to the evapotranspiration of oil palm (Röll et al., 2015).

Information about the daily stand transpiration supports oil palm agricultural practices, especially water management. The results can be used for model development to estimate oil palm water requirements and apply water conservation in oil palm plantations. Water conservation is essential to conserve excess water in the rainy season and improve SM in the dry season. High SM in the dry season, where Qs and VPD are pretty high, can increase oil palm productivity (Brum et al., 2020). Several techniques to conserve water in an oil palm plantation, such as silt pit, ridge terrace, or cover crops (Ariyanti et al., 2016). Bare soil should be avoided on the plantation’s floor because it can elevate water losses from the ground due to the evaporation process and make the soil vulnerable to erosion and nutrient leaching (Satriawan et al., 2021).

**CONCLUSION**

![Figure 5. A bottom-up view of the petiole segment from sample palm No. 1 (left) and palm No. 2 (right) after soaking in a container of 1% safranin solution and left to transpire for 72 hr. Some parts were damaged during the preparation of the sample.](image-url)
This study showed that SF on oil palm increased after 06:30 am, reached the peak by mid-day, tended to be a plateau until 03:00 pm, and then decreased thereafter. Environment variables that had a major contribution in affecting SF were $Q_s > VPD > SM > RF$. Frond water potential ($\Psi_{frond}$) was negatively correlated to the SF. However, the measurement of only $\Psi_{frond}$ may not be sufficient to understand the SF movement in oil palm, it needs to be accomplished with the data of gradient of water potential in the continuum of soil-plant-atmosphere.

Frond water potential decreased as the SF increased, it reach the minimum value when the SF reached the maximum value. Environment variables that had a major contribution to the $\Psi_{frond}$ fluctuation was not as high as their contribution to the dynamics of SF. This indicated that changes in environmental conditions might cause more impacts on atmospheric water potential ($\Psi_{atmosphere}$), so there would be changes in gradient potential between $\Psi_{atmosphere}$ and $\Psi_{frond}$ that decrease or increase the SF rate.

This study also revealed that daily stand transpiration of the 14 years old oil palm estimated by SF measurement was about 0.82-1.66 mm day$^{-1}$. The stand transpiration comprised about 30% of the stand evapotranspiration. Data of stand transpiration are useful for improving agronomic practices, especially in water management.

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