Recent results from an ecohydrological study of forest species in drained tropical peatlands

Ismail [a,*], Ali Torabi Haghighi [a], Hannu Marttila [a], Oka Karyanto [b], Bjørn Kløve [a]

[a] *Water, Energy, and Environmental Engineering Research Unit, University of Oulu, P.O.Box 8000, Pentti Kaiteran katu 1, Oulu, 90014, Finland*
[b] *Faculty of Forestry, Universitas Gadjah Mada, Agro street 1, Bulaksumur, Yogyakarta, 55281, Indonesia*

ARTICLE INFO

ABSTRACT

Ecohydrological studies in tropical peatland have mostly focused on a small number of non-native commercial species. However, studies of native species are urgently needed as they are considered to be a possible solution in the restoration of millions of hectares of degraded tropical peatlands. We investigated peatland species on Padang Island, Indonesia, to assess their responses to changing environmental factors, particularly the high fluctuation of the water table due to intensive peatland draining. We monitored the sap-flux velocity and radial growth of six trees (four native and one non-native peatland species) in high temporal resolution using sap-flux meters and dendrometers up to seven months. Monitoring also included hydrological and micrometeorological parameters. We found that sap-flux velocity in the monitored species was mainly controlled by air vapor pressure deficits, photosynthetic active radiation, and to some extent, by wind speed and water-table depth. We also observed a species-specific correlation between daily sap-flux velocity and daily radial growth. Non-native *Acacia crassicarpa* had up to twice the radial growth of native species. This growth of non-native species was significantly higher at a shallow water-table depth, while native species did not show the same relationship. The interaction between water-table depth, sap-flux velocity, and radial growth in daily timescale was not straightforward, presumably because of the complex carbon-allocation mechanism in trees.

1. Introduction

In recent decades, millions of hectares (ha) of tropical peatlands have been converted into commercial plantations for a small number of monoculture non-native species (Miettinen et al., 2016). Palm oil and pulpwood are the two major non-native commercial species that currently dominate industrial-scale plantations on tropical peatlands, while rubber is another major non-native species but mostly appears on small-scale farms. Because of the poor tolerance of these species to waterlogged soil, tropical peatlands were intensively drained. This peatland draining has led to surface subsidence and severe land degradation (Hooijer et al., 2012; Mishra et al., 2021; Wijedasa et al., 2017). The cultivation of non-native species has also led to other disastrous impacts, such as water scarcity (Merten et al., 2016; Taufik et al., 2020), floods (Sumarga et al., 2016; Wijedasa et al., 2017), and immense carbon emissions (Hooijer et al., 2012; Jauhiainen et al., 2012). Pulpwood plantations occupied 2.5 million ha of land areas in Indonesia, up to half of these on peatlands (Kuru and Wood, 2018). Among the few pulpwood species in the tropic, *Acacia crassicarpa* is the only species that grows in

drained peatlands (Laurén et al., 2021; Martins et al., 2020). It is a fast-growing (Laurén et al., 2021; Mendham and White, 2019) and light-demanding species yet survives in low-fertility and high-acidity lands (Otsamo et al., 1999; Suhartati et al., 2013). There is a concern that *A. crassicarpa* also consumes more water, leading to water scarcity in drought season. Similar to *Acacia mangium* (Jambul et al., 2020), the other tropical pulpwood species (Mendham and White, 2019), *A. crassicarpa* may also be an invasive species (Mawazin and Octavia, 2019) and outcompete local species.

Tropical peatlands are the most effective terrestrial carbon sink when undisturbed (Page et al., 2011), where there is high biodiversity of native species (Giesen and Page, 2016). Native species display adaptive characteristic to waterlogged tropical peatlands such as stilt roots, extensive buttresses, pneumatophores, or sclerophyllous leaves (Graham, 2014; Osaki and Tsuji, 2015; Ripin et al., 2017; Tata et al., 2021). Seedlings grow on the hummock where the peat is relatively dry (Page and Rieley, 2018). Tropical peatlands are low in nutrients, where trees are stunted and grow slower than trees on mineral soil (Junaedi, 2018; Page and Rieley, 2018; Worbes et al., 2017). In general, tree-stand
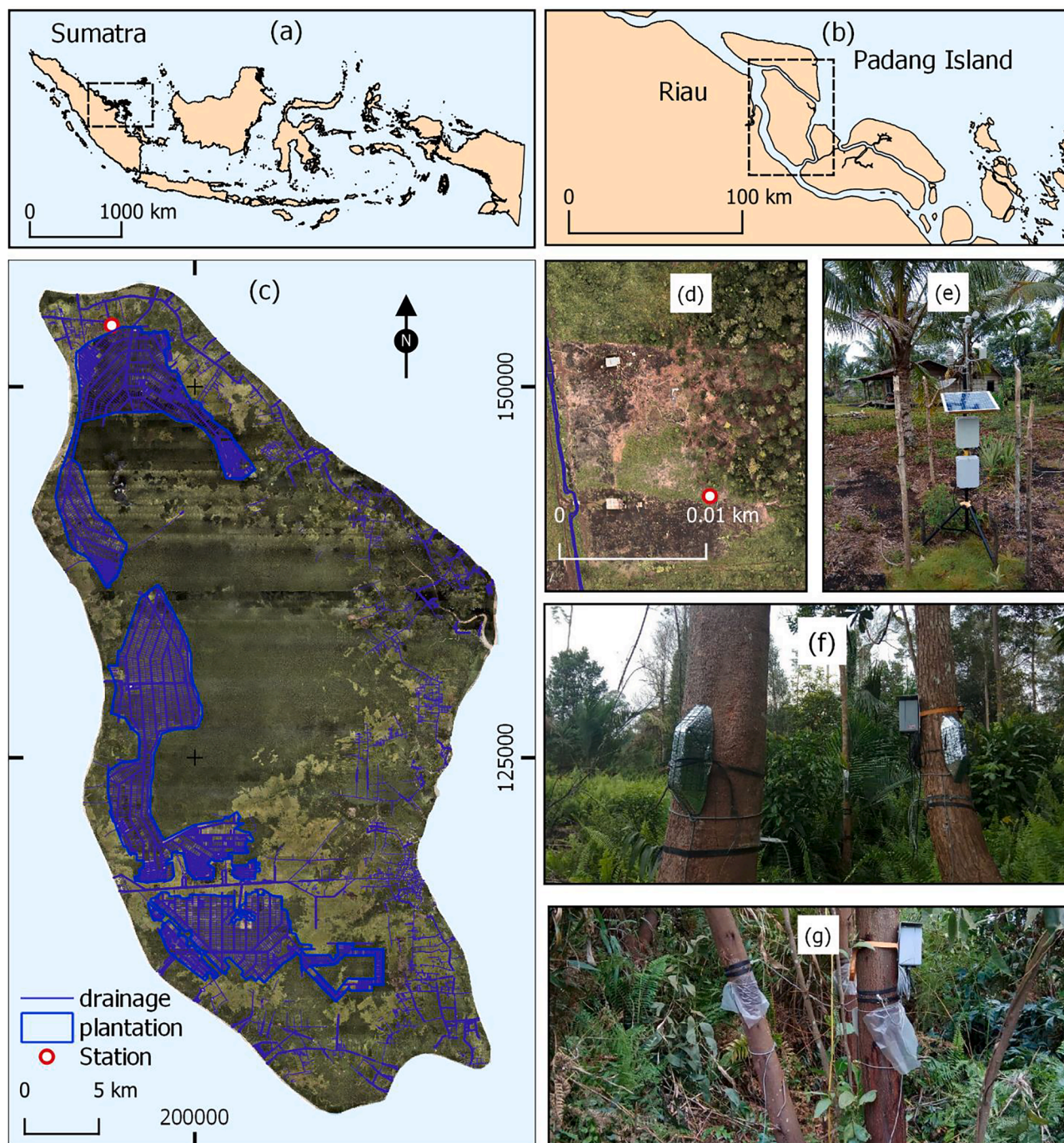

Fig. 1. (a) Indonesian archipelago with the Sumatra mainland in the west and (b) Padang Island in the east of the Riau province of the Sumatra mainland. (c) Padang Island with the drainage network and (d) the monitoring station in the northern part of the island, (e) equipped with multiple sensors for hydrological and micrometeorological parameters, (f and g) as well as sap-flux and dendrometers.

structures vary based on peat depth, shifting from tall and closed-canopy forests in shallow peat near rivers to open-canopy pole forests away from the river, where the peat layer tends to be thicker and nutrient levels are even lower (Kuniyasu and Tetsuya, 2002; Osaki and Tsuji, 2015; Page and Rieley, 2018). The *Dipterocarpaceae* family is the most dominant family in Southeast Asia (Blackham et al., 2014; Mirmanto, 2010; Ripin et al., 2017). Giesen & Page (2016) identified many peatland species, with over hundred species categorized as opportunistic pioneers (i.e., having distinct strategies to cope with unfavorable environment for resource competition to optimize growth) or secondary forest species. Natural forest regeneration of degraded tropical peatlands is slow (Hoscilo, 2009); some species are less adaptable to degraded peatlands

(Blackham et al., 2014). Several native species are already endangered due to intensive forest disturbances and slow regeneration (Kalima et al., 2020).

To mitigate the damage of peatland degradation, ecosystem restoration is urgently needed (Dohong et al., 2018; Yuwati et al., 2021). Indonesia alone aims to restore over two million ha of degraded peatlands across the country (BRG [Peatland Restoration Agency] 2016). While traditional plantations need intensive drainage (Hooijer et al., 2012), the native species of tropical peatlands that can grow at a shallow water-table depth (WTD) offer an option to support restoration initiatives and the more sustainable use of peatland resources and areas (Blackham et al., 2014). *Cratoxylum arborescens* and *Shorea uliginosa*
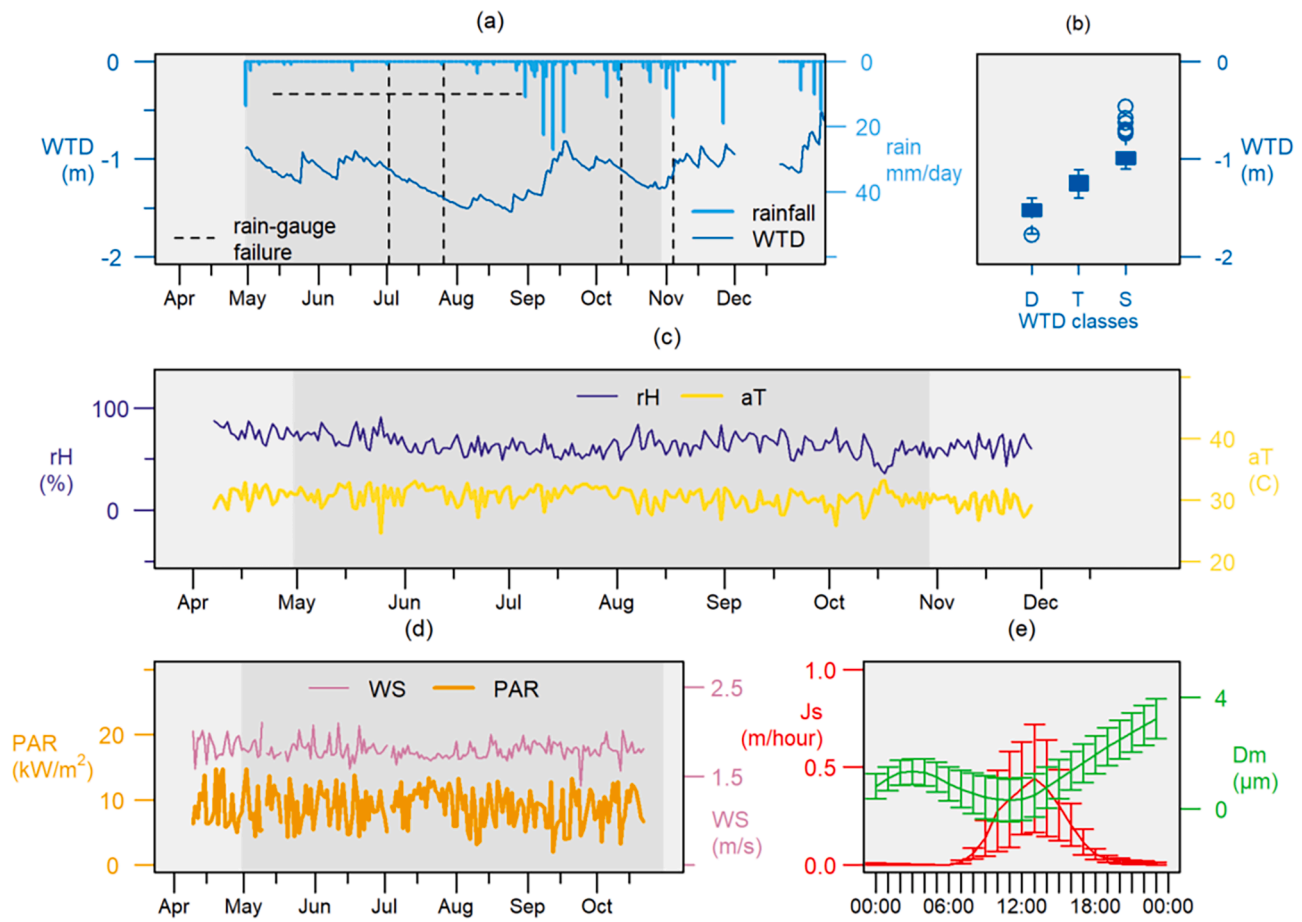
Fig. 2. Hydrological and micrometeorological parameters of (a) water-table depth (WTD) and rainfall, (b) classification of WTD into deep, transitional, and shallow, (c) relative humidity (rH) and air temperature (aT), (d) Photosynthetic Active Radiation (PAR) and windspeed (WS). Darker backgrounds represent overlapping timelines. (e) diurnal variation (mean and standard deviation) in sap-flux velocity and dendrometer reading for *Cratoxylum arborescens*.

Foxw which belong to *Dipterocarpaceae* family are some of the few native species to be widely recommended for restoration (Rochmayanto et al., 2021; Suwito et al., 2021). However, due to their lower economic value (Tata et al., 2021), ecohydrological studies on native species are limited, hence our understanding of native species and the interaction with peatland ecosystem is poor. Ecohydrological studies in the tropics have predominantly been conducted on commercial species, such as oil palm (Hardanto et al., 2017; Meijide et al., 2017; Röll et al., 2015), pulpwood (Hardie et al., 2018; Martins et al., 2020; Mendham and White, 2019), and rubber (Giambelluca et al., 2016; Hardanto et al., 2017).

Contrary to what is commonly believed, Worbes et al., (2017) found that some native species of tropical peatlands do develop tree rings; they argue that the formation is related to the seasonality of rain and drought. This indicates a connection between water availability and the growth in tropical peatlands as has been observed in other ecosystems (Báreková et al., 2020; Sheil, 2003). Spannl et al., 2016 found that the growing season in the tropic is consistent during the rainy season, while Raffelsbauer et al., (2019) observed that prolonged dry days could induce stem shrinkage, in which the shrinkage intensity and the stem recovery time are species specific. Few ecohydrological studies have been conducted for native peatland species to understand how these species respond to changing environmental factors (e.g., Graham, 2014; Junaedi, 2018; Lampela et al., 2017; Tata et al., 2021). (Graham, 2014; Tata et al., 2021) observed that native peatland species grow best at different light intensities, while (Graham, 2014; Hirano et al., 2015) argued that drawdown of WTD can induce plant water stress.

Past studies have mostly been carried out on the species seedling (Lampela et al., 2017) or conducted as simulation studies (Graham,

2014; Tata et al., 2021), while studies at a tree-stand level on native species are rare (e.g., Junaedi, 2018). Therefore, we carried on ecohydrological monitoring on standing trees of several native species on Padang Island, Sumatra, Indonesia. One non-native species was also selected for comparison. Monitoring included two physiological vegetation parameters: sap-flux velocity and radial growth. Sap-flux velocity is an indicator for water uptake/transpiration while growth monitoring is important for understanding the tree's response to environmental factors (Drew and Downes, 2009; Siegmund et al., 2016). Studies that investigate both parameters (sap-flux velocity and growth) and their connection have mostly been carried out in non-peatland ecosystems (e. g., Báreková et al., 2020; Deslauriers et al., 2007; Heinrich et al., 2018; McLaughlin et al., 2003; Winters et al., 2018). Our study aims to improve the understanding of species native to tropical peatland in response to the changing environmental conditions, particularly the high fluctuation of WTD that is caused by intensive peatland draining. In this study, we 1) investigated the influence of hydrological (WTD) and micrometeorological parameters in water uptake and growth, 2) examined the variation in vegetation responses to WTD fluctuation within and between species, and 3) assessed whether non-native *A. crassicarpa* outperforms the native species in higher water uptake and growth.

2. Materials and methods

2.1. Study area

Padang Island (N 1.16 E 102.35) is situated on the east coast of the

Table 1

Timeline monitoring for hydrological (rainfall and water-table depth/WTD), micrometeorological (relative humidity/rH, air temperature/aT, Photosynthetic Active Radiation /PAR, and wind speed/WS), and vegetation parameters.

Parameter	Timeline	Species	Timeline	
			Sap flux	Dendrometer
Rainfall	20.08.2017 - 26.03.2018	*C. arborescens*	06.04.2017 - 16.05.2018	03.06.2017 - 04.08.2017
WTD	01.05.2017 - 26.03.2018	*S. uliginosa foxw*	06.04.2017–03.07.2018	09.06.2017 - 05.09.2017
rH	08.04.2017 – 29.11.2017	*K. malaccensis*	06.04.2017–16.05.2018	–
aT	08.04.2017 – 29.11.2017	*T. glabra*	06.04.2017–23.06.2017	01.07.2017 - 07.09.2017
PAR	10.04.2017 – 22.10.2017	*A. crassicarpa 53*	08.04.2017–18.08.2017	07.04.2017 - 15.06.2017
WS	10.04.2017 – 22.10.2017	*A. crassicarpa 62*	08.04.2017–22.09.2017	07.04.2017 - 26.05.2017

Riau province in Sumatra (Fig. 1). It lies close to the equator, where daylight remains constant the year around, from 6:00 to 18:00, with an average air temperature of 28 °C and annual rainfall ranging 1000–3000 mm. The island is slightly over 100,000 ha in size, covered by raised peatlands up to 10 m in thickness in the center. Commercial pulpwood plantations of *A. crassicarpa* with intensive drainage cover

about a third of the island, mainly on the western coast (Fig. 1c). Another third is covered by degraded peat swamp forest, while the rest of the island is occupied with settlements and small-scale farms, mainly rubber and sago. Non-native rubber crops require drainage but are much less intensive than typical drainage for pulpwood plantation. The drainage for plantations and farms has changed the island's hydrology,
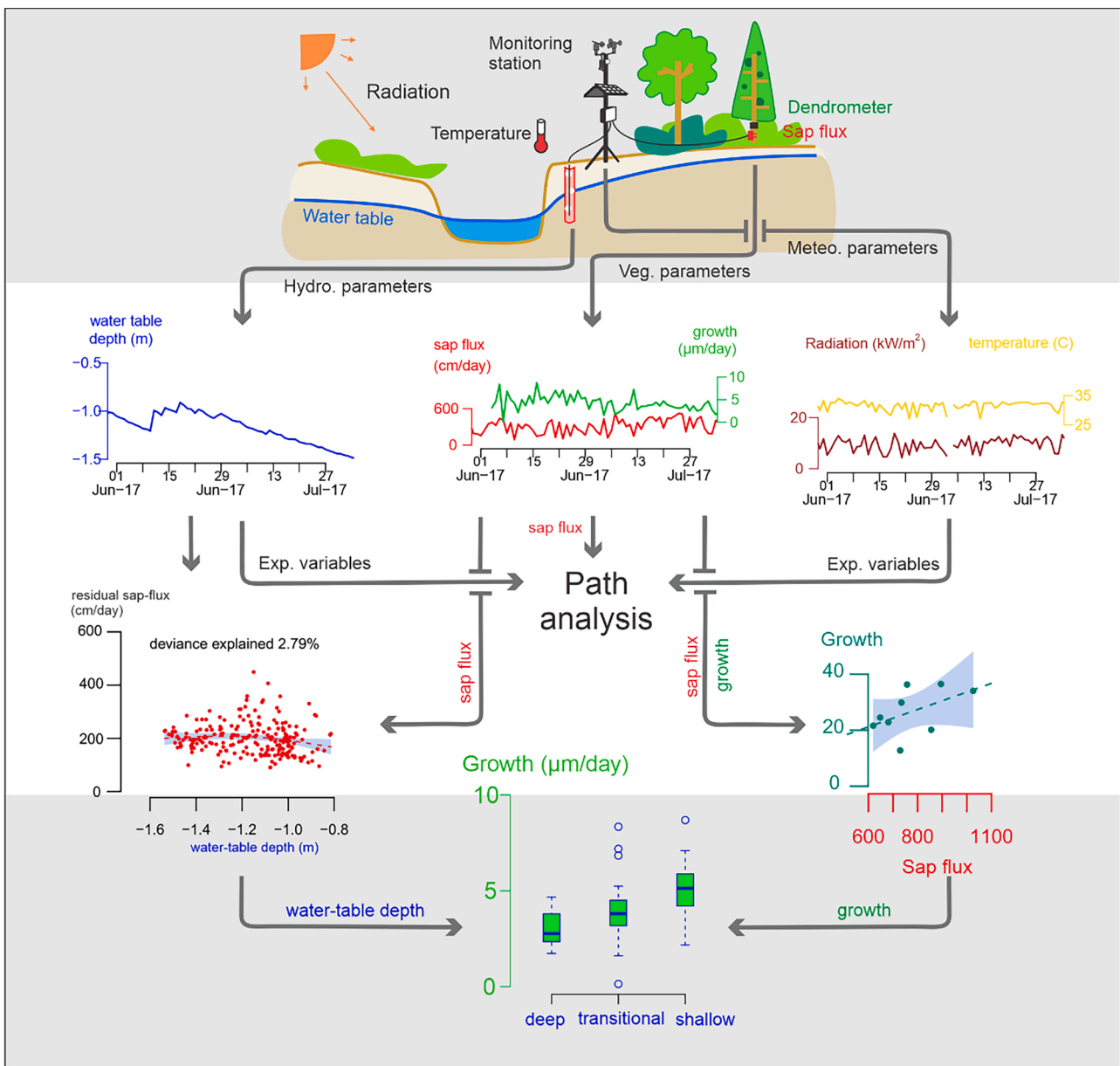

Fig. 3. flowchart for data analysis. Hydrological and micrometeorological parameters were fed into path analysis as explanatory variables for temporal variability in sap-flux velocity. Water-table depth (WTD) classes and sap-flux velocity were used to explain the temporal variability in radial growth.

where WTD varies across different land use and drainage intensity (Ismail et al., 2021). Sago farms do not require drainage as sago is a wetland species that is tolerant to shallow WTD. In the past, the island has suffered from peat fires, mainly caused by land-clearing practices (Susanti et al., 2018).

2.2. Measurement of vegetation, hydrological, and micrometeorological parameters

A monitoring station was installed in the north of the island (Fig. 1c) at approximately 10 m from a plantation's outlet drainage (Fig. 1d). The peat depth at this monitoring station was >7 m. The WTD near the drainage fluctuated from a −0.5 m depth to deeper than −1.8 m (Ismail et al., 2021). The monitoring station was equipped with multiple sensors for vegetation, hydrology, and micrometeorological parameters (Fig. 1e). Six nearby trees were selected for vegetation monitoring, based mainly on species recommendations for restoration (Alimah 2014; Graham, 2014; Rochmayanto et al., 2021; Suwito et al., 2021; Tata et al., 2021; Yulianti et al., 2010). Four of the six trees were native species *Cratoxylum arborescens* (Geronggong), *Shorea uliginosa Foxw* (Meranti Bakau), *Tetramerista glabra* (Punak), and *Koompassia malaccensis* (Kempas). Sap-flux sensors (at 5-cm depth) and dendrometers were installed for each native species (Fig. 1f), with the stem diameter at breast height (DBH) and height estimates were 27 cm and 13 m, 73 cm and 17 m, 80 cm and 19 m, and 103 cm and 23 m for *C. arborescens, S. uliginosa Foxw, T. glabra,* and *K. malaccensis,* respectively. This variation in DBH, nevertheless, was inevitable for this location, particularly for *C. arborescens* as the only other tree in this species with a closer DBH was far from the monitoring station. Native species were all evergreen with broad leaves, and in each case the main stem appeared tall and straight, having few branches at height of 5 m. Sap-flux sensors and dendrometers were also installed for each of two stands *Acacia crassicarpa* individual trees, having a DBH of 53 cm with 21 m height, and 62 cm with 23 m height (Fig. 1g). In contrast to native species, both stands of evergreen *A. crassicarpa* had many small branches along the main stem with smaller leaves, and thus appeared greener with denser canopy than native species. All native and non-native species are wild trees at the edge of the severely degraded natural forest. We used homemade sap-flux meter, thermal dissipation method, following the instruction of Davis et al., (2012), and DC Ecomatik Circumference Dendrometers (ICT international) with CR1000 datalogger (Campbell Scientific). Other sensors were also installed for *WTD* (OEM HC-801 submersible pressure level transducer, Diwi Taiwan, set inside a perforated tube buried underneath), rainfall (tipping bucket rain gage), wind speed, air temperature, Photosynthetic Active Radiation, and relative humidity. Sensors for micrometeorological parameters were bundled sensors assembled for weather stations (MISOL Electric, China). Monitoring began in April 2017 (Fig. 2 and Table 1), and sensors were set to record measurements every 20 min. However, due to sensor failure and vandalism, monitoring only lasted couple of months, and thus data availability varied between sensors (Table 1).

2.3. Data analysis

A brief overview of data analysis is presented in Fig. 3. Data records from hydrological and micrometeorological sensors were converted to standard units: m for *WTD*, mm/day for rainfall, °C for air temperature (*aT*), % for relative humidity (*rH*), kW/m^2 for photosynthetic active radiation (*PAR*), and m/s for wind speed (*WS*). Vapor pressure deficit (*VPD*) in kPa was calculated from *aT* and *rH* as follows (Zhao et al., 2016):

$$VPD = 0.611 \exp\left(\frac{17.502 \, aT}{aT + 240.91}\right)(1 - rH). \tag{1}$$

Sap-flux velocity (*Js*) in m^3/m^2 /sec was calculated as (Davis et al.,

2012):

$$J_s = 0.000119 \left(\frac{\Delta T_0 - \Delta T}{\Delta T}\right)^{1.231}, \tag{2}$$

where *ΔT* was temperature difference in the heater and reference probe, while *ΔT$_0$* was the maximum daily value of *ΔT* that represent zero sap flux. *Js* was later resampled hourly and then summed up to get the daily velocity in cm/day. A rough estimate of daily water uptake is obtained by multiplying *Js* with the sapwood area, derived using an allometric equation developed for tropical species by Meinzer et al., (2001). Meinzer et al., (2001) found that variation in DBH explains up to 98% of the variation in sapwood area. The dendrometer reading (*Dm*) of stem girth was converted into a radial measurement by dividing girth by 2π (Vieira et al., 2013) then adjusted to start at the baseline 0 μm. Daily radial growth as *SRI* (stem radial increment) was calculated from the daily accumulation of GRO (stem growth) at point *t* during the day by the Zero-Growth approach developed by Zweifel et al., (2016), using the following equation:

$$GRO_t = \begin{cases} Dm_t - max(Dm_{<t}) & Dm_t \geq max(Dm_{<t}) \\ 0 & Dm_t < max(Dm_{<t}) \end{cases}, \tag{3}$$

where Dm_t is the dendrometer reading at time *t* while max($Dm_{<t}$) is the precedent maximum *Dm*. By the Zero-Growth approach, GRO becomes size-irrelevant (hence set as 0) when stem is shrinking or expanding but below the precedent maximum *Dm*.

We used various regression analyses, including 1) multivariate regression, 2) partial-correlation analysis, 3) path analysis, and 4) GAM (generalized additive model) to examine the explanatory variables for *Js*, as well as the interaction between explanatory variables. Explanatory variables were the daylight average of *VPD, PAR, WS*, and *WTD*. Parameters of *aT* and *rH* were already represented by *VPD*, while rainfall was represented by WTD. Multivariate regressions were used to identify significant predictors, while partial-correlation analysis was used to confirm the influence of each significant predictor, particularly for PAR and VPD, known to strongly correlate with one another (Siegmund et al., 2016). The interaction between explanatory variables and their indirect effect through mediator variables was examined using path analysis (Chen et al., 2020) since environmental parameters such as weather variables also correlated with one another to some extent (O'Brien et al., 2004). The models for path analysis were developed by identifying possible interactions between explanatory variables from current understandings of plant-environment interaction (Chen et al., 2020). WTD, PAR, and WS were set as the exogenous variables with VPD and *Js* as the endogenous variables. In particular, VPD was a mediator which may be influenced by WTD (*i.e.*, deep WTD may drive drier relative air humidity), PAR, and WS.

Previous studies have found that *VPD* and PAR have a very strong influence on *Js* (Kume et al., 2007; Suárez et al., 2021; Zhao et al., 2016) that may conceal the influence of other parameters, *i.e.*, other explanatory variables appear insignificant despite being otherwise. We extended the statistical analysis for explanatory variables, specifically for *WTD*. Firstly, we extracted the residual *Js* from the path-analysis model with significant predictors other than WTD. The use of residual *Js* was to remove the variability in *Js* explained by variables other than WTD. WTD was then classified into three classes, shallow (< −1.0 m), transitional (−1 to −1.4 m), and deep (> −1.4 m), defined by the *WTD* range during the monitoring period. We then compiled residual *Js* for each WTD class and assessed the possible correlation between WTD and residual *Js*. GAM was used to examine the relationship between residual *Js* and actual WTD, in which such model can accommodate non-linear relationships such as quadratic and polynomial (Duursma et al., 2011). To avoid overfitting (i.e., fitting the noise) by GAM, the function base was limited to 3. The influence of *Js* on growth or *SRI* was examined using regression and path analysis. The assessment of SRI for each WTD class was also carried out to determine the growth response of species to
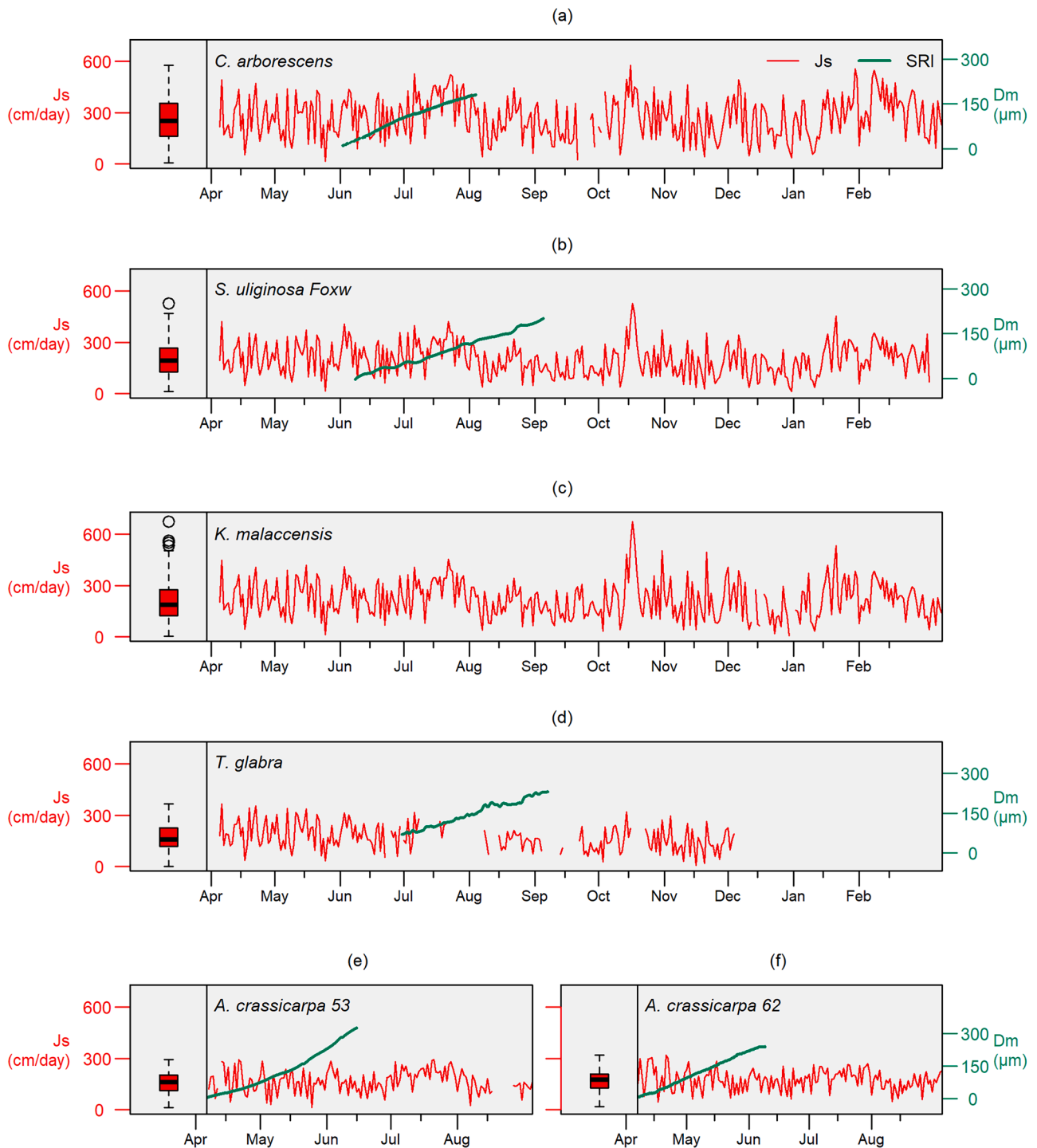
Fig. 4. Sap-flux velocity (*Js*) and adjusted dendrometer reading (*Dm*) of native species (a) *Cratoxylum arborescens*, (b) *Shorea uliginosa foxw*, (c) *Koompassia mala-ccensis,* (d) *Tetramerista glabra*, and (e and f) non-native species *Acacia crassicarpa* with 53-cm and 62-cm diameters at breast height. Boxplots on the left represent the range and median of *Js*.

changing WTD, and the significance was examined using an unpaired *welch t*-test. All multivariate regression (e.g., path analysis, GAM) to analyze *Js* were applied on each species independently, except for *T. glabra* due to the short timeline monitoring in sap flux. Meanwhile, *K. malaccensis* was excluded from the growth analysis due to dendrometer failure. However, results were interpreted on a species or species-group basis, i.e., native versus non-native species. Data analyses were carried out using R 4.1 software (R Core Team, 2022) with packages "ppcor" (Kim, 2015) for partial-correlation analysis, "Lavaan

0.6–11" (Rosseel, 2012) and "lavaanPlot" (Lishinski, 2021) for path analysis, and "mgcv" 1.8–28 (Wood, 2011) for GAM.

3. Results

3.1. Temporal variability in hydrological, micrometeorological, and vegetation parameters

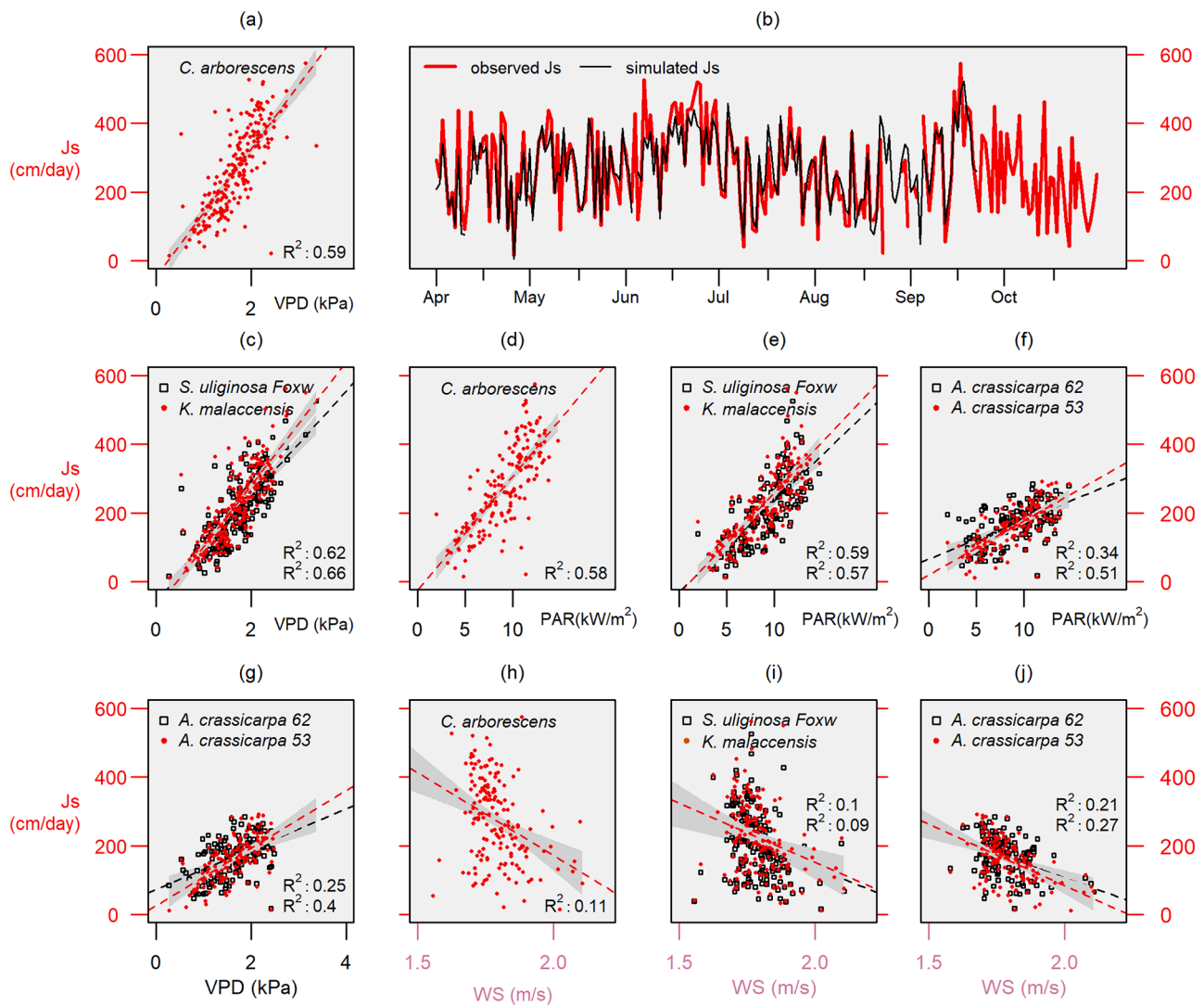The *WTD* at the monitoring station ranged from −0.5 to −1.8 m

Fig. 5. Sap-flux velocity (*Js*) versus vapor pressure deficit (VPD) of (a) native species *Cratoxylum arborescens*, (c) *Shorea uliginosa Foxw* and *Koompassia malaccensis*, and (g) non-native *Acacia crassicarpa* with 62-cm and 53-cm diameters breast height. (b) Time series of observed and simulated *Js* of *C. arborescens* by multivariate regression. Photosynthesis active radiation (PAR) versus *Js* for (d) *C. arborescens*, (e) *S. uliginosa Foxw* and *K. malaccensis*, and (f) *A. crassicarpa* 62 and 53. Wind speed (WS) versus *Js* for (h), (i) *S. uliginosa Foxw* and *K. malaccensis*, and (j) *A. crassicarpa* 62 and 53.

below the surface (Fig. 2a). This temporal change in *WTD* was mainly controlled by rainfall (0–20 mm/day), as WTD rose in response to each rainfall event. Unfortunately, due to a power issue with the solar panel, the rain gage was inoperable during May-August 2017, which was the main period of *Js*-SRI measurement. However, rainfall events can be predicted using a hydrograph of WTD (Fig. 2a). There were only a few sudden rises in WTD during May-June 2017 and September-October 2017, while WTD decreased consistently in June-August 2017 which indicates a drier season during Js-SRI measurement (see Ismail et al., (2021) for details on this hydrological process). The air temperature (*aT*), and relative humidity (*rH*) fluctuated greatly (Fig. 2c) with ranges 25–35 °C, and 80–100%, respectively. The daily average PAR and wind speed (WS) also fluctuated considerably (Fig. 2c), 5–15 kW/m^2 for *PAR* and 1.5–2.0 m/s for WS. The diurnal *Js* occurred mainly during the daylight and reached a peak just after midday, during hour 12:00 (Fig. 2e). The daily *Js* had high temporal variability within species (Fig. 4), with *Js* fluctuating mainly within 50–350 cm/day, with a maximum of up to 600 cm/day. However, temporal variability in *Js* between species appear similar. Rough estimates of daily range water uptake in overall measurement and cumulative water uptake (April-August 2017 when measurement of all species overlapped) were

90–200 Kg/day and 18×10^3 kg (*C. arborescens*), 385–816 Kg/day and 79×103 Kg (*S. uliginosa Foxw*), 750–1 674 Kg/day and 156×10^3 Kg (*K. malaccensis*), 211–387 Kg/day and 35×10^3 Kg (*A. crassicarpa 53*), and 407–483 Kg/day and 48×10^3 Kg (*A. crassicarpa 62*). Overall, native species had higher daily cumulative water uptake than non-native species except for *C. arborescens* which had the smallest DBH. The *Dm* of all species generally show a steady increase, accumulating up to 300 μm radial growth within two months. Nevertheless, *Dm* had diurnal variation as stem was shrinking in the early morning before expanding again after midday and reached a maximum just after midnight (Fig. 2e).

3.2. Environmental parameters as explanatory variables for sap-flux velocity

Multivariate regression with four environmental parameters (WTD, VPD, PAR, and WS) used as explanatory variables, suggests that VPD, PAR, and WS were the main significant predictors on *Js* for most of the measured species (Fig. 5). *Js* had strong positive linear correlations with VPD (R^2 0.25–0.62; Fig. 5a, 5c, and 5g) and with PAR (R^2 0.34–0.59; Fig. 5d, 5e, and 5f), but a weak inverse linear correlation with WS (R^2 0.09–0.27; Fig. 5h, 5i, and 5j). PAR strongly correlated with aT and rH,
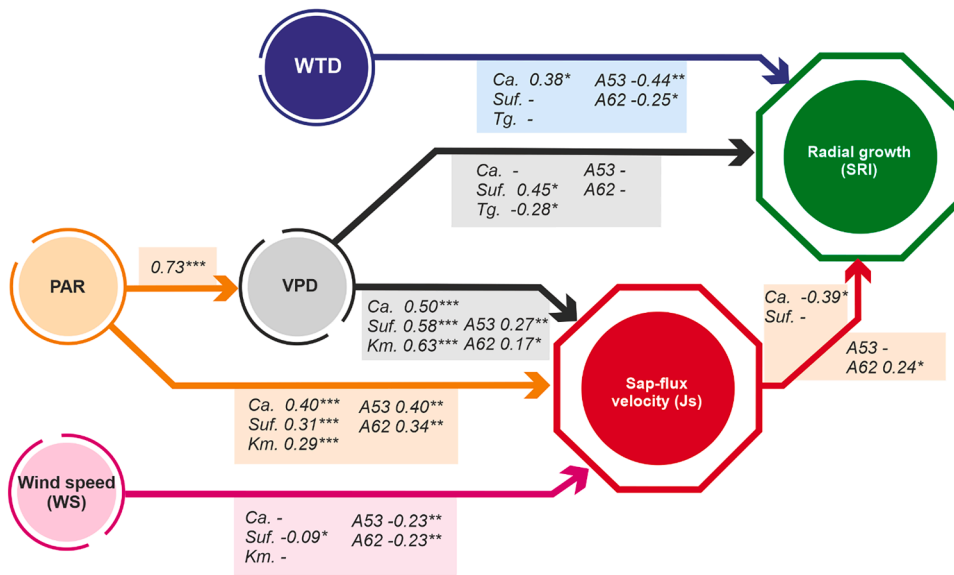
Fig. 6. Path analysis using water-table depth (WTD), Photosynthetic Active Radiation (PAR), and wind speed (WS) as exogenous variables (non-mediate explanatory variables) and vapor pressure deficit (VPD) as a mediator to explain the variability in *Js* and *SRI* (stem radial increment) for native species *Cratoxylum arborescens* (ca), *Shorea uliginosa Foxw* (Suf), *Koompassia malaccensis* (Km), *Tetramerista glabra* (Tg), and non-native species *Acacia crassicarpa* having 53 and 62-cm DBH (A53 and A62). The asterisks represent the significance of PCs (path coefficients), while - shows no significance. All non-significant arrows have been removed.

Table 2

Standardized total effect of Photosynthetic Active Radiation (PAR), wind speed (WS), and vapor pressure deficit (VPD) on sap-flux velocity (*Js*) for each species.

Parameters	*C. arborescens*	*S. uliginosa foxw*	*K. malaccensis*	*A. crassicarpa 53*	*A. crassicarpa 62*
PAR	0.40*	0.31*	0.29*	0.40*	0.34*
WS	−0.08	−0.09*	−0.06	−0.23*	−0.23*
VPD	0.50*	0.58*	0.63*	0.17*	0.27*
R^2	0.70	0.74	0.74	0.39	0.59

as did VPD. However, their individual effect of PAR and VPD on *Js* remained. Partial-correlation analysis with PAR and VPD as explanatory variables for *Js* indicated a significant correlation between *Js* and PAR if the effect of VPD was excluded (partial correlation estimates 0.30–0.45, *p_values* <0.05), and vice versa (partial correlation estimates 0.25–0.64, *p_values* <0.05, see Table 4 in Appendix I). Meanwhile, WS and WTD had no significant correlation with either PAR or VPD. Path analyses (Fig. 6 and Table 2) supported the results from multivariate regression and partial correlation analysis, in which VPD, PAR, and WS were the main significant predictors (*p_values* <0.05). PAR had an indirect effect to *Js* through VPD as a mediator, with total indirect and direct effect ranging from 0.53 to 0.76. Standardized path coefficients (PCs) of VPD-Js for native species were much higher (0.50–0.63) than coefficients for non-native species (0.17–0.27). WS was only significant (*p_values* <0.05) for *S. uliginosa Foxw* and *A. crassicarpa* and was not significant for *C. arborescens* and *K. malaccensis* (the *p_values* were 0.09 and 0.07, slightly above the threshold). WS had no indirect effect on *Js* through VPD, and neither correlated with PAR nor WTD. WTD, the parameter of interest, was neither a significant predictor of *Js* (*p_values* >0.05) for any species, nor had any correlation with any other environmental parameters (PAR, VPD, and WS). All three significant environmental parameters (PAR, VPD, and WS) explained the 39–74% variation in *Js*.

Although *WTD* was not a significant predictor for *Js* based on the path analysis, visual observation shows there was a tendency towards correlation between residual *Js* and WTD (Fig. 7). Residual *Js* tended to increase during transitional *WTD* (−1.0 to −1.4 m) for all native and non-native species. The connection between residual *Js* and *WTD* classes appears non-linear, e.g., residual *Js* was slightly lower when *WTD* was shallow or deep (Fig. 7 right). Despite this tendency, the ranges of residual *Js* for these 3 *WTD* classes mostly overlapped. The deviance explained by the GAM quadratic model in residual *Js* was <10% (Fig. 7 right panels), with the lowest score belonging to *C. arborescens* (Figure not shown). There seems to be no difference between native and non-native species in WTD-*Js* interaction other than non-native species having slightly higher deviance explained than native species.

3.3. Environmental parameters, sap-flux velocity, and growth

The daily average *SRI* for native species were quite similar: 2.73 (SD 0.95), 2.28 (SD 1.92), and 2.38 (SD 3.87) μm/day for *C. arborescens, S. uliginosa Foxw*, and *T. glabra* respectively (Fig. 8). By contrast, the daily average *SRI* for non-native *A. crassicarpa* was 4.72 (SD 2.81) and 3.80 (SD 1.80) μm/day for 53-cm and 62-cm DBH, respectively (Fig. 8c), about twice the *SRI* of native species. This difference in SRI between native and non-native species was significant (*t*-test *p_value* <0.05). Path analysis shows that significant predictors of SRI vary between species (Fig. 6, Table 3) with a wide range of explained variance (R^2 = 0.08–0.42). The effect of VPD was only significant for *S. uliginosa Foxw* (PC 0.45) and *T. glabra* (PC −0.28), while WS and PAR had no significant effects for any species. WTD is a significant predictor of SRI for native *C. arborescens* (PC 0.38) and both non-native *A. crassicarpa* 53 and 62 (PCs −0.44 and −0.25 respectively). It is worth bearing in mind that the intensity of PCs of different environmental parameters are only comparable within the same species. However, the sign of PCs (+/-) represent whether correlation is positive linear or inverse linear. For example, while WTD had a positive linear correlation with SRI of *C. arborescens*, the corresponding correlations for both non-native *A. crassicarpa* 53 and 62 were inverse linear. This suggests that the WTD-SRI interaction was species specific (Fig. 8 right). Among native species, *C. arborescens* showed a linear WTD-SRI relationship as SRI tended to increase over shallow WTD (*t*-test *p_value* <0.05), while no relationship was observed for *S. uliginosa Foxw*, and *T. glabra* (*t*-test *p_value* >0.05). Overall, native species did not show a drop in SRI over shallow WTD. Non-native *A. crassicarpa* at both DBHs (53 cm and 62 cm) shows an inverse relationship because the SRI tends to be lower when WTD was shallow (*t*-test *p_values* <0.05). This is different to the native species.
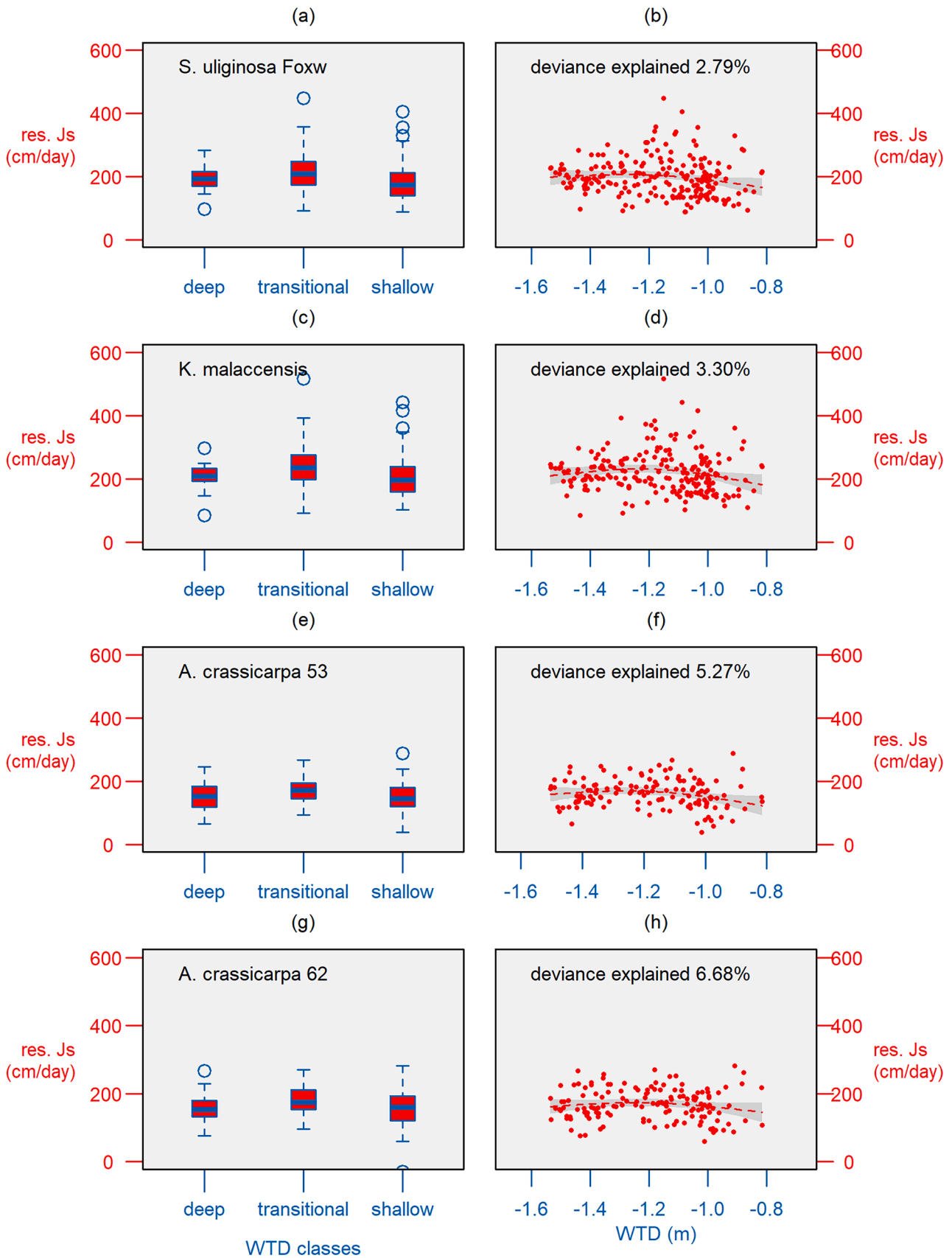
Fig. 7. (left) Residual sap-flux velocity (*Js*) versus water-table depth (WTD) classes and (right) the GAM quadratic model between residual *Js* and WTD for native species (*Shorea uliginosa Foxw* and *Koompassia malaccensis*) and non-native species *Acacia crassicarpa*.
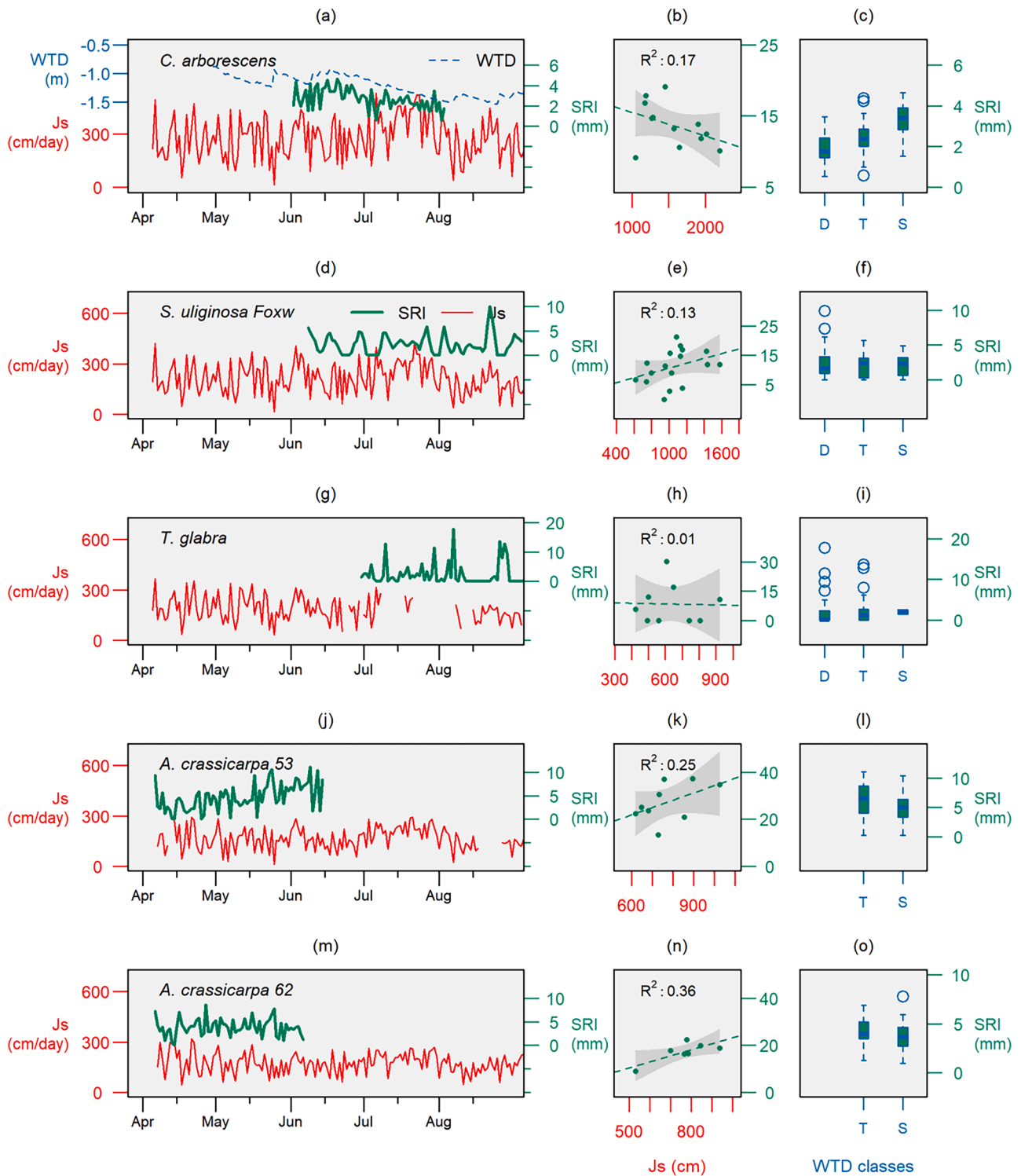
Fig. 8. (left) sap-flux velocity (*Js*), stem radial increment (SRI), and water table depth (WTD), (center) 5-day cumulative SRI versus 5-day cumulative *Js*, and (right) SRI versus WTD classes: deep(D), transitional (T), and shallow (S).

On the other hand, *Js* was only significant for *C. arborescens* and *A. crassicarpa 62*, and both PCs, −0.39 and 0.24 respectively, also show opposite correlation. However, in comparison to *A. crassicarpa 62*, *Js* was not significant for *A. crassicarpa 53* which indicates variation within species. *A. crassicarpa 53* seemed to be more sensitive to WTD than *A. crassicarpa 62* which may be prompted by its lower DBH. Overall, *Js* tends to have an inverse linear correlation with the SRI of native species (PCs −0.39 and −0.08), but positive linear correlation with the SRI of

non-native species (PCs 0.23 and 0.24, Table 3). Nevertheless, the correlation of 5-day cumulative *Js* and SRI tend to be positive linear, except for *C. arborescens*, which kept the inverse linear correlation (Fig. 8 center).

Table 3
Standardized total effect of sap-flux velocity (*Js*), Water-table depth (WTD), Photosynthetic Active Radiation (PAR), wind speed (WS), and vapor pressure deficit (VPD) on stem radial increment (SRI) for each species.

Parameters	*C. arborescens*	*S. uliginosa foxw*	*T. glabra*	*A. crassicarpa 53*	*A. crassicarpa 62*
Js	−0.39*	−0.08		0.23	0.24*
WTD	0.38*	−0.12	0.02	−0.44*	−0.25*
PAR	−0.09	−0.35	−0.24	−0.23	−0.11
WS	−0.01	−0.14	−0.05	−0.06	0.21
VPD	0.27	0.45*	−0.28*	0.14	0.18
R²	0.42	0.13	0.08	0.24	0.20

4. Discussion

4.1. Impact of environmental parameters on sap-flux velocity/water uptake

In our study, the native species generally had higher *Js* and cumulative water uptake than the non-native *A. crassicarpa*. This does not support the current assumption of high water uptake by *A. crassicarpa*. However, more studies are needed to examine this hypothesis. The comparison of water uptake between native and non-native species can be different in stand level over a longer period, e.g., plantation versus forest. Our *Js* or daily water uptake were substantially higher than some estimates reported in tropical forest (e.g., Hardanto et al., 2017; Horna et al., 2011) but were close to estimates reported by (Davis et al., 2012; Zhao et al., 2016) also in tropical forest. The discrepancies can be attributed to differences in DBHs and VPD, which profoundly impact *Js* or water uptake. Zhao et al., (2016) had reported VPD measurement of >3 kPa during the wet season, which was consistently higher than their VPD in the dry season.

Among all the environmental parameters in our study, VPD, PAR, and to some extent WS, had profound impacts on *Js* in most of the species, while WTD explained only a small amount of variation in *Js*. These results of a high impact of VPD and PAR on *Js* mirror those found for other species in tropical (Kume et al., 2007; O'Brien et al., 2004; Suárez et al., 2021; Zhao et al., 2016) and non-tropical ecosystems (Bodo and Arain, 2021; Duursma et al., 2011; Martin et al., 2001). Higher VPD increases the water-potential gradient between leaves and atmosphere, prompting stomata to diffuse more water into the atmosphere to balance the contrast water potential, driving more upward movement of water from roots to leaves. Despite the significance of VPD for *Js* in all species, the impact of VPD on *Js* was more profound in native species than in non-native species (Fig. 6), which might be because native species are more sensitive to certain environmental conditions. The *Js* of non-native *A. crassicarpa* was more sensitive to PAR (PCs 0.34–0.40) than VPD (PCs 0.17–0.27), which can be attributed to their characteristic as light-demanding species and their greater resistance to other environmental condition. Native species show the opposite characteristic, i.e., their *Js* is less sensitive to PAR (PCs 0.29–0.4) than to VPD (PCs 0.50–0.63). The sensitivity of native species to light availability varies across different species (Graham, 2014). *C. arborescens* is considered as a light demanding species while *K. malaccensis* was classified as a general species (Graham, 2014). Currently, there is a global trend in rising VPD, which might lead to even higher tree's water uptake in drained peatlands. However, there is a limit when water uptake begins to level off or even begins to decrease after passing the VPD threshold. Meanwhile, non-native species are more sensitive to WS than native species with invers linear correlation (PC-0.23). Ma et al. (2008) also found a negative correlation between WS and *Js* for *Acacia mangium*, despite the correlation being insignificant. Schymanski & Or, (2016) argued that increasing WS can lower transpiration that is attributed to water use efficiency and higher carbon uptake under certain conditions. In our study, non-native *A. crassicarpa* seemed to have efficient water use which was indicated by higher SRI, despite their lowere lower *Js* (more about *Js*-SRI in Section 4.2). On the other hand, we found

non-linear quadratic but weak correlation between *Js* and *WTD* for all species, which may explain why *WTD* was not a significant predictor in the path analysis. Path analysis was simply an extension of multivariate linear regression in which relations among variables should be linear (Rosseel, 2012). We expect that the contrast in *Js* response to WTD between native and non-native species will be more visible when WTD is near the surface or waterlogged. Miyazawa et al., (2014) observed contrasting species responses in sap flux to groundwater table depth in a non-peatland ecosystem. The temporal variability in *Js* across various WTD in our study, however, did not reflect the species responses to waterlogged conditions because *WTD* never rose above a −0.4 m depth during measurement. Overall, the *Js* of native species tended to be more sensitive to VPD, while *Js* of non-native species was more sensitive to PAR and WS.

On the other hand, there are other controlling factors for *Js* which were not the focus of our study, such as variation in DBH, root system, or radial variation within the same tree. Variations in DBH and/or root depth also influence variation in *Js* between and within species (Kume et al., 2007). Trees with large DBH tend to have a wider leaf area index, which leads to higher water demands for photosynthesis. Unfortunately, literature surrounding root systems for peatland species is rare. Tata et al. (2021) studied the roots of the seedlings of two native species and reported that *C. arborescens* developed adventitious roots to survive waterlogged peatland. In a typical *A. crassicarpa* plantation, roots can be found over −1 m deep, although most of the roots were near the ground surface. Sulistiyanto, (2004) reported that most of the root biomass (74.2%) in peat swamp forest was within a depth of −0.25 m, while WTD during our measurement was deeper all the time. Nevertheless, we cannot find any information for the root systems of specific native species on a standing-tree level. Furthermore, *Js* also varies within the same tree, i.e., radial variation (Bodo and Arain, 2021; Poyatos et al., 2007). Our *Js* measurement represents one point in the tree sapwood and does not therefore account for radial variation. This variation in DBH/leaf area index, root system, and radial variation within tree should be considered when information is available.

4.2. Impact of environmental parameters, water uptake, and peatland draining on growth

The growth rate of non-native species was found to be significantly higher than the growth rate of native species, which could be attributed to different carbon allocation mechanisms between species or optimization of water uptake. Sugars produced from photosynthesis are primarily used for maintenance of living cells and growth of new leaves and roots, before allocating carbon for wood growth. In peatlands, roots are shallow but have an extensive horizontal network (Dezzeo et al., 2021). Nutrient deficiency leads to more carbon being allocated to the root system at the expense of shoot growth (Poorter et al., 2012), which may lead to slower shoot growth for peatland species (Anadon-Rosell et al., 2022). Meanwhile, growth for shoot systems is also distributed for height/length (primary growth) and radial stem (secondary growth). Junaedi, (2018) observed different patterns of height growth of native and non-native peatland species which may affect radial growth. Junaedi, (2018) reported SRI of around 2.08 cm/year for *C. arborescens*

and 6 cm/year for *A. crassicarpa*, which were much higher than our results (Fig. 8), presumably because their measured trees were younger (1.5–5 years) and much smaller in DBH (<20 cm). The non-native *A. crassicarpa* was shown to have constant radial growth while their height growth substantially decreased when the species past 3 years old; the radial and height growth of native species leveled off with smaller drop in their growth (Junaedi, 2018). Nyadzi et al., (2002) also reported higher growth for non-native peatland species. Other studies usually reported growth in volume (*e.g.*, Laurén et al., 2021). This difference in radial growth suggests that *A. crassicarpa* can optimize water use for growth, which is a typical trait of invasive species (Mawazin and Octavia, 2019; Jelbert et al., 2019).

Nevertheless, we found inconsistent responses of SRI toward environmental parameters on daily scale (Figs. 6 and 7). The impact of environmental parameters appears to be more consistent for *Js* than for SRI. The significant predictors and their correlation (i.e., positive or inverse linear) with SRI varied widely between species. VPD was found to be significant only for *S. uliginosa foxw* and *T. glabra*, although the explained variance was very small in both cases (R^2 0.13 and 0.08, Table 3), much smaller than the explained variance for other species. For *T. glabra*, the significance of VPD may be attributed to the absence of *Js* as an explanatory variable; *Js* was found to be a significant predictor for *C. arborescens* and *A. crassicarpa 62*. In contrast, despite being the same species as *A. crassicarpa 62, Js* was not a significant predictor for *A. crassicarpa 53*. Overall, daily *Js* did not explain much of the variation in daily SRI. The correlation of cumulative *Js*-SRI may be observed better with a longer measurement period, as their correlation appears to be more consistent on a 5-day basis (Fig. 8 center). However, the Zero-Growth approach provides an alternative plausible mechanistic process to explain the diurnal water uptake-stem growth interaction. The Zero-Growth approach is named after the underlying assumption that no stem growth takes place during stem shrinkage, i.e., during the day when stem is shrinking and expanding before reaching the precedent maximum stem radius (Zweifel et al., 2016). This shrinking is induced by water deficit in the early morning before reversing to expands as hysteresis response to water uptake during the day (Fig. 2e).

The response of SRI toward WTD also varied between species with particularly contrasting behavior between non-native *A. crassicarpa* and native *C. arborescens*. The SRI of *A. crassicarpa 53* was found to be more sensitive to WTD than the SRI of *A. crassicarpa 62*. However, both *A. crassicarpa 62* and *A. crassicarpa 53* shows lower tolerance to shallow WTD with lower growth. In contrast, *C. arborescens* had lower radial growth in deeper WTD (Fig. 8b) which may result from a low tolerance of the species to drought (Graham, 2014). *C. arborescens* is known to the local community as a flood-resistant species. Meanwhile, *S. uliginosa Foxw* and *T. glabra* do not show any impact of WTD on their SRI. This WTD-SRI interaction suggests the low tolerance of *A. crassicarpa* to shallow WTD, which is the primary cause of intensive drainages on tropical peatlands where *A. crassicarpa* is the most dominant commercial pulpwood species.

Previous studies have shown that the correlations between environmental parameters, water uptake, and stem growth is not straightforward and varies significantly between species and ecosystem, which may explain the inconsistency of significant variables for SRI in our study. Hardie et al., (2018) shows that stem growth of *A. mangium* and *Eucalyptus pellita* in tropical mineral soil was not influenced by *WTD*, while Hung et al., (2016) found that the growth of an *Acacia* hybrid was more affected by soil water deficit than by temperature. (Ježík et al., 2011; Siegmund et al., 2016) observed that the correlation between stem growth, hydrological, and micrometeorological parameters varied over time, i.e., the correlation may be strong in a certain year but weak in other years. Winters et al., (2018) unexpectedly found that cambial growth of *Acacia raddiana* and *Acacia tortilis* in an arid environment took place for most of the dry season. McLaughlin et al., (2003) observed contrast growth response between faster- and slower-growing trees toward environmental parameters. (Báreková et al., 2020; Deslauriers

et al., 2007) found no conclusive connection or low correlation between *Js* and stem increment. This complexity of growth-environment interaction highlights the need for more studies of native species in tropical peat swamp forests.

4.3. Peatland restoration and direction for future studies

The limited observation and uncertainty from our study may only allow for tentative recommendations for restoration, in favor of native species which are currently under intensive pressure from logging and competition from non-native species. The higher SRI of *C. arborescens* in shallow WTD (Fig. 8c) shows the potential of *C. arborescens* for restoration, as has been suggested in other studies (Graham, 2014; Suwito et al., 2021; Tata et al., 2021). *C. arborescens* is a pioneer species, less prone to fire, has fast recovery (Mojiol et al., 2014; Suwito et al., 2021; Yulianti et al., 2010), and its chance of survival in degraded peatland is high (Mojiol et al., 2014; Junaedi, 2018; Tata et al., 2021). *S. uliginosa Foxw* and *T. glabra* show less growth sensitivity to changes in WTD, which may also indicate their potential for restoration. Revegetation of these native species, as well as *C. arborescens*, are important to preserve peatland diversity as they have suffered from intensive logging. Their timber is widely used for construction by local communities (Kalima et al., 2020). *S. uliginosa Foxw* is already listed as a threatened species (Azwin and Sadjati, 2018), while *K. malaccensis* is one of the few species that hosts honeybee hives, which is crucial for ecosystem balance in tropical peatland. For this reason, the peatland restoration program in Indonesia stresses the importance of providing alternative livelihood options for local communities from unsustainable logging (Yuwati et al., 2021). On the other hand, the significantly higher growth rate of *A. crassicarpa* shows its potential to outcompete native species which is a major risk for the diversity of peat swamp forest. This urges the importance of hydrological restoration in drained peatlands to restore the near-pristine saturated peatland which allows native species to thrive and preserve diversity.

Nevertheless, more studies with longer timeline monitoring, more environmental and vegetation parameters, and better monitoring devices are needed to provide strong recommendation for restoration strategies. For example, studies on the survival and regeneration of various native species (e.g., Lampela et al., 2017) can benefit selection for pioneer species among overwhelming numbers of native species. Ecohydrological data from tropical peatlands are still rare, and thus, we recommend extending future studies of waterlogged conditions to examine the survival of these species in restored degraded peatland, where WTD rises near the surface. A WTD of −0.4 m is understood as the threshold for healthy tropical peatlands and the minimum WTD for restored peatland in Indonesia (Kemenkunham [Ministry of Law and Human Rights Republic of Indonesia] 2016). Other factors, such as tree phenology, photosynthesis measurements, or carbon leveling (e.g., Shinde et al., 2018) are also recommended to be included in the monitoring. Understanding these parameters will benefit future analysis to disentangle the carbon allocation process in the trees, and their connection with the water status and stem growth. Instrument quality and safety concern should also be considered. Our studies relied heavily on homemade sensors for cost efficiency to accommodate the diversity of peatland species. However, when conducting monitoring remotely, high quality sensors from reputable brands are recommended to minimize sensor failures and lost data. Safety concern is a major risk in a remote area that is prone to social conflict, which is rampant in many regions in Indonesia (Uda et al., 2017). Overall, despite the limitations of our study, it has paved the way for future ecohydrological studies on tropical peatlands which described technical challenges and missing link that should be considered, and our results serve as early evidence requiring further investigation.

Table 4

Partial correlation estimates between Exp. (explanatory) variable and sap-flux velocity (*Js*) when Exc. (excluded) variable is excluded. VPD is vapor pressure deficit and PA is photosynthesis active radiation.

Species	Exp. variable	Exc. variable	estimate	*p_value*
C. arborescens	VPD	PAR	0.53	3.42e-13
C. arborescens	PAR	VPD	0.45	1.41e-9
S. uliginosa Foxw	VPD	PAR	0.60	6.49e-18
S. uliginosa Foxw	PAR	VPD	0.43	6.69e-9
K. malaccensis	VPD	PAR	0.64	1.66e-21
K. malaccensis	PAR	VPD	0.37	4.14e-7
A. crassicarpa 53	VPD	PAR	0.25	3.79e-3
A. crassicarpa 53	PAR	VPD	0.45	9.03e-8
A. crassicarpa 62	VPD	PAR	0.35	1.02e-2
A. crassicarpa 62	PAR	VPD	0.35	2.73e-5

5. Conclusion

In order to improve our understanding of the ecohydrological processes in tropical peatlands, we monitored the hydrological, micrometeorological, and vegetation parameters of six trees (four native and one non-native species) on Padang Island. We observed the profound impact of VPD and PAR, as well as to some extent, the impact of WS and WTD on temporal variability (i.e., day-to-day fluctuation) in *Js* of the measured native and non-native species. For any species, daily *Js* was slightly higher when WTD was between −1.4 to −1.0 m. Correlation between daily *Js* and daily SRI was species specific. Nevertheless, non-native *A. crassicarpa* had lower SRI in shallow WTD, while native species did not share a similar relationship. Non-native species had almost twice the radial-growth rate of native species. There was no evidence of higher water uptake by non-native *A. crassicarpa*. Overall, the interaction between WTD, *Js*, and SRI was not straightforward, presumably due to the large variation of *Js* within species and within the tree, complex carbon-allocation mechanisms, and unmeasured parameters such as tree phenology. Despite the uncertainties, lessons learned from our measurement pave the way for future ecohydrological studies in tropical peatland with recommended monitoring techniques, for example, large-scale sensor deployment and the study of other parameters in a longer monitoring timeline.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

Acknowledgement

Appendix

Appendix I. Partial correlation coefficient

References

Alimah, D., 2014. Studi Karakteristik dan Potensi Punak (Tetramerista glabra) Sebagai Jenis Tanaman Rawa Gambut Multiguna. Galam 7 (2), 1–8. Retrieved from. https ://foreibanjarbaru.or.id/wp-content/uploads/2016/07/Galam-Volume-VII-Nomor-2-Tahun-2014-Studi-Karakteristik-dan-Potensi-Punak-Tetramerista-Glabra-Sebagai-Jenis-Tanaman-Rawa-Gambut-Multiguna.pdf.

Anadon-Rosell, A., Scharnweber, T., Arx, G.v., Peters, R.L., Smiljanić, M., Weddell, S., Wilmking, M., 2022. Growth and Wood Trait Relationships of Alnus glutinosa in Peatland Forest Stands With Contrasting Water Regimes. Front. Plant. Sci. 12, 788106 https://doi.org/10.3389/fpls.2021.788106.

Azwin, Sadjati, E, 2018. Respon Stek meranti Bakau (Shorea uliginosa Foxw.) Terhadap Pemberian Rootone F dan Berbagai Media Tanam. J. Kehutanan 13 (2). Retrieved from. https://journal.unilak.ac.id/index.php/forestra/article/download/1564/1098.

Báreková, A., Bárek, V., Kováčová, M., Novotná, B., Kišš, V., 2020. Climate conditions impact on sap flow into plants and their dendrometric changes. J. Ecolog. Engin. 21 (6), 224–228. https://doi.org/10.12911/22998993/124077.

Blackham, G.V., Webb, E.L., Corlett, R.T., 2014. Natural regeneration in a degraded tropical peatland, Central Kalimantan, Indonesia: implications for forest restoration. For. Ecol. Manage. 324, 8–15. https://doi.org/10.1016/j.foreco.2014.03.041.

Bodo, A.V., Arain, M.A., 2021. Radial variations in xylem sap flux in a temperate red pine plantation forest. Ecol. Process 10, 24. https://doi.org/10.1186/s13717-021-00295-4.

BRG, 2016. Mengawali Restorasi Gambut Indonesia (Initiating Peatland Restoration in Indonesia). Badan Restorasi Gambut/Peatland Restoration Agency, Jakarta. Retrieved September 2018, from. https://brg.go.id/files/Publikasi/BRG%202016%20report_29.05.17.pdf.

Chen, Z., Zhang, Z., Sun, G., Chen, L., Xu, H., Chen, S., 2020. Biophysical controls on nocturnal sap flow in plantation forests in a semi-arid region of northern China. Agric. For. Meteorol. 284, 107904. https://doi.org/10.1016/j.agrformet.2020.107904.

Davis, T.W., Kuo, C.-M., Liang, X., Yu, P.-.S., 2012. Sap Flow Sensors: construction, Quality Control and Comparison. sensors 12, 954–971. https://doi.org/10.3390/s120100954.

Deslauriers, A., Anfodillo, T., Rossi, S., Carraro, V., 2007. Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees. Tree. Physiol. 27 (8), 1125–1136. https://doi.org/10.1093/treephys/27.8.1125.

Dezzeo, N., Grandez-Rios, J., Martius, C., Hergoualc'h, K., 2021. Degradation-driven changes in fine root carbon stocks, productivity, mortality, and decomposition rates in a palm swamp peat forest of the Peruvian Amazon. Carbon Balance Manage. 16, 33. https://doi.org/10.1186/s13021-021-00197-0.

Dohong, A., Aziz, A.A., Dargusch, P., 2018. A Review of Techniques for Effective Tropical Peatland Restoration. Wetlands 38 (2), 275–292. https://doi.org/10.1007/s13157-018-1017-6.

Drew, D.M., Downes, G.M., 2009. The use of precision dendrometers in research on daily stem size and wood property variation: a review. Dendrochronologia 27 (2), 159–172. https://doi.org/10.1016/j.dendro.2009.06.008.

Duursma, R.A., Barton, C.V., Eamus, D., Medlyn, B.E., Ellsworth, D.S., Forster, M.A., Tissue, D.T., Linder, S., McMurtrie, R.E., 2011. Rooting depth explains [CO2] × drought interaction in Eucalyptus saligna. Tree Physiol. 31, 922–931. https://doi.org/10.1093/treephys/tpr030.

Giambelluca, T.W., Mudd, R.G., Liu, W., Ziegler, A.D., Kobayashi, N., Kumagai, T., Kasemsap, P., 2016. Evapotranspiration of rubber (Hevea brasiliensis) cultivated at two plantation sites in Southeast Asia. Water Resour. Res. 52, 660–679. https://doi.org/10.1002/2015WR017755.

Giesen, W., Page, S., 2016. Unique Southeast Asian Peat Swamp Habitat Have relatively Few Distinct Plant Species. In: 15th International Peat Congress 2016. International Peatland Society (IPS), Kuching, Malaysia, pp. 730–734. Retrieved from. https://peatlands.org/assets/uploads/2019/06/ipc16p730-734a199giesen.page_.pdf.

Graham, L.L., 2014. Tropical Peat Swamp Forest Silviculture in Central Kalimantan: A series of Five Research Papers. Kalimantan Forest and Carbon Partnership (KFCP), Jakarta. https://doi.org/10.13140/RG.2.1.1071.9126.

Hardanto, A., Röll, A., Niu, F., Hendrayanto, A.M., Hölscher, D, 2017. Oil Palm and Rubber Tree Water Use Patterns: effects of Topography and Flooding. Front. Plant. Sci. 8, 452. https://doi.org/10.3389/fpls.2017.00452.

Hardie, M., Mendham, D., Corkrey, R., Hardiyanto, E., Maydra, A., Siregar, S., Wibowo, A., 2018. Effects of Eucalypt and Acacia plantations on soil water in Sumatra. New For. 49, 87–104. https://doi.org/10.1007/s11056-017-9607-3.

Heinrich, I., Balanzategu, D., Bens, O., Blasch, G., Blume, T., Böttcher, F., Heine, I., 2018. Interdisciplinary Geo-ecological Research across Time Scales in the Northeast German Lowland Observatory (TERENO-NE). Vadoze Zone J. 17, 1–25. https://doi.org/10.2136/vzj2018.06.0116.

Hirano, T., Kusin, K., Limin, S., Osaki, M., 2015. Evapotranspiration of tropical peat swamp forests. Glob. Chang. Biol. 21 (5), 914–1927. https://doi.org/10.1111/gcb.12653.

Hooijer, A., Page, S., Jauhiainen, J., Lee, W.A., Lu, X.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.

Horna, V., Schuldt, B., Brix, S., Leuschner, C., 2011. Environment and tree size controlling stem sap flux in a perhumid tropical forest of Central Sulawesi, Indonesia. Ann. For. Sci. 68, 1027–1038. https://doi.org/10.1007/s13595-011-0110-2.

Hoscilo, A., 2009. Fire regime, Vegetation Dynamics and Land Cover Change in Tropical peatland, Indonesia. University of Leicester. Phd thesesRetrieved from. https://lra.le.ac.uk/bitstream/2381/9932/1/PhD%20thesis_Agata%20Hoscilo.pdf.

Hung, T.T., Almeida, A.C., Eyles, A., Mohammed, C., 2016. Predicting productivity of Acacia hybrid plantations for a range of climates and soils in Vietnam. For. Ecol. Manage. 367, 97–111. https://doi.org/10.1016/j.foreco.2016.02.030.

Ismail, I., Haghighi, A.T., Marttila, H., Kurniawan, U., Karyanto, O., Kløve, B., 2021. Water table variations on different land use units in a drained tropical peatland island of Indonesia. Hydrol. Res. 52 (6), 1372–1388. https://doi.org/10.2166/nh.2021.062.

Jambul, R., Limin, A., Ali, A.N., Slik, F., 2020. Invasive Acacia mangium dominance as an indicator for heath forest disturbance. Environmen. Sustainab. Indic. 8, 100059 https://doi.org/10.1016/j.indic.2020.100059.

Jauhiainen, J., Hooijer, A., Page, S., 2012. Carbon dioxide emission from an Acacia plantation on peatland in Sumatra, Indonesia. Biogeosciences 9, 617–630. https://doi.org/10.5194/bg-9-617-2012.

Jelbert, K., Buss, D., McDonald, J., Townley, S., Franco, M., Stott, I., Hodgson, D., 2019. Demographic amplification is a predictor of invasiveness among plants. Nat. Commun. 10, 5602. https://doi.org/10.1038/s41467-019-13556-w.

Ježík, M., Blaženec, M., Střelcová, K., Ditmarová, Ľ., 2011. The impact of the 2003–2008 weather variability on intra-annual stem diameter changes of beech trees at a submontane site in central Slovakia. Dendrochronologia 29 (4), 227–235. https://doi.org/10.1016/j.dendro.2011.01.009.

Junaedi, A., 2018. Growth performance of three native species for pulpwood plantation in drained peatland of Pelalawan District, Riau. Indones. J. Forestry Res. 5, 119–132. https://doi.org/10.20886/ijfr.2018.5.2.119-132.

Kalima, T., Suharti, S., Sumarhani, S., Trethowan, L.A., 2020. Tree species diversity and ethnobotany of degraded peat swamp Forest in Central Kalimantan. Reinwardtia 19, 27–54. https://doi.org/10.14203/reinwardtia.v19i1.3819.

Kemenkunham, 2016. *Peraturan Pemerintah Nomor 57 Tahun 2016 (Goverment Policy No. 57 Year 2016)*. Retrieved October 2018, from Peraturan.go.id: Kementrian Hukum Dan Hak Asasi Manusia Republik Indonesia. Ministry of Law and Human Rights Republic of Indonesia. http://peraturan.go.id/pp/nomor-57-tahun-2016.html.

Kim, S., 2015. ppcor: Partial and Semi-Partial (Part) Correlation. https://CRAN.R-project.org/package=ppcor.

Kume, T., Takizawa, H., Yoshifuji, N., Tanaka, K., Tantasirin, C., Tanaka, N., Suzuki, M., 2007. Impact of soil drought on sap flow and water status of evergreen trees in a tropical monsoon forest in northern Thailand. For. Ecol. Manage 238, 220–230. https://doi.org/10.1016/j.foreco.2006.10.019.

Kuniyasu, M., Tetsuya, S., 2002. Environments and People of Sumatran Peat Swamp Forests I: distribution and Typology of Vegetation. Southeast Asian Stud. 40 (1), 74–86. Retrieved from. https://www.jstage.jst.go.jp/article/tak/40/1/40_KJ00000434259/_pdf.

Kuru, G., Wood, T., 2018. Forestry in Indonesia. NZ J. Forestry 63, 36–43. Retrieved from. http://www.nzjf.org.nz/free_issues/NZJF63_3_2018/B5495F92-EDDB-4fcb-BD03-91660E317138.pdf.

Lampela, M., Jauhiainen, J., Sarkkola, S., Vasander, H., 2017. Promising native tree species for reforestation of degraded tropical peatlands. For. Ecol. Manage. 394, 52–63. https://doi.org/10.1016/j.foreco.2016.12.004.

Laurén, A., Palviainen, M., Page, S., Evans, C., Urzainki, I., Hökkä, H., 2021. Nutrient Balance as a Tool for Maintaining Yield and Mitigating Environmental Impacts of Acacia Plantation in Drained Tropical Peatland—Description of Plantation Simulator. Forests 12 (3), 312. https://doi.org/10.3390/f12030312.

Lishinski, A., 2021. lavaanPlot: Path Diagrams For 'Lavaan' Models. Retrieved from. https://CRAN.R-project.org/package=lavaanPlot.

Ma, L., Lu, P., Zhao, P., Rao, X.-q., Cai, X.-a., Zeng, X.-p., 2008. Diurnal, daily, seasonal and annual patterns of sap-flux-scaled transpiration from an Acacia mangium plantation in South China. Ann. For. Sci. 65, 402. https://doi.org/10.1051/forest:2008013.

Martin, T., Brown, K., Kučera, J., Meinzer, F., Sprugel, D., Hinckley, T., 2001. Control of transpiration in a 220-year-old Abies amabilis forest. For. Ecol. Manage 152, 211–224. https://doi.org/10.1016/S0378-1127(00)00604-6.

Martins, G.S., Yuliarto, M., Antes, R., Sabki, Prasetyo, A., Unda, F., Acosta, J.J., 2020. Wood and Pulping properties variation of acacia crassicarpa A.Cunn. ex Benth. and Sampling Strategies for Accurate Phenotyping. Forests 11 (10), 1043. https://doi.org/10.3390/f11101043.

Mawazin, Octavia, D, 2019. Uji eradikasi Acasia crassicarpa di hutan gambut. Pros Sem Nas Masy Biodiv Indon 5 (2), 324–329. https://doi.org/10.13057/psnmbi/m050232.

McLaughlin, S.B., Wullschleger, S.D., Nosal, M., 2003. Diurnal and seasonal changes in stem increment and water use by yellow poplar trees in response to environmental stress. Tree Physiol. 23 (6), 1125–1136. https://doi.org/10.1093/treephys/23.16.1125.

Meijide, A., Röll, A., Fan, Y., Herbst, M., Niu, F., Tiedemann, F., Knohl, A., 2017. Controls of water and energy fluxes in oil palm plantations: environmental variables and oil palm age. Agric. For. Meteorol. 239, 71–85. https://doi.org/10.1016/j.agrformet.2017.02.034.

Meinzer, F.C., Goldstein, G., Andrade, J.L., 2001. Regulation of water flux through tropical forest canopy trees: do universal rules apply? Tree Physiol. 21 (1), 19–26. https://doi.org/10.1093/treephys/21.1.19.

Mendham, D.S., White, D.A., 2019. A review of nutrient, water and organic matter dynamics of tropical acacias on mineral soils for improved management in Southeast Asia. Aust. For. 82, 45–56. https://doi.org/10.1080/00049158.2019.1611991.

Merten, J., Röll, A., Guillaume, T., Meijide, A., Tarigan, S., Agusta, H., Hölscher, D., 2016. Water scarcity and oil palm expansion: social views and environmental processes. Ecol. Soc. 21 (2), 5. https://doi.org/10.5751/ES-08214-210205.

Miettinen, J., Shi, C., Liew, S.C., 2016. Land cover distribution in the peatlands of Peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. Glob. Ecol. Conserv. 6, 67–68. https://doi.org/10.1016/j.gecco.2016.02.004.

Mirmanto, E., 2010. Vegetation analyses of Sebangau peat swamp forest, Central Kalimantan. Biodiversitas 11 (2), 82–88. https://doi.org/10.13057/biodiv/d110206.

Mishra, S., Page, S.E., Cobb, A.R., Lee, J.S., Jovani-Sancho, A.J., Sjögersten, S., Wardle, D.A., 2021. Degradation of Southeast Asian tropical peatlands and integrated strategies for their better management and restoration. J. Appl. Ecol. 58, 1370–1387. https://doi.org/10.1111/1365-2664.13905.

Miyazawa, Y., Tateishi, M., Komatsu, H., Ma, V., Kajisa, T., Sokh, H., Kumagai, T., 2014. Tropical tree water use under seasonal waterlogging and drought in central Cambodia. J. Hydrol (Amst) 515, 81–89. https://doi.org/10.1016/j.jhydrol.2014.04.049.

Mojiol, A.R., Wahyudi, W., Nasly, N., 2014. Growth Performance of Three Indigenous Tree Species (Cratoxylum arborescens Vahl. Blume, Alstonia spathulata Blume, and Stemonurus scorpioides Becc.) Planted at Burned Area in Klias Peat Swamp Forest, Beaufort, Sabah, Malaysia. J. Wetlands Environm. Manag. 2 (1), 66–78. https://doi.org/10.20527/jwem.v2i1.32.

Nyadzi, G., Otsyina, R., Ong, C., 2002. Growth and Water Resource Utilization of Acacia Crassicarpa, Senna Siamea and Leucaena Pallida Tree Species Established in Rotational Woodlots Agroforestry System in Western Tanzania. In: *12th ISCO Conference*. Beijing. Retrieved from. https://www.tucson.ars.ag.gov/isco/isco12/VolumeIII/GrowthandWaterResourceUtilization.PDF.

O'Brien, J.J., Oberbauer, S.F., Clark, D.B., 2004. Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. Plant Cell Environ. 27 (5), 551–567. https://doi.org/10.1111/j.1365-3040.2003.01160.x.

Osaki, M., Tsuji, N., 2015. Tropical Peatland Ecosystems. Springer.

Otsamo, A., Hadi, T.S., Kurniati, L., Vuokko, R., 1999. Early performance of 12 Acacia crassicarpa provenances on an imperata cylindrica dominated grassland in South Kalimantan, Indonesia. J. Trop. For. Sci. 11 (1), 36–46.

Page, S., Rieley, J., 2018. Tropical Peat Swamp Forests of Southeast Asia. In: Finlayson, C.M., Milton, G.R., Prentice, R.C., Davidson, N.C. (Eds.), The Wetland Book. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-4001-3_5.

Page, S., Rieley, J., Banks, C., 2011. Global and regional importance of the tropical peatland carboon pool. Glob. Chang. Biol. 17, 798–818. https://doi.org/10.1111/j.1365-2486.2010.02279.x.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol. 193 (1), 30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x.

Poyatos, R., Čermák, J., Llorens, P., 2007. Variation in the radial patterns of sap flux density in pubescent oak (Quercus pubescens) and its implications for tree and stand transpiration measurements. Tree Physiol. 27, 537–548. https://doi.org/10.1093/treephys/27.4.537.

R Core Team, 2022. R: A language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. https://www.R-project.org/.

Raffelsbauer, V., Spannl, S., Peña, K., Pucha-Cofrep, D., Steppe, K., Bräuning, A., 2019. Tree Circumference Changes and Species-Specific Growth Recovery After Extreme Dry Events in a Montane Rainforest in Southern Ecuador. Front Plant Sci. 10, 342. https://doi.org/10.3389/fpls.2019.00342.

Ripin, Astiani, D., Burhanuddin, 2017. Jenis-Jenis Pohon Penyusun Vegetasi Hutan Rawa Gambut di Semenanjung Kampar Kecamatan Teluk meranti Provinsi Riau (Tree Species of Peat swamp Forest Vegetation in Semenanjung Kampar Subdistrict Riau Province). J. Hutan Lestari 5 (3), 807–813. Retrieved from. https://jurnal.untan.ac.id/index.php/jmfkh/article/download/21709/17549.

Rochmayanto, Y., Priatna, D., Wibowo, A., Salminah, M., Salaka, F.J., Lestari, N.S., Suryadi, D., 2021. Strategi Dan Teknik Restorasi Ekosistem Hutan Rawa Gambut. IPB Press, Bogor, Indonesia. Retrieved from. https://sustainability-dashboard.com/documents/115225/0/Priatna_Strategi+dan+Teknik+Restorasi+Hutan+Rawa+Gambut_EBOOK.pdf/90b38dc7-9c31-9092-695b-dcf38a0cb57d?t=1629972588569.

Röll, A., Niu, F., Meijide, A., Hardanto, A., Hendrayanto, Knohl, A., Hölscher, D, 2015. Transpiration in an oil palm landscape: effects of palm age. Biogeosciences 12, 5619–5633. https://doi.org/10.5194/bg-12-5619-2015.

Rosseel, Y., 2012. lavaan: an R Package for Structural Equation. J. Stat. Softw 48 (2), 1–36. https://doi.org/10.18637/jss.v048.i02.

Schymanski, S.J., Or, D., 2016. Wind increases leaf water use efficiency. Plant, cell, & Environment 39 (7), 1448–1459. https://doi.org/10.1111/pce.12700.

Sheil, D., 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Can. J. For. Res. 33, 2027–2035. https://doi.org/10.1139/x03-121.

Shinde, S., Naik, D., Cumming, J.R., 2018. Carbon allocation and partitioning in Populus tremuloides are modulated by ectomycorrhizal fungi under phosphorus limitation. Tree Physiol. 38 (1), 52–65. https://doi.org/10.1093/treephys/tpx117.

Siegmund, J.F., Sanders, T.G., Heinrich, I., Maaten, E.v., Simard, S., Helle, G., Donner, R. V., 2016. Meteorological Drivers of Extremes in Daily Stem Radius Variations of Beech, Oak, and Pine in Northeastern Germany: an Event Coincidence Analysis. Front. Plant. Sci. 7, 733. https://doi.org/10.3389/fpls.2016.00733.

Spannl, S., Volland, F., Pucha, D., Peters, T., Cueva, E., Bräuning, A., 2016. Climate variability, tree increment patterns and ENSO-related carbon sequestration reduction of the tropical dry forest species Loxopterygium huasango of Southern Ecuador. Trees 30, 1245–1258. https://doi.org/10.1007/s00468-016-1362-0.

Suárez, J.C., Casanoves, F., Bieng, M.A., Melgarejo, L.M., Rienzo, J.A., Armas, C., 2021. Prediction model for sap flow in cacao trees under different radiation intensities in the western Colombian Amazon. Scient. Report 11, 10512. https://doi.org/10.1038/s41598-021-89876-z.

Suhartati, S., Aprianis, Y., Pribadi, A., Rochmayanto, Y., 2013. Kajian Dampak Penurunan Daur Tanaman Acacica crassicarpa A. Cunn Terhadap Nilai Produksi dan

Sosial. J. Penelitian Hutan Tanaman 10 (2). https://doi.org/10.20886/jpht.2013.10.2.109-117.

Sulistiyanto, Y., 2004. Nutrient Dynamics in Different Sub-Types of Peat Sawmp Forest in Central Kalimantan, Indonesia. The University of Nottingham. Ph.D. thesisRetrieved from. http://eprints.nottingham.ac.uk/12597/1/404784.pdf.

Sumarga, E., Hein, L., Hooijer, A., Vernimmen, R., 2016. Hydrological and economic effects of oil palm cultivation in Indonesian peatlands. Ecol. Soc. 21 (2), 52. https://doi.org/10.5751/ES-08490-210252.

Susanti, A., Karyanto, O., Affianto, A., Ismail, Pudyatmoko, S., Aditya, T., Nainggolan, H. A., 2018. Understanding the impacts of recurrent peat fires in Padang Island – Riau Province, Indonesia. J. Ilmu Kehutanan 12, 117–126. https://doi.org/10.22146/jik.34126.

Suwito, D., Suratman, Poedjirahajoe, E, 2021. The Potency of Cratoxylum arborescens Blume (Geronggang) and Combrecarpus rotundatus Dans (Tumih) as Natural Regeneration in Degraded Tropical Peat Swamp Forest. JISDeP 2 (3). https://doi.org/10.46456/jisdep.v2i3.185.

Tata, H.L., Nuroniah, H.S., Ahsania, D.A., Anggunira, H., Hidayati, S.N., Pratama, M., Kolka, R., 2021. Flooding tolerance of four tropical peatland tree species in a nursery trial. Biorxiv. https://doi.org/10.1101/2021.12.26.474202.

Taufik, M., Minasny, B., McBratney, A.B., Dam, J.C., Jones, P.D., Lanen, H.A., 2020. Human-induced changes in Indonesian peatlands increase drought severity. Environ. Res. Lett. 15, 084013 https://doi.org/10.1088/1748-9326/ab96d4.

Uda, S.K., Hein, L., Sumarga, E., 2017. Towards sustainable management of Indonesian tropical peatlands. Wetlands Ecol. Manage. 25, 683–701. https://doi.org/10.1007/s11273-017-9544-0.

Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2013. Seasonal and daily cycles of stem radial variation of Pinus pinaster in a drought-prone environment. Agric. For. Meteorol. 18, 173–181. https://doi.org/10.1016/j.agrformet.2013.06.009.

Wijedasa, L.S., Jauhiainen, J., Könönen, M., Lampela, M., Vasander, H., Leblanc, M.-.C., Clements, G.R., 2017. Denial of long-term issues with agriculture on tropical peatlands will have devastating consequences. Glob. Chang. Biol. 23, 977–982. https://doi.org/10.1111/gcb.13516.

Winters, G., Otieno, D., Cohen, S., Bogner, C., Ragowloski, G., Paudel, I., Klein, T., 2018. Tree growth and water-use in hyper-arid Acacia occurs during the hottest and driest season. Oecologia 188, 695–705. https://doi.org/10.1007/s00442-018-4250-z.

Wood, S., 2011. Fast stable restricted maximum likelihood and. J R Stat Soc Series B Stat. Methodol. 73 (1), 3–36.

Worbes, M., Herawati, H., Martius, C., 2017. Tree Growth Rings in Tropical Peat Swamp Forests of Kalimantan, Indonesia. Forests 8, 336. https://doi.org/10.3390/f8090336.

Yulianti, R., Marsono, D., Yunianto, T., 2010. Analisis Vegetasi Hutan Rawa Gambut Pascakebakaran di Wilayah Desa Sebangau dan Desa Taruna Jaya. Majalah Geografi Indonesia 24, 1. https://doi.org/10.22146/mgi.13341.

Yuwati, T.W., Rachmanadi, D., Pratiwi, Turjaman, M., Indrajaya, Y., Nugroho, H., Bastoni, 2021. Restoration of Degraded Tropical Peatland in Indonesia: a Review. Land (Basel) 10 (11), 1170. https://doi.org/10.3390/land10111170.

Zhao, X.-.W., Zhao, P., Zhu, L.-.W., Zhao, X.-.H., 2016. Applying time series models to estimate time lags between sap flux and micro-meteorological factors. Écoscience 23 (1–2), 13–27. https://doi.org/10.1080/11956860.2016.1202885.

Zweifel, R., Haeni, M., Buchmann, N., Eugster, W., 2016. Are trees able to grow in periods of stem shrinkage? New Phytol. 211 (3), 839–849. https://doi.org/10.1111/nph.13995.