

# Water-use characteristics of *Syzygium antisepticum* and *Adinandra integerrima* in a secondary forest of Khao Yai National Park in Thailand with implications for environmental management

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**Background.** Forests in Southeast Asia have been disrupted by widespread deforestation and land use change; hence, many reforestation projects have emerged in this region. However, planting trees efficiently is difficult because the changing environments and tree size could affect water consumption by different tree species under climate variability. Thus, the information regarding water-use characteristics of different tree species and sizes is important for selecting tree species for reforestation.

**Methods.** We estimated tree water use ( $T$ ) of dominant species including *Syzygium antisepticum* and *Adinandra integerrima*, hereafter  $Sa$  and  $Ai$ , respectively, in a secondary tropical forest in Khao Yai National Park, Thailand, using sap flow data, and compared  $T$  between species and size classes. Additionally, we evaluated the responses of  $T$  of both species in each size class to environmental factors including soil moisture and vapor pressure deficit (VPD) which represent soil and atmospheric humidity, respectively.

**Results.** Results showed consistently higher  $T$  in  $Sa$  compared to  $Ai$  across ranges of VPD and soil moisture. Under low soil moisture,  $T$  of  $Sa$  responded to VPD, following a saturating exponential pattern while  $Ai$  had unchanged water use across VPD, regardless of tree size. No responses of  $T$  to VPD were observed in either species when soil water was moderate. When soil moisture was high,  $T$  of both species significantly increased and reached saturation at high VPD, albeit the responses were less sensitive in large trees. Our results imply that  $Ai$  may be suitable for reforestation in areas where droughts frequently occur through its conservative water-use behavior, thus benefiting downstream ecosystems with increased runoff. In contrast,  $Sa$  may benefit areas with frequent floods because it has high water consumption during high water availability, thus deterring runoff from forests when storms come. However, mixed planting species should be appropriate for reforestation in areas where extreme events rarely occur because both species can maintain water use rates at moderate soil moisture, regardless of tree size. This study emphasizes the dependency of  $T$  responses to VPD on tree species and size. Such information will benefit tree species selection for reforestation that adapt well to environments and support policy design on forest and water management. Depending on the purposes of reforestation,  $Sa$  and  $Ai$  may provide either benefits or negative effects to the ecosystems.

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## Abstract

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environmental factors including soil moisture and vapor pressure deficit (VPD) which represent soil and atmospheric humidity, respectively.

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## Introduction

Over an annual timescale, precipitation is coarsely partitioned into evapotranspiration and runoff in the forest water cycle. Because tree water use ( $T$ ) constitutes 40–90% of evapotranspiration (Jasechko et al. 2013; Deb Burman et al. 2019), the quantity of  $T$  affects the amount of precipitation that ultimately contributes to runoff, impacting the downstream ecosystems. With the projected increases of global climate change impacts,  $T$  may be altered through changes in environmental conditions including temperature and precipitation regimes, severity of weather and climate extremes such as droughts and floods (Menezes-Silva et al. 2019). Such changes will certainly affect the responses of  $T$  to environmental factors, therefore governing the outflow from forests. Thus, evaluating such responses would provide insights into environmental management that involves water cycling, such as predicting runoff from forests which may result in floods or droughts in the downstream ecosystems.

The variations of  $T$  are mainly related to tree size (Meinzer et al. 2005; Jung et al. 2011) and environmental factors including soil water availability, solar radiation, and vapor pressure deficit (VPD) which represents atmospheric humidity (Xu et al. 2020; Gutierrez Lopez et al. 2021). Several previous studies reported significant variations of  $T$  with tree size. The relationship between tree diameter and  $T$  were found among several species of angiosperms (Meinzer et al. 2005), *Eucalyptus crebra* and *Callitris glaucophylla* in evergreen woodland in Australia (Zeppel and Eamus 2008), and trees in a temperate mixed-deciduous forest in South Korea (Jung et al. 2011). Additionally, different tree sizes have been linked to different

responses to droughts with large trees being more vulnerable than small trees to drought because of greater exposure to atmospheric demand (Bennett et al. 2015; Stovall et al. 2019). However, information of the effects of tree size on  $T$  is still lacking in secondary tropical forests. The effects of environmental factors on  $T$  vary in different forest types and regions. For example, when soil moisture is not limited,  $T$  strongly responds to VPD, which increases when the air humidity decreases, and solar radiation in an old-growth spruce forest in the Ore Mountains, Germany (Clausnitzer et al. 2011). Under soil water stress, Brum et al. (2018) found that  $T$  could decrease with increasing VPD during an extreme drought in an Amazonian tropical rainforest. On the other hand, Spanner et al. (2022) found that the sensitivity of  $T$  to soil moisture varied with species, with some increasing and some decreasing during the dry period in an old-growth upland forest in central Amazon. Thus, changing environmental conditions can alter the response patterns of  $T$ .

Forests in Southeast Asia provide a wide range of important ecosystem services to many people and communities. Unfortunately, these forests have been disrupted by widespread deforestation and land use change (Stibig et al., 2014; Zeng et al. 2018), resulting in various stages of forests in the same area (Curtis et al. 2018). In particular, the areas that were previously used for agricultural purposes have been abandoned for several years, and naturally or artificially transformed into secondary forests. Consequently, many of the degraded forests may not contribute much to improving biodiversity and mitigating climate change through carbon dioxide removal from the atmosphere. Therefore, reforestation projects have emerged in many countries in the tropics, highlighting the use of native species to avoid competition with other native trees, which can help restoring biodiversity and sequestering carbon (Hooper et al. 2002). However, planting more trees in forests may raise some concerns because trees are potentially heavy water users and might deplete water resources (Jackson et al. 2005). Also, reforestation may not be desirable in certain areas because it may reduce water availability for the existing trees and increase evapotranspiration rate (Van Kantén and Vaast 2006) and thus leading to reductions in runoff (Li et al. 2014). With these regards, an appropriate selection of tree species for planting is among the priority tasks for forest restoration since species-specific water-use characteristics play an important role in changing the components of the forest hydrologic cycle (van Dijk and Keenan 2007). However, the availability of such information is still limited in tropical forests, especially in secondary ones. Hence, it is imperative to evaluate the response patterns of  $T$  to environmental factors in secondary tropical forests that would offer necessary information on species-specific water-use characteristics.

Khao Yai National Park (KYNP) is a UNESCO world heritage site. Most of the areas of KYNP consist of a mosaic of different stages of vegetation succession with more than 60% of the forests undergoing different stages of regeneration while the remainder are old-growth forests. Thus, secondary forests in KYNP are important to biodiversity conservation and climate change mitigation through the regulation of atmospheric carbon. With these regards, this study was performed in a secondary tropical forest at KYNP, representing a young forest aged ~10 years. In this study site, the dominant tree species include *Syzygium antisepticum* and *Adinandra*

*integerrima*. *Syzygium antisepticum* can be found as the dominant species in other tropical forests such as tropical evergreen swamp forest in Cambodia (Theilade et al. 2011), dry evergreen forest in northeastern Thailand (Bunyavejchewin 1999) and tropical coastal sand dune in southern Thailand (Marod et al. 2020). *Adinandra integerrima* can be found in other parts of Thailand, such as Doi Inthanon National Park in the northern region (Georgiadis 2022) and other countries in the tropics, such as Cambodia, China, Laos, and Vietnam (Tagane et al. 2020). Despite the widespread presence of these species in Thailand and neighboring countries of Southeast Asia, the information of water-use characteristics of both species is still lacking. Therefore, this study aims to (1) estimate  $T$  of *Syzygium antisepticum* and *Adinandra integerrima* in a secondary tropical forest in KYNP and compare  $T$  of both species in different tree size classes, and (2) evaluate the responses of  $T$  to environmental factors of both species in different tree size classes. The collected data covered a period from 18 September 2020 to 26 November 2022, including a wide range of environmental conditions. The outcome from this study would improve the understanding of species-specific water-use characteristics in secondary forests which can support policy design on the management of tropical forests and water resources. In addition, findings from this study may provide a recommendation for selecting appropriate tree species for forest restoration in the tropical region.

## Materials & Methods

### *Study site and measurements of the environmental variables*

The study site was conducted in Khao Yai National Park, Thailand (14°26'31" N, 101°22'55" E). Khao Yai National Park covers an area of about 200 km<sup>2</sup> in Nakhon Ratchasima, Saraburi, Prachinburi and Nakhon Nayok Provinces in Thailand. This region is dominated by monsoon climate, where dry season usually lasts from November to April and from May to October for wet season (Brockelman et al. 2017). Based on recorded data between 1994-2018, the overall mean annual temperature was 22.4 °C. The mean annual rainfall was 2,100 mm. Khao Yai National Park is characterized by different stages of forest succession comprising primary forests and various stages of secondary forests. In this study, we performed the study in a secondary forest representing a young forest which is in Nakhon Nayok Province. The study site has an area of 2 ha and the age of approximately 10 years (Chanthorn et al. 2017). Its mean canopy height is 15 m and stem density of 1,226 trees ha<sup>-1</sup>. The soil type of this plot is gray brown soil. In 2020, a 20 m tall tower was constructed for installing weather sensors above the forest canopy in the plot. Environmental conditions that influence  $T$  including atmospheric humidity, solar radiation, and soil moisture have been continuously monitored since then. Air temperature ( $T$ , °C), relative humidity (RH, %) and photosynthetically active radiation (PAR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were measured by a temperature and relative humidity probe (EE181-PT, Campbell Scientific) and a quantum sensor (LI190R-PT, Campbell Scientific), respectively. Soil moisture sensors (Water content reflectometer, CS616-PT-U, Campbell Scientific) were installed to monitor volumetric soil moisture ( $\theta$ , m<sup>3</sup>m<sup>-3</sup>) at 5, 10, 15 and 30 cm depth because trees may access water from multiple depths in the soil (Wang et al. 2019). We randomized the points to install soil moisture

sensors around the tower. Two soil moisture sensors were installed at each depth of 5, 10 and 15 cm. However, soil moisture at 30 cm depth was monitored by one soil moisture sensor because soil moisture at subsoil was less sensitive to changing environmental conditions than topsoil (Rong et al. 2017). Rainfall (mm) was measured by tipping rain gauge bucket (TE525MM-PT, Campbell Scientific). All sensors were connected to a datalogger (CR1000 series; Campbell Scientific, Logan, UT) which recorded data every 30 minutes. Air temperature and relative humidity are used to calculate vapor pressure deficit (VPD, kPa), which is the difference between actual vapor pressure and saturated vapor pressure (SVP), from the following equations (Monteith and Unsworth 1990)

$$SVP = 610.7 \times 10^{\frac{7.5T}{237.5 + T}} \quad (1)$$

$$VPD = (1 - \frac{RH}{100}) \times SVP \quad (2)$$

To facilitate the cross-site comparison, Relative Extractable Water (REW), which represents the availability of soil water in the rooting zone, was used in the analysis and was calculated according to Granier et al. (2000)

$$REW = \frac{\theta - \theta_m}{\theta_{FC} - \theta_m} \quad (3)$$

where  $\theta_m$  is minimum volumetric soil moisture and  $\theta_{FC}$  is the soil water at field capacity. In the plot where soil water at field capacity has not been measured, we used maximum volumetric soil moisture during the study period as  $\theta_{FC}$  for the REW calculation (Tor-ngern et al. 2018).

### ***Species selection and tree sampling***

The tree species were chosen based on the relative abundance of basal area in this plot, which was calculated from the basal area of one species relative to total basal area of all species within the site. To compare species difference in tree water use, two dominant tree species with similar leaf phenology were selected for this study. As a result, *Syzygium antisepticum* and *Adinandra integerrima*, hereafter *Sa* and *Ai*, respectively, which have evergreen leaf habit, were chosen to measure water flow rate. To compare differences in  $T$  due to tree size, we selected trees of both species based on the distribution of tree diameter in this plot. We partitioned the tree size classes into 10-cm intervals and sampled 3 trees in both species for each size class. However, due to the limitation in distance between measured trees to the data logger, 4 trees of *Sa* and 5 trees of *Ai* were selected for the measurement (Table 1).

### ***Sap flux measurement and scaling up from the point measurement to whole-tree water use***

Sap flux density ( $J_s$ ), which represents water mass flowing through a unit area per time in trees, was measured using self-constructed thermal dissipation probes (TDPs) (Granier 1985). Each TDP set contains one non-heated and one heated probe being supplied with a constant ~0.2 W electrical power. Before inserting TDPs into the stems, debarking around the drilling point was done before drilling the holes for TDP installation. Two holes were drilled with approximately 10-15 cm spacing between two probes. Based on previous studies in pine trees, the patterns of radial variation in  $J_s$  along the sapwood depth were observed with higher  $J_s$  in the outer sapwood layers than that in the inner sapwood layers (Ford et al. 2004; Oishi et al. 2008). Therefore, ignoring radial variation of  $J_s$  may produce error when scaling up from  $J_s$  to  $T$ . However,

previous studies in tropical forests that use similar sap flow sensors only measured  $J_s$  at the outer sapwood because of the unknown pattern of sapwood area in tropical tree species (Horna et al. 2011; Raquel Salas-Acosta et al. 2022). In addition, most tropical trees have diffuse-porous wood without distinct annual rings and tend to have sap flow rate that is relatively uniform along the radial sapwood depth (Lu et al. 2004). Therefore, we assumed that  $J_s$  was uniform along the sapwood depth of the selected trees when scaling from single-point measurements to the whole-tree level, and only measured  $J_s$  at the outer 2-cm sapwood at breast height (~1.3 m above ground). In addition, azimuthal variation of  $J_s$  may produce variation when scaling up from  $J_s$  to  $T$  (Lu et al. 2000; James et al. 2002; Tateishi et al. 2008). This variation depends on the effect of forest canopy shading by neighboring trees. In other words, trees may be obstructed from sunlight by canopy shading from surrounding trees leading to varying  $J_s$  along the circumference. In this study, the surrounding trees were similarly distributed around the measured trees. Nevertheless, we installed two sensors in the north and the south directions in some trees which may be influenced by canopy shading at certain time during the day. Data from TDPs were recorded as 30-minute means of voltage difference between the probes ( $\Delta V$ , mV) by the same data logger (CR1000, Campbell Scientific, Logan, UT, USA) that recorded environmental data. For the analysis, the voltage difference was converted to  $J_s$  ( $\text{g m}^{-2} \text{s}^{-1}$ ) using an empirical equation (Granier 1987)

$$J_s = 118.99 \times 10^{-6} \times \left( \frac{\Delta V_m - \Delta V}{\Delta V} \right)^{1.231} \quad (4)$$

where  $\Delta V_m$  is the maximum voltage difference under no flow conditions which usually occur at night and when VPD is low. The Baseliner program version 4.0 was used to select  $\Delta V_m$  to calculate  $J_s$  (Oishi et al. 2016). The program automatically determines maximum daily  $\Delta V$  to represent  $\Delta V_m$ . Maximum voltage difference may occur every night if air humidity is very high, or VPD reaches 0 kPa, resulting in potentially zero water flow. However, this assumption is not valid for many ecosystems due to nighttime transpiration or recharge of stem water (Phillips and Oren 1998). For these reasons, no universal rule exists for identifying  $\Delta V_m$ . The Baseliner software takes an approach to  $\Delta V_m$  estimation by first identifying points in time where flow is likely zero and allowing the user to visually inspect and modify those points.

To scale up from  $J_s$  to  $T$ , we employed the following approach. Daily sum  $J_s$  ( $\text{g m}^{-2} \text{day}^{-1}$ ) was considered in the analysis to avoid issues related to nighttime recharge of stem water that may increase as soil moisture becomes more depleted (Phillips and Oren 1998). When nighttime recharge increases with decreasing soil moisture, the proportions of sap flux at night relative to sap flux during the day become larger. This problem can be avoided when calculating  $T$  as daily sum (Phillips and Oren 1998). For trees with sensors in the north and the south direction, daily sum  $J_s$  from both sensors were averaged to a mean daily  $J_s$  ( $J_{\text{mean}}$ ) for each of them (Kunert et al. 2012). The following equation was used to estimate  $T$

$$T = 1800 \times 10^{-7} \times J_{\text{mean}} \times A_s \quad (5)$$

where  $T$  is daily tree water use ( $\text{L d}^{-1}$ ),  $J_{\text{mean}}$  is mean daily sum  $J_s$  ( $\text{g m}^{-2} \text{day}^{-1}$ ) and  $A_s$  is sapwood area ( $\text{cm}^2$ ). In both species,  $A_s$  was estimated based on an allometric equation which



was derived from 13 dominant species in an old growth and a secondary forest (the same plot as this study site) at Khao Yai National Park as follows (Yaemphum et al. 2022)

$$y = 0.728x^{1.998} \quad (6)$$

where  $y$  is sapwood area ( $\text{cm}^2$ ),  $x$  is diameter at breast height (cm).

### Data analysis

For the analysis, we used the environmental data and  $T$  between 18 September 2020 to 26 November 2022. The data covered a period of two years which represents a wide range of environmental conditions. To avoid potential effects of wet canopy conditions that may inhibit  $T$  when leaf surface is covered with water droplets (Aparecido et al. 2016), we selected the days under rain-free condition to perform the analysis. To compare  $T$  of two dominant tree species,  $Sa$  and  $Ai$ , we performed an independent t-test by selecting  $T$  under non-limiting soil moisture and high light condition. The steps for selecting  $T$  included (1) partitioning  $T$  data of each day into each species, (2) selecting the days that have REW values falling above the mean plus two standard deviations of each group of REW data and then selecting the days with PAR values that were higher than the mean plus two standard deviations of each group of PAR data. After the steps of data selection, we had two subsets of data with different species under non-limiting soil moisture and high light conditions. Then, an independent t-test was used to compare the selected data from the  $Sa$  and  $Ai$  and thus testing the difference of  $T$  between species.

To compare  $T$  in different tree size classes, trees were categorized into two size classes based on the size distribution of each species as presented in Table 1 into large trees ( $\text{DBH} \geq 10$  cm for  $Ai$  and  $\text{DBH} \geq 20$  cm for  $Sa$ ) and small trees ( $\text{DBH} < 10$  cm for  $Ai$  and  $\text{DBH} < 20$  cm for  $Sa$ ). We analyzed the difference of  $T$  of each species in different tree size classes using an independent t-test by selecting  $T$  under non-limiting soil moisture and high light condition. The criteria for selecting  $T$  under non-limiting soil moisture and high light conditions of both species in different tree size classes were (1) selecting the days falling above the mean plus two standard deviations of REW and then (2) selecting the days falling above the mean plus two standard deviations of PAR. After this step, we had two subsets of data in each species with different tree size classes under non-limiting soil moisture and high light conditions. An independent t-test was then used to test the difference of  $T$  of each species in different tree size classes.

To evaluate the responses of  $T$  to environmental factors including VPD and REW, we performed a boundary line analysis (Schäfer et al. 2000) to obtain the response of  $T$  to environmental factors under non-limiting conditions. Trees in both species were categorized into two size classes based on the size distribution of sampled trees as mentioned above. After that,  $T$  from all trees in the same category was averaged to mean  $T$  ( $T_{\text{mean}}$ ) for each day. Tree water use varies with VPD, REW and PAR (Phillips and Oren 2001). Based on our data during the study period, VPD and PAR were highly correlated ( $r = 0.79$ ,  $p = <0.001$ ), therefore we focused on VPD and REW as environmental driving variables. We performed boundary line analysis after partitioning data into three REW classes based on the REW distribution including low soil moisture ( $\text{REW} < 0.1$ ), intermediate soil moisture ( $\text{REW} 0.1-0.4$ ) and high soil moisture ( $\text{REW} > 0.4$ ). With two classes of tree size (large and small), we had six subsets of data in both species.



Each subset was subjected to the boundary line, designed to select data representing maximum  $T_{\text{mean}}$  for each tree size in each REW class along the range of VPD. The upper boundary line was derived by (1) partitioning  $T_{\text{mean}}$  data of each REW class into at least five VPD intervals for appropriate number of data points in regression analysis (at least five data points per analysis), (2) calculating the mean and standard deviation of  $T_{\text{mean}}$  in each interval, (3) removing outliers using Dixon's test, (4) selecting the data falling above the mean plus one standard deviation and (5) averaging the selected data for each VPD interval. For each tree size and REW classes, the mean  $T_{\text{mean}}$  values of all VPD intervals obtained in step (5) were analyzed by regression analysis. All regression analyses were performed in SigmaPlot version 12.0 (Systat Software, Inc., San Jose, CA USA). An F-test was used to compare fitting results on different datasets with the same function (e.g., the analysis of  $T$  response to VPD in all REW classes). Data management and analysis were performed with Rstudio, version 1.3.1073 (The R Foundation for Statistical Computing, <http://www.R-project.org>).

## Results

### *Environmental conditions in the study site*

During the study period, there were 52% rainy and 48% rain-free days. The average daily VPD and PAR inversely corresponded with rainfall, being low when rainfall occurred and vice versa. The maximum and minimum values of PAR during the study period were 575 and 57.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, with an average of  $345.76 \pm 103.47 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The average daily VPD was  $0.34 \pm 0.23 \text{ kPa}$ . Our data showed that VPD and PAR were highly correlated ( $r = 0.79$ ,  $p < 0.001$ ). Volumetric soil moisture of all depths was averaged into  $\theta_{\text{average}}$ . The maximum and minimum  $\theta_{\text{average}}$  during the study period were 0.2 and 0.04  $\text{m}^3 \text{m}^{-3}$ , respectively. The  $\theta_{\text{average}}$  was then used to calculate REW with the average value of  $0.44 \pm 0.25$ . Figure 1 summarizes the environmental conditions during the study period.

### *Tree water use of Syzygium antisepticum and Adinandra integrerrima*

Tree water use of both species during the study period are shown in Figure 2. The average  $T$  values with one standard deviation of  $Sa$  and  $Ai$  were  $21.48 \pm 7.73$  and  $10.01 \pm 4.04 \text{ L d}^{-1}$ , respectively. Comparing  $T$  between both species, we found that  $T$  of  $Sa$  was significantly higher than that of  $Ai$  under high soil moisture and high light conditions ( $p < 0.0001$ ; Figure 3A). Considering the difference in sizes for each species, under high soil moisture and high light conditions,  $T$  of large trees was significantly higher than that of small trees in both  $Sa$  and  $Ai$  ( $p < 0.0001$  for both; Figure 3B and 3C).

### *Responses of tree water use to environmental factors in different tree size classes*

Figure 4 summarizes results of the responses of  $T$  to VPD under various REW ranges, with the resulting regression statistics in Table 2. At low soil moisture ( $\text{REW} < 0.1$ , black circles),  $T$  of  $Sa$  increased with increasing VPD and gradually saturated at high VPD while that of  $Ai$  did not respond to the changing VPD, regardless of tree size. Under intermediate soil moisture condition ( $\text{REW } 0.1\text{-}0.4$ , gray squares),  $T$  of both species in both sizes did not respond to VPD. Under high

soil moisture ( $REW > 0.4$ , red triangles),  $T$  of both species in both sizes followed the saturating exponential pattern as previously described in the case of low soil moisture. However, the sensitivity of increasing  $T$  at low VPD was different between the species and size class. In both species,  $T$  of large trees was less sensitive to rising VPD than small ones (Table 2).

## Discussion

Overall, the environmental data during the study period represent a wide range of environmental conditions which facilitates the analysis of  $T$  responses to the environments. The maximum  $T$  of *Sa* in our data ( $47.54 \text{ L d}^{-1}$ ) was higher than the values that were found in  $T$  of *Syzygium cordatum* in a peat swamp forest in South Africa (Clulow et al. 2013), ranging from  $30 \text{ L d}^{-1}$  in the winter to  $45 \text{ L d}^{-1}$  in the summer. Moreover, our average  $T$  of *Sa* was within the range of  $T$  found in *Eugenia natalitia* ( $2$  to  $28 \text{ L d}^{-1}$ ), which is the same family as *Sa*, as reported by the same study. Although we did not find studies that reported  $T$  values of *Ai* or similar genus,  $T$  of *Ai* was within the range of  $T$  ( $10$  to  $1,180 \text{ L d}^{-1}$ ) found in 93 tree species from 52 reviewed publications that estimated whole-plant water use for trees growing in worldwide natural forests or plantations (Wullschleger et al. 1998). The study reported that the rates of water use ranged from  $10 \text{ L d}^{-1}$  for trees in a 32-year-old plantation of *Quercus petraea* L. ex Liebl. in eastern France to  $1,180 \text{ L d}^{-1}$  for an overstory tree, *Euperua purpurea* Bth., growing in the Amazonian rainforest. Overall,  $T$  values of both species in this study were within the wide ranges found in previous studies in tropical settings (Table 3).

Previous studies showed that the variation of  $J_s$  among trees of different ages and sizes is relatively low (Kumagai et al. 2007; Jaskierniak et al. 2016); thus, sapwood area may be a major determinant of  $T$  in this study. In fact, based on our data,  $J_s$  of trees in different tree size classes were marginally different in *Sa* and *Ai* ( $p = 0.01$  and  $0.02$ , respectively). Additionally, higher water use in large trees may imply their deeper access to groundwater whereas small trees may only consume water from shallow soil as previously shown in a study investigating water use by *Acer saccharum* Marsh. in different sizes (Dawson 1996). Moreover, other research in tropical forests reported that large trees consume much more water relative to small trees as indicated by the positive relationship between water consumption and tree size (O'Grady et al. 1999; Meinzer et al. 2001; Horna et al. 2011; Aparecido et al. 2016).

The response pattern of saturating exponential function of  $T$  with VPD found in this study is similar to the one observed in various tree species in a wide range of tropical forests, including a lowland tropical forest of Central and northern South America (Meinzer et al. 1993), a primary lowland tropical forest in eastern Amazon (Brum et al. 2018) and a per-humid tropical forest of Central Sulawesi in Indonesia (Horna et al. 2011). Under dry conditions, our results indicate that *Sa* was sensitive to increasing VPD while *Ai* can maintain their water use rate regardless of changes in VPD, regardless of tree size. This implies that *Ai* may be more tolerant to drought than *Sa* and may have strong control over their water use under low soil moisture, regardless of tree size, which can prevent it from negative effects from droughts. This result agreed with a previous study that investigated drought tolerance of both species in this site (Unawong et al.

2022). Based on tree hydraulic measurement, the study reported that xylem pressure at 50% loss of hydraulic conductivity ( $P_{50}$ ) of *Ai* and *Sa* were  $-5.97$  and  $-4.71$  MPa, respectively. It is implied that species with lower  $P_{50}$  have greater resistance to embolisms, thus allowing better adaptation to the environments where water stress frequently occurs (Maherali et al. 2004). When comparing  $T$  in different size classes of *Sa*, large trees were less sensitive to rising VPD at lower VPD ranges. The less sensitivity of large trees to rising VPD leads to slower decrease in water consumption rate to save water than small trees, resulting in potentially greater vulnerability to hydraulic failure during drought in large trees. Previous studies have shown size-dependent sensitivity to droughts in many ecosystems. A synthetic study using data on tree growth and mortality, which were collected during 40 drought events in forests worldwide, showed that droughts consistently exerted negative impacts on the growth and mortality rates of larger trees (Bennett et al. 2015). Greater vulnerability of large trees to drought could be affected by the higher exposure to radiation and atmospheric demand because of increasing tree height (Roberts et al. 1990; Nepstad et al. 2007). Moreover, large trees have to transport water to greater height, which is against the effects of gravity, thus facing greater hydraulic failure (Ryan et al. 2006; Zhang et al. 2009). Thus, large *Sa* may be at higher risk to hydraulic failure when drought is more pronounced, plausibly leading to increasing mortality rates (Choat et al. 2018). At moderate soil water, the results indicated that both species could maintain their tree water use, regardless of tree size. Under high soil moisture condition,  $T$  of both species in both sizes also followed the saturating exponential pattern as in the case of low soil moisture condition. However, the sensitivity of increasing  $T$  at low VPD was different between sizes. In both species,  $T$  of large sizes was less sensitive to rising VPD than small ones. In other words, when the air becomes dry, small trees may decrease water consumption rate faster to save water than large trees. This may be partly because small trees mainly use shallow soil water whereas large trees can access water from deeper soil (Brum et al. 2018), allowing less sensitivity to droughts in large trees.

### ***Implications for environmental management***

The results from this study imply that *Sa* may provide ecosystem disservice in dry areas due to its high water consumption which results in low water supply for the downstream community, but it may slow down runoff in the region that experiences heavy precipitation. In contrast, *Ai* may provide ecosystem benefits by conservatively using water, even under drought conditions, but may increase runoff when storms come with high rainfall. Another implication is that *Ai* may be suitable for reforestation in the area where droughts frequently occur in downstream ecosystems through its conservative water-use behavior, thus maintaining runoff from the forests during drought. Moreover, because *Ai* showed relatively constant water use regardless of tree size, the species would still provide such benefits to the ecosystems even when it grows larger in the future. In contrast, *Sa* may be appropriate for reforestation in the area with frequent floods because it has high water consumption during high water availability which may decelerate runoff from forests into downstream ecosystems. This would benefit the downstream ecosystems when storms occur. Regardless, mixed planting species seem to be suitable for reforestation in

the area where extreme events do not frequently occur because both species can maintain their water use at moderate soil moisture regardless of tree size, therefore preventing the depletion of soil water availability. In addition, mixed planting species could reduce the competition for limited water resources because the differences in root structures of different tree species lead to less competition for water (Schwendenmann et al. 2015). Nevertheless, reforestation projects should emphasize the use of native species to avoid competition with other native trees in the site (Hooper et al. 2002).

## Conclusions

We estimated tree water use ( $T$ ) of dominant tree species including *Syzygium antisepticum* ( $Sa$ ) and *Adinandra integerrima* ( $Ai$ ) in a secondary tropical forest in Khao Yai National Park from sap flux density ( $J_s$ ) which was continuously monitored with custom-made thermal dissipation probes and compared  $T$  of both species in different tree size classes. In addition, we evaluated the responses of  $T$  to environmental factors of both species in different tree size classes. The results showed that  $T$  of  $Sa$  was significantly higher than  $Ai$  and that large trees had higher  $T$  than small ones which was related to relatively lower sapwood area in the small trees. Further analysis on the response patterns of  $T$  showed that  $Sa$  was more sensitive to increasing VPD than  $Ai$  while  $Ai$  can maintain their water use regardless of tree size under low soil moisture. This implies that  $Ai$  may be able to cope with negative effects from droughts and retain such capacity when they grow. With ample soil moisture, both species can maintain their tree water use regardless of tree size. When soil moisture becomes high,  $T$  of both species in both sizes increased with rising VPD and then saturated at high VPD. Nevertheless,  $T$  of both species in large size was less sensitive to rising VPD than small size which may be explained by the deeper access to groundwater in large trees. For the implications for management, our results suggest that  $Ai$  may be suitable for reforestation in the area where droughts frequently occur in the downstream ecosystem through its conservative water-use behavior and may benefit downstream ecosystems with continuous runoff from the forest despite droughts. Moreover,  $Ai$  has conservative water-use behavior regardless of tree size. Thus,  $Ai$  would still provide these benefits to ecosystems when they grow larger in the future. In contrast,  $Sa$  seems suitable for reforestation in the area with frequent floods because it has high water consumption during high water availability which may slow down runoff from forest into downstream ecosystems when storms come. However, mixed planting species may be suitable for reforestation in the area that extreme events do not frequently occur because both species can maintain their water use at moderate soil moisture regardless of tree size which prevent the depletion of soil water availability. In this case, depending on the purposes of reforestation,  $Sa$  and  $Ai$  may provide either benefits or negative effects to the ecosystems. In conclusion, this study highlights the dependency of responses of  $T$  to environmental conditions on tree species and size. Such information would benefit the selection of tree species for reforestation that could adapt well to certain environments and support policy design on the management of tropical forests and water resources. Nevertheless, a

further study involving additional field measurements of physiological parameters of trees, such as root depth, is needed to support the proposed findings.

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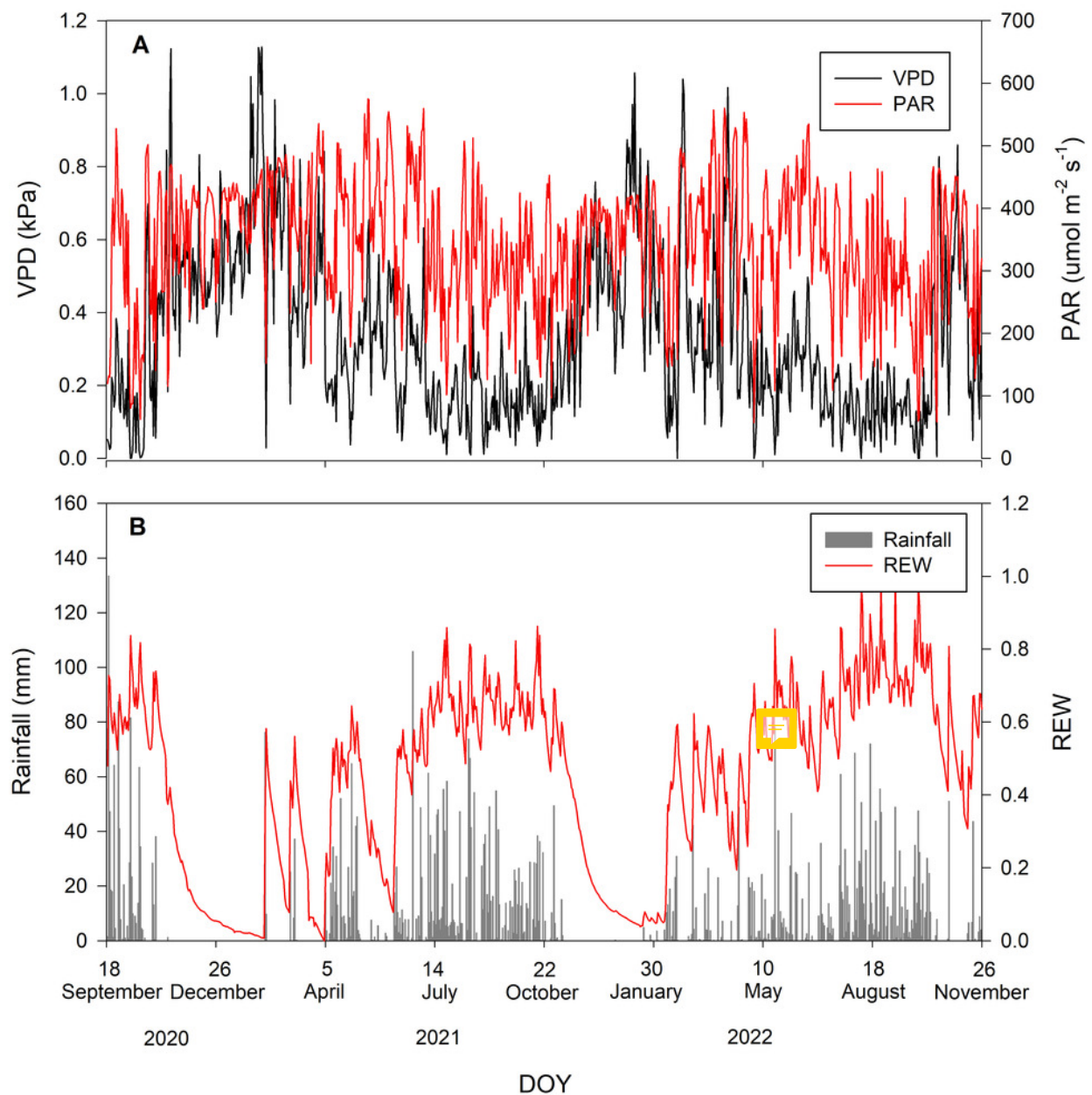
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# Figure 1

Figure 1 Environmental conditions during the study period.

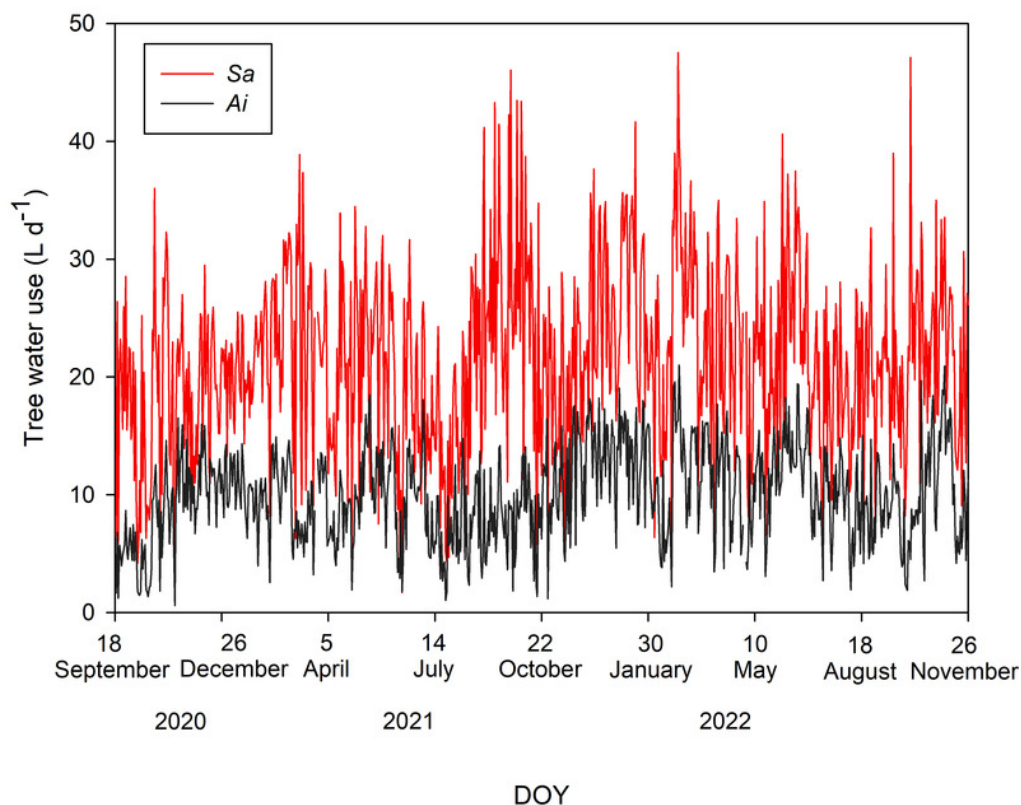
Daily values of **(A)** vapor pressure deficit (VPD in kPa; black line) and photosynthetically active radiation (PAR in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; red line) and **(B)** rainfall (mm; gray bar) and relative extractable water (REW; red line).



# Figure 2

Figure 2 Daily tree water use.

Daily sum of tree water use ( $L\ d^{-1}$ ) of *Syzygium antisepticum* (red line) and *Adinandra integerrima* (black line) throughout the study period from 18 September 2020 to 26 November 2022.

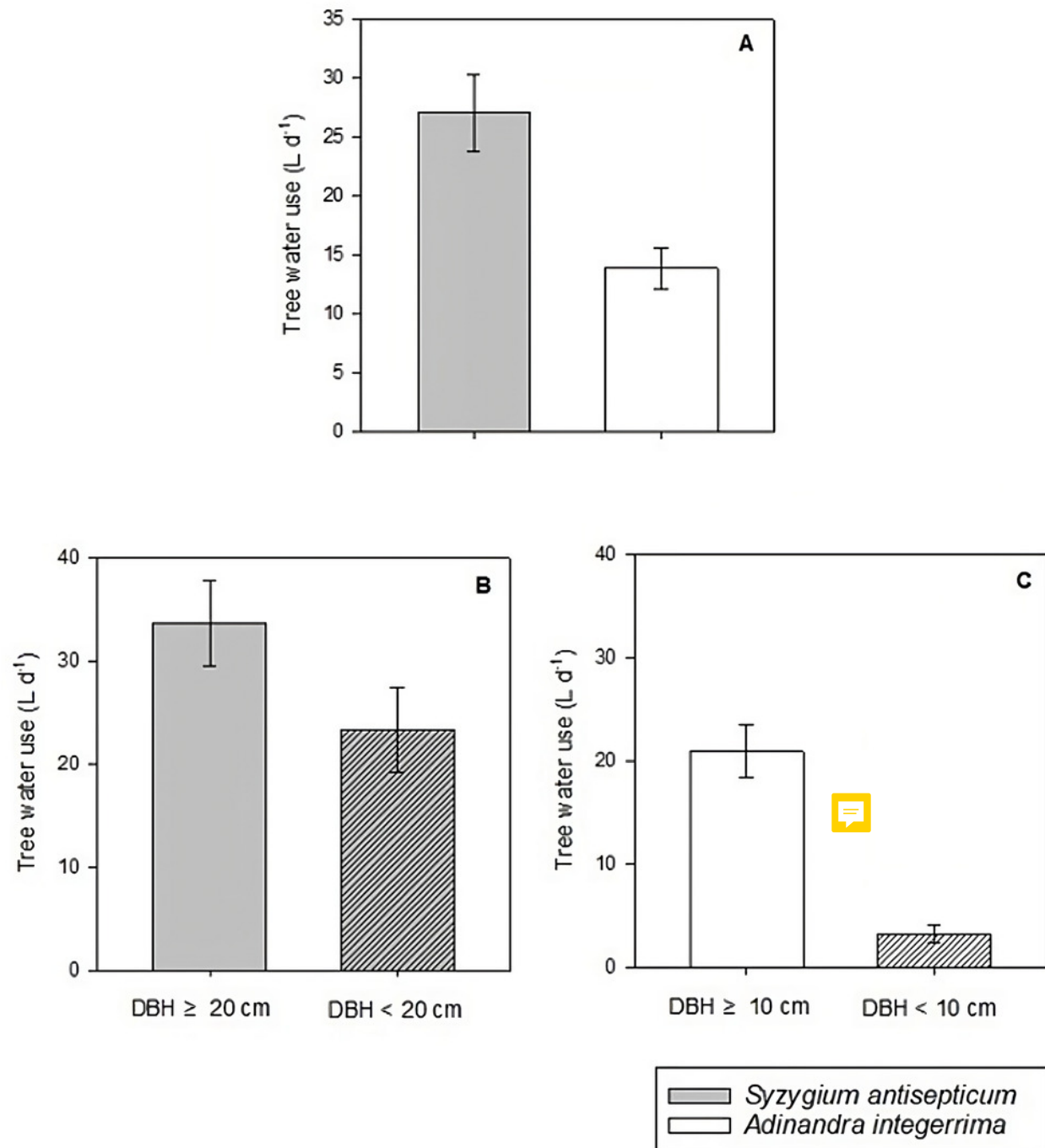


# Figure 3

Figure 3 Comparison of tree water use between class size and species.

Average tree water use ( $T$ ;  $L\ d^{-1}$ ) under non limiting soil moisture and high light conditions during the study period. Comparison between **(A)** *Syzygium antisepticum* and *Adinandra integerrima* and between different size classes of **(B)** *Syzygium antisepticum* and **(C)** *Adinandra integerrima*.

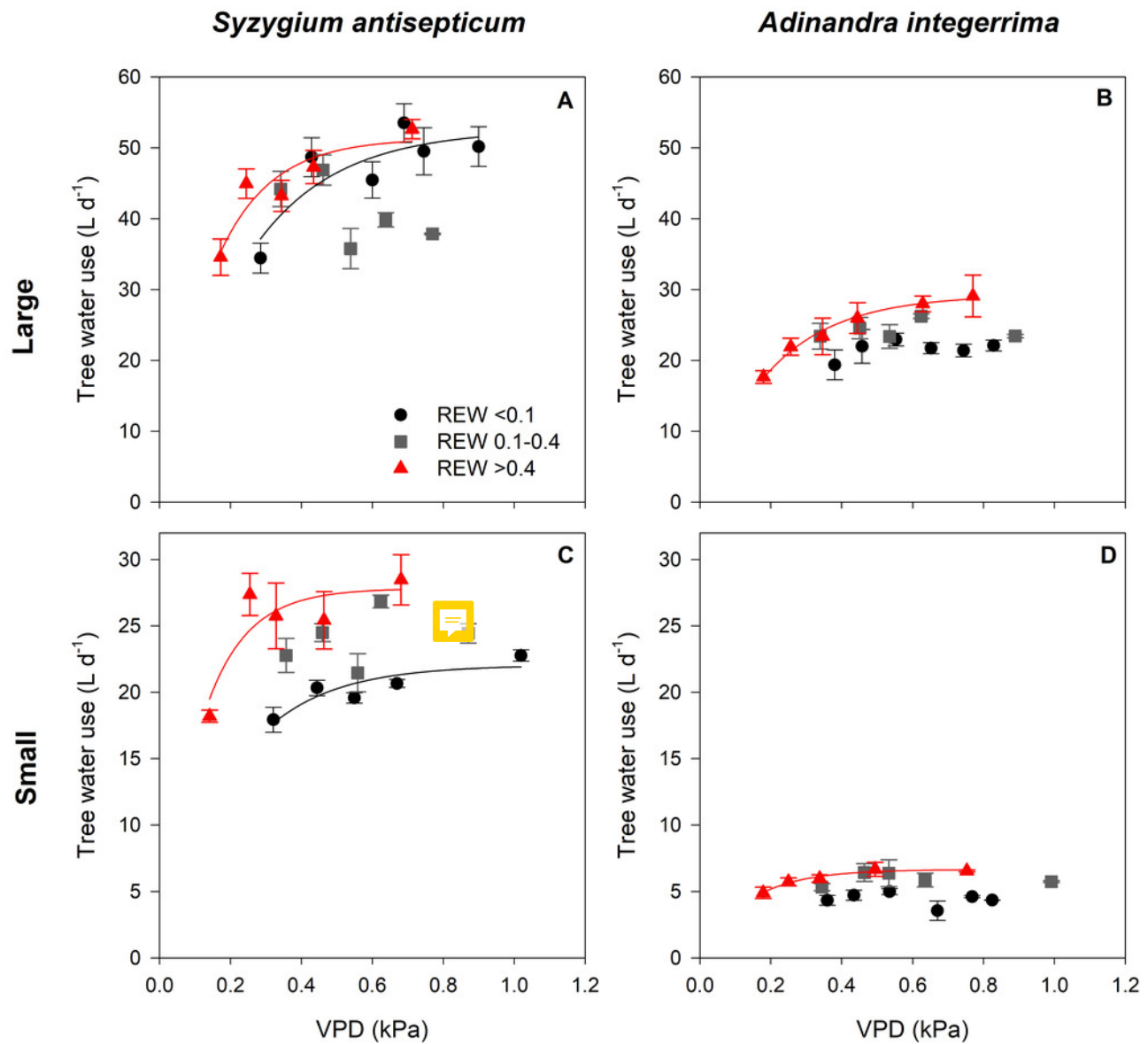




# Figure 4

Figure 4 Relationship between tree water use and vapor pressure deficit under different soil moisture conditions.

Relationship between tree water use ( $T$ ;  $L\ d^{-1}$ ) and vapor pressure deficit (VPD; kPa) of *Syzygium antisepticum* in **(A)** large and **(C)** small size classes and *Adinandra integerrima* in **(B)** large and **(D)** small size classes under low soil moisture condition (REW  $<0.1$ , circles), under intermediate soil moisture condition (REW  $0.1-0.4$ , squares), and under high soil moisture condition (REW  $>0.4$ , triangles).



# **Table 1**(on next page)

Table 1 Information of the selected study trees. DBH refers to the diameter at breast height in cm. Sapwood area (in cm<sup>2</sup>) was estimated using an allometric equation derived from dominant species in the study site (Yaemphum et al. 2022).

**Table 1** Information of the selected study trees. DBH refers to the diameter at breast height in cm. Sapwood area (in cm<sup>2</sup>) was estimated using an allometric equation derived from dominant species in the study site (Yaemphum et al. 2022).

Species	DBH (cm)	Sapwood area (cm <sup>2</sup> )
<i>Adinandra integerrima</i>	13.7	135.92
<i>Adinandra integerrima</i>	6.5	30.64
<i>Adinandra integerrima</i>	11	87.67
<i>Adinandra integerrima</i>	5.3	20.38
<i>Adinandra integerrima</i>	11.3	92.51
<i>Syzygium antisepticum</i>	24.8	444.88
<i>Syzygium antisepticum</i>	22.4	363.02
<i>Syzygium antisepticum</i>	18.7	253.09
<i>Syzygium antisepticum</i>	17.8	229.34



## Table 2 (on next page)

Table 2 Summary of regression statistics.

$T$  is tree water use ( $L\ d^{-1}$ ), VPD is vapor pressure deficit (kPa) and  $r^2$  is the coefficient of determination and p value for each regression result. The analyses were based on significance level of 0.05. n/a indicates no significant relationship was found.



- 1 **Table 2** Summary of regression statistics.  $T$  is tree water use ( $L\ d^{-1}$ ), VPD is vapor pressure
- 2 deficit (kPa) and  $r^2$  is the coefficient of determination and  $p$  value for each regression result. The
- 3 analyses were based on significance level of 0.05. n/a indicates no significant relationship was
- 4 found.

Species	Size classes	REW classes	Relationships	$r^2$	p
<i>Syzygium antisepticum</i> (Sa)	Small (DBH < 20 cm)	< 0.1	$T = 22.04 \times (1 - e^{-5.03 \times VPD})$	0.77	0.049
		0.1 – 0.4	n/a	0.14	0.538
		> 0.4	$T = 27.82 \times (1 - e^{-8.55 \times VPD})$	0.80	0.042
	Large (DBH $\geq$ 20 cm)	< 0.1	$T = 56.63 \times (1 - e^{-4.30 \times VPD})$	0.76	0.023
		0.1 – 0.4	n/a	0.44	0.56
		> 0.4	$T = 51.34 \times (1 - e^{-6.75 \times VPD})$	0.85	0.027
<i>Adinandra integerrima</i> (Ai)	Small (DBH < 10 cm)	< 0.1	n/a	0.13	0.868
		0.1 – 0.4	n/a	0.21	0.440
		> 0.4	$T = 6.65 \times (1 - e^{-7.53 \times VPD})$	0.96	0.003
	Large (DBH $\geq$ 10 cm)	< 0.1	n/a	0.45	0.143
		0.1 - 0.4	n/a	0.11	0.589
		> 0.4	$T = 29.25 \times (1 - e^{-5.08 \times VPD})$	0.99	<0.0001





# **Table 3**(on next page)

Table 3 Summary of water use of tropical forest trees reviewed in this study.

Mean values ( $\pm$  SD if available) are presented. The abbreviations are DBH, diameter at breast height ( $\sim$ 1.3 m above ground); *T*, tree water use ( $\text{L d}^{-1}$ ); TDP, thermal dissipation probes; HPM, heat pulse method. NA indicates not available data.

**Table 3** Summary of water use of tropical forest trees reviewed in this study. Mean values ( $\pm$  SD if available) are presented. The abbreviations are DBH, diameter at breast height ( $\sim 1.3$  m above ground);  $T$ , tree water use ( $L\ d^{-1}$ ); TDP, thermal dissipation probes; HPM, heat pulse method. NA indicates not available data.

Reference	Location		Species	Method	DBH (cm)	Tree height (m)	$T$ (L d <sup>-1</sup> )	Period
Dye 1996	Frankfort State Forest in South Africa (24°49' S, 30°43' E)	Site 1 (3-year-old trees)	<i>Eucalyptus grandis</i>	HPM	14.7 ± 1.17	14.7 ± 1.01	45.8	July 1993
		Site 2 (9-year-old trees)	<i>Eucalyptus grandis</i>	HPM	29.7 ± 4.53	34.3 ± 1.15	68.0	
Eamus et al. 2000	North Australian Tropical Transect -Dry site (130°45' E, 12°30' S) -Intermediate site (132°39' E, 14°40' S) - Wet site (133°46' E, 17°07' S)	<i>Eucalyptus miniate</i> <i>Eucalyptus tetrodonta</i> <i>Eucalyptus latifolia</i> <i>Eucalyptus Capricornia</i> <i>Eucalyptus spp.</i> <i>Eucalyptus terminalis</i>	HPM	8.8 – 30.4	NA	16.1	August–September 1998 (Dry season)	
				4.9 – 48.7			17.9	March–April 1999 (Wet season)
				9.7 – 48.7				
				6.1– 35.6				
				6.1- 35.6				
				9.1– 41.6				
Dierick and Hölscher 2009	The Philippines (10°45'55"N, 124°47'25"E) and (10°44'10"N, 124°48'16"E)	<i>Shorea contorta</i> <i>Parashorea malaanonan</i> <i>Hopea malibato</i> <i>Hopea plagata</i> <i>Swietenia macrophylla.</i> <i>Vitex parviflora</i>	TDP	18.2 ± 7 12 ± 0.4 11.6 ± 2.4 6.6 ± 1.0 14.6 ± 1.3 20.4 ± 5.5 22.1 ± 3.7 16.3 ± 2.7 19.8 ± 7.3 21.9 ± 4.0	16.1 ± 3.5 13.1 ± 1.6 13.3 ± 1.8 9.4 ± 1.2 14.2 ± 1.5 12.7 ± 1.6 11.2 ± 0.6 13.2 ± 1.1 13.8 ± 3.0 18.1 ± 2.4	18.4 ± 19.5 10.6 ± 1.2 9.1 ± 8.5 4.0 ± 1.9 25.5 ± 4.1 30.7 ± 14.6 61.7 ± 17.0 32.8 ± 16.5 44.6 ± 18.5 27.6 ± 7.8	June to August 2006 and July to September 2007	

		<i>Myrica javanica</i> <i>Sandoricum koetjape</i> <i>Durio zibethinus</i> <i>Gmelina arborea</i>					
Dierick et al. 2010	The Philippines (10°45'55"N, 124°47'25"E) and (10°44'10"N, 124°48'16"E)	<i>Shorea contorta</i> <i>Parashorea malaanonan</i> <i>Hopea malibato</i> <i>Hopea plagata</i> <i>Swietenia macrophylla</i> <i>Vitex parviflora</i> <i>Myrica javanica</i> <i>Sandoricum koetjape</i> <i>Durio zibethinus</i> <i>Gmelina arborea</i>	TDP	18.2 ± 7 12 ± 0.4 11.6 ± 2.4 6.6 ± 1.0 14.6 ± 1.3 20.4 ± 5.5 22.1 ± 3.7 16.3 ± 2.7 19.8 ± 7.3 21.9 ± 4.0	16.1 ± 3.5 13.1 ± 1.6 13.3 ± 1.8 9.4 ± 1.2 14.2 ± 1.5 12.7 ± 1.6 11.2 ± 0.6 13.2 ± 1.1 13.8 ± 3.0 18.1 ± 2.4	18.4 ± 14.4 10.6 ± 1.1 9.1 ± 6.7 4.0 ± 1.3 25.5 ± 3.6 20.7 ± 9.3 43.2 ± 12.5 23.4 ± 12.6 32.9 ± 14.8 19.8 ± 6.1	June to August 2006 and July to September 2007
	Indonesia (1.552°S, 120.020°E)	<i>Theobroma cacao</i> <i>Gliricidia sepium</i>	TDP	10.1 ± 1.6 15.0 ± 2.5	4.5 ± 0.8 10.9 ± 2.1	10.0 ± 4.5 13.9 ± 4.1	February 2007 (Dry season)
	Panama (9.317°N, 79.633°W)	<i>Luehea seemannii</i> <i>Anacardium excelsum</i> <i>Hura crepitans</i>	TDP	11.8 ± 1.6 10.1 ± 0.6 18.0 ± 2.3 12.0 ± 0.6 11.5 ± 1.3	8.7 ± 1.0 6.4 ± 0.4 5.4 ± 1.0 11.7 ± 1.1 7.4 ± 0.3	13.1 ± 3.6 10.5 ± 2.8 14.6 ± 7.6 9.9 ± 2.2 7.9 ± 0.6	June to September 2007 (Wet season)

			<i>Cedrela odorata</i> <i>Tabebuia rosea</i>					
Clulow et al. 2013	Nkazana Peat swamp forest site (28°10.176' S, 32°30.070' E)		<i>Syzygium cordatum</i> <i>Shirakiopsis elliptica</i>	HPM	NA	22.5 6.8	30 - 45 2 - 12	4 September 2009 to 4 May 2011
	Dune forest site (28°12.017' S, 32°31.633' E)		<i>Drypetes natalensis</i> <i>Eugenia natalitia</i> <i>Mimusops caffra</i>	HPM	NA	4.5 7.5 7.2	5 - 45 2 - 28 1 - 4	
Chen et al. 2014	Northwest China (38°11' N, 109°28' E)		<i>Ziziphus jujuba</i>	TDP	6.69-11.46	1.39-1.63	12.52 – 19.47	May to October 2012 (growth season)
Cavaleri et al. 2014	Lowland wet forest on Hawaii Island (19°42.15' N, 155°2.40' W)	invaded forest plots	<i>Metrosideros polymorpha</i> <i>Cecropia obtusifolia</i> <i>Macaranga mappa</i> <i>Melastoma septemnervium</i>	TDP	9.0 – 42.0 7.0 – 27.0 6.0-17.0 7.0 – 19.0	NA	2 - 25	February to November 2008
		Removal plots	<i>Metrosideros polymorpha</i>	TDP	9.0 - 42.0	NA	5 - 43	
Hardanto et al. 2017	rubber monoculture		<b>Rubber trees</b> <i>Hevea brasiliensis</i>	TDP	20.3 ± 0.6	13.4 ± 0.4	25.6 ± 3.7	June to August 2013
	jungle rubber		<b>Rubber trees</b> <i>Hevea brasiliensis</i>	TDP	17.8 ± 0.5	140. ± 0.5	24.1 ± 4.2	

		<b>Admixed native trees</b> <i>Cratoxylum sumatranum</i> <i>Callerya atropurpurea</i> <i>Ixonanthes petiolaris</i> <i>Santiria griffithii</i> <i>Macaranga cf. sumatrana</i> <i>Artocarpus nitidus</i> <i>Alstonia angustifolia</i> <i>Streblus elongates</i> <i>Artocarpus integer</i> <i>Porterandia anisophylla</i> <i>Timonius wallichianus</i>	TDP	18.03 ± 0.3	14.0 ± 0.2	26.7 ± 2.2	
Brum et al. 2018	Mature lowland Amazon forest (2°31'0 S, 48°53'W)	Canopy trees	HPM	30-109	NA	68 ± 87	October 2015 to April 2016
		Subcanopy trees	HPM	10-30	NA	11 ± 10.04	