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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Abstract

Background. Southeast Asia has experienced widespread deforestation and change in land use. Consequently, many reforestation projects have been initiated in this region. However, it is imperative to carefully choose the tree species for planting, especially in light of the increasing climate variability and the potential alteration of plantation on the watershed water balance. Thus, the information regarding water-use characteristics of various tree species and sizes is critical in the tree species selection 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).

39 **Results.** Results showed consistently higher T in Sa compared to Ai across ranges of VPD and
40 soil moisture. Under low soil moisture, T of Sa responded to VPD, following a saturating
41 exponential pattern while Ai maintained T across different VPD levels, irrespective of tree size.
42 No responses of T to VPD were observed in either species when soil water was moderate. When
43 soil moisture was high, T of both species significantly increased and saturated at high VPD,
44 albeit the responses were less sensitive in large trees. Our results imply that Ai may be suitable
45 for reforestation in water-limited areas where droughts frequently occur to minimize
46 reforestation impact on water availability to downstream ecosystems. In contrast, Sa should be
47 planted in regions with abundant and reliable water resources. However, a mixed species
48 plantation should be generally considered to increase forest resilience to increasing climate
49 variation.
50

Introduction

52 Over an annual timescale with negligible change in total water storage, precipitation is coarsely
53 partitioned into evapotranspiration and runoff in the forest water cycle (Wang and Tang 2014).
54 Because tree water use (T) constitutes 40–90% of evapotranspiration (Jasechko et al. 2013; Deb
55 Burman et al. 2019), the quantity of T affects the amount of precipitation that ultimately
56 contributes to runoff, impacting the downstream ecosystems. With the projected increases of
57 global climate change impacts, T may be altered through changes in environmental conditions
58 including temperature and precipitation regimes, severity of weather and climate extremes such
59 as droughts and floods (Menezes-Silva et al. 2019). Such changes will certainly affect the
60 responses of T to environmental factors, therefore governing the outflow from forests. Thus,
61 evaluating such responses would provide insights into environmental management that involves
62 water cycling, such as predicting runoff from forests which may result in floods or droughts in
63 the downstream ecosystems.
64   The variations of T are mainly related to tree size (Meinzer et al. 2005; Jung et al. 2011)
65 and environmental factors including soil water availability, solar radiation, and vapor pressure
66 deficit (VPD) which represents atmospheric humidity (Xu et al. 2020; Gutierrez Lopez et al.
67 2021). Several previous studies reported significant variations of T with tree size. The
68 relationship between tree diameter and T was found among several species of angiosperms
69 (Meinzer et al. 2005), *Eucalyptus crebra* and *Callitris glaucophylla* in evergreen woodland in
70 Australia (Zeppel and Eamus 2008), and trees in a temperate mixed-deciduous forest in South
71 Korea (Jung et al. 2011). Additionally, different tree sizes have been linked to different
72 responses to droughts with large trees being more vulnerable than small trees to drought because
73 of greater exposure to atmospheric demand (Bennett et al. 2015; Stovall et al. 2019). However,
74 information of the effects of tree size on T is still lacking in secondary tropical forests. The
75 effects of environmental factors on T vary in different forest types and regions. For example,
76 when soil moisture is not limited, T strongly responds to VPD, which increases when the air
77 humidity decreases, and solar radiation in an old-growth spruce forest in the Ore Mountains,
78 Germany (Clausnitzer et al. 2011). Under soil water stress, Brum et al. (2018) found that T could

79   decrease with increasing VPD during an extreme drought in an Amazonian tropical rainforest.
80   On the other hand, Spanner et al. (2022) found that the sensitivity of T to soil moisture varied
81   with species, with some increasing and some decreasing during the dry period in an old-growth
82   upland forest in the central Amazon. Thus, changing environmental conditions can alter the
83   response patterns of T.
84   Forests in Southeast Asia provide a wide range of important ecosystem services to many
85   people and communities. Unfortunately, these forests have been disrupted by widespread
86   deforestation and land use change (Stibig et al., 2014; Zeng et al. 2018), resulting in various
87   stages of forests in the same area (Curtis et al. 2018). In particular, the areas that were previously
88   used for agricultural purposes have been abandoned for several years, and naturally or artificially
89   transformed into secondary forests. Consequently, many of the degraded forests may not
90   contribute much to improving biodiversity and mitigating climate change through carbon dioxide
91   removal from the atmosphere. Therefore, reforestation projects have emerged in many countries
92   in the tropics, highlighting the use of native species to avoid competition with other native trees,
93   which can help restore biodiversity and sequester carbon (Hooper et al. 2002). However, planting
94   more trees in existing secondary forests may raise some concerns because trees are potentially
95   heavy water users and might deplete water resources (Jackson et al. 2005). Also, reforestation
96   may not be desirable in certain areas because it may reduce water availability for the existing
97   trees and increase the evapotranspiration rate (Van Kanten and Vaast 2006) and thus leading to
98   reductions in runoff (Li et al. 2014). With these regards, an appropriate selection of tree species
99   for planting is among the priority tasks for forest restoration since species-specific water-use
100   characteristics play an important role in changing the components of the forest hydrologic cycle
101   (van Dijk and Keenan 2007). However, the availability of such information is still limited in
102   tropical forests, especially in secondary ones. Hence, it is imperative to evaluate the response
103   patterns of T to environmental factors in secondary tropical forests that would offer necessary
104   information on species-specific water-use characteristics.
105   Khao Yai National Park (KYNP) is a UNESCO world heritage site. Most of the areas of
106   KYNP consist of a mosaic of different stages of vegetation succession with more than 60% of
107   the forests undergoing different stages of regeneration while the remainder are old-growth
108   forests. Thus, secondary forests in KYNP are important to biodiversity conservation and climate
109   change mitigation through the regulation of atmospheric carbon. With these regards, this study
110   was performed in a secondary tropical forest at KYNP, representing a young forest aged ~10
111   years. In this study site, the dominant tree species include *Syzygium antisepticum* and *Adinandra*
112   *integerrima*. *Syzygium antisepticum* can be found as the dominant species in other tropical
113   forests such as tropical evergreen swamp forests in Cambodia (Theilade et al. 2011), dry
114   evergreen forests in northeastern Thailand (Bunyavejchewin 1999) and tropical coastal sand
115   dune in southern Thailand (Marod et al. 2020). *Adinandra integerrima* can be found in other
116   parts of Thailand, such as Doi Inthanon National Park in the northern region (Georgiadis 2022)
117   and other countries in the tropics, such as Cambodia, China, Laos, and Vietnam (Tagane et al.
118   2020). Despite the widespread presence of these species in Thailand and neighboring countries

119   of Southeast Asia, the information on the water-use characteristics of both species is still lacking.
120   Therefore, this study aims to (1) estimate T of *Syzygium antisepticum* and *Adinandra integerrima*
121   in a secondary tropical forest in KYNP, and (2) evaluate the responses of T to environmental
122   factors of both species in different tree size classes. The collected data covered a period from 18
123   September 2020 to 26 November 2022, including a wide range of environmental conditions. The
124   outcome of this study would improve the understanding of species-specific water-use
125   characteristics in secondary forests which can support policy design on the management of
126   tropical forests and water resources. In addition, findings from this study may provide a
127   recommendation for selecting appropriate tree species for forest restoration in the tropical region.
128
129   **Materials & Methods**
130   ***Study site and measurements of the environmental variables***
131   The study was conducted in Khao Yai National Park, Thailand (14°26′31″ N, 101°22′55″ E).
132   Khao Yai National Park covers an area of about 200 km^2 in Nakhon Ratchasima, Saraburi,
133   Prachinburi and Nakhon Nayok Provinces in Thailand. This region is dominated by monsoon
134   climate, where the dry season usually lasts from November to April and from May to October for
135   the wet season (Brockelman et al. 2017). Based on recorded data between 1994-2018, the overall
136   mean annual temperature was 22.4 °C. The mean annual rainfall was 2,100 mm. Khao Yai
137   National Park is characterized by different stages of forest succession comprising primary forests
138   and various stages of secondary forests. In this study, we performed the study in a secondary
139   forest representing a young forest in Nakhon Nayok Province. The study site has an area of 2 ha
140   and an age of approximately 10 years (Chanthorn et al. 2017). Its mean canopy height is 15 m
141   and its tree density of 1,226 trees ha^{-1}. The soil is gray-brown ultisol which was degraded by
142   shifting agriculture by burning before regeneration (Chanthorn et al., 2016, 2017). The bulk
143   density was 1.24 g cm^{-3} and soil texture was sandy clay-loam with the sand contents of 64.4%
144   and 56.4% as measured in September 2020 and February 2021, respectively (Rodtassana et al.
145   2021). In 2020, a 20 m tall tower was constructed for installing weather sensors above the forest
146   canopy in the plot. Environmental conditions that influence T including atmospheric humidity,
147   solar radiation, and soil moisture have been continuously monitored since then. Air temperature
148   (T, °C), relative humidity (RH, %), and photosynthetically active radiation (PAR, µmol m^{-2} s^{-1})
149   were measured by a temperature and relative humidity probe (EE181-PT, Campbell Scientific)
150   and a quantum sensor (LI190R-PT, Campbell Scientific), respectively. Soil moisture sensors
151   (Water content reflectometer, CS616-PT-U, Campbell Scientific) were installed to monitor
152   volumetric soil moisture at 5, 10, 15, and 30 cm depth because tree roots may access water from
153   multiple depths in the soil (Wang et al. 2019). We randomized the points to install soil moisture
154   sensors around the tower. Two soil moisture sensors were installed at each depth of 5, 10, and 15
155   cm. However, soil moisture at 30 cm depth was monitored by one soil moisture sensor because
156   soil moisture in subsoil was less sensitive to changing environmental conditions than topsoil
157   (Rong et al. 2017). Rainfall (mm) was measured by tipping rain gauge bucket (TE525MM-PT,
158   Campbell Scientific). All sensors were connected to a datalogger (CR1000 series; Campbell

159 Scientific, Logan, UT) which recorded data every 30 minutes. Air temperature and relative
160 humidity are used to calculate vapor pressure deficit (VPD, kPa), which is the difference
161 between actual vapor pressure and saturated vapor pressure (SVP), from the following equations
162 (Monteith and Unsworth 1990)

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

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

165 Because we did not have any information regarding rooting depth, which determines the depth of
166 soil moisture data to be used in the analysis, we used the average of soil moisture data from all
167 soil water probes, covering soil depth up to 30 cm, as the soil moisture data (θ, m³m⁻³) for further
168 analysis. Based on previous studies in the central Amazon which reported the most fine root
169 distribution within 20 cm soil depth (Noguchi et al. 2014), we assumed that the average soil
170 moisture across 30 cm depth represents the soil water that largely influences tree water use. To
171 facilitate the cross-site comparison with other or future studies, Relative Extractable Water
172 (REW) was used in the analysis and was calculated according to Granier et al. (2000)

$$REW = \frac{\theta - \theta m}{\theta FC - \theta m} \tag{3}$$

174 where θ is the average soil moisture of all sensors across 30-cm soil depth, θ_m is minimum
175 volumetric soil moisture and θ_{FC} is the soil water at field capacity. In the plot where soil water at
176 field capacity has not been measured, maximum volumetric soil moisture during the study period
177 can be used as θ_{FC} for the REW calculation (Tor-ngern et al. 2018). Accordingly, we used the
178 maximum and minimum $\theta_{average}$ that were determined from our data during the study period to
179 represent θ_{FC} and θ_m, respectively.

180 ***Species selection and tree sampling***
181 The tree species were chosen based on the relative abundance of basal area in this plot, which
182 was calculated from the basal area of one species relative to total basal area of all species within
183 the site. To examine the difference in tree water use, two dominant tree species with similar leaf
184 phenology were selected for this study. As a result, *Syzygium antisepticum* and *Adinandra*
185 *integerrima,* hereafter *Sa and Ai,* respectively, which have evergreen leaf habit, were chosen to
186 measure water flow rate. We attempted to select trees to cover the range of size distribution
187 within the plot, based on the inventory data from the site (unpublished data, personal
188 communication with Dr. Wirong Chanthorn), by partitioning the tree size classes into 10-cm
189 intervals and sampled 3 trees from each size class. However, due to the requirement of trees
190 being within 25 m radius from the data logger, 4 trees of *Sa* and 5 trees of *Ai* were selected for
191 the measurement (Table 1).

192 ***Sap flux measurement and scaling up from the point measurement to whole-tree water use***
193 Sap flux density (J_s), which represents water mass flowing through a unit area per time in trees,
194 was measured using self-constructed thermal dissipation probes (TDPs) (Granier 1985). Each
195 TDP set contains one non-heated and one heated probe being supplied with a constant ~0.2 W
196 electrical power. Before inserting TDPs into the stems, debarking around the drilling point was
197 done before drilling the holes for TDP installation. Two holes were drilled with approximately

198   10-15 cm spacing between two probes. Based on previous studies in pine trees, the patterns of

199   radial variation in J_s along the sapwood depth were observed with higher J_s in the outer sapwood

200   layers than in the inner sapwood layers (Ford et al. 2004; Oishi et al. 2008). Therefore, ignoring

201   the radial variation of J_s may produce an error when scaling up from J_s to T. However, previous

202   studies in tropical forests that use similar sap flow sensors only measured J_s at the outer sapwood

203   because of the unknown pattern of sapwood area in tropical tree species (Horna et al. 2011;

204   Raquel Salas-Acosta et al. 2022). In addition, most tropical trees have diffuse-porous wood

205   without distinct annual rings and tend to have a sap flow rate that is similar along the radial

206   sapwood depth (Lu et al. 2004). Therefore, we assumed that J_s was uniform along the sapwood

207   depth of the selected trees when scaling from single-point measurements to the whole-tree level,

208   and only measured J_s at the outer 2-cm sapwood at breast height (~1.3 m above ground). In

209   addition, azimuthal variation of J_s may produce variation when scaling up from J_s to T (Lu et al.

210   2000; James et al. 2002; Tateishi et al. 2008). This variation depends on the effect of forest

211   canopy shading by neighboring trees. In other words, trees may be obstructed from sunlight by

212   canopy shading from surrounding trees leading to varying J_s along the circumference. In this

213   study, the surrounding trees were equally distributed around the measured trees. Nevertheless,

214   we installed two sensors in the north and the south directions in some trees which may be

215   influenced by canopy shading at certain times during the day. Data from TDPs were recorded as

216   30-minute means of voltage difference between the probes (ΔV, mV) by the same data logger

217   (CR1000, Campbell Scientific, Logan, UT, USA) that recorded environmental data. For the

218   analysis, the voltage difference was converted to J_s (g m^{-2} s^{-1}) using an empirical equation

219   (Granier 1987)

220    $$J_s = 118.99 \text{ x } 10^{-6} \text{ x } \left(\frac{\Delta V_m - \Delta V}{\Delta V}\right)^{1.231} \tag{4}$$

221   where ΔV_m is the maximum voltage difference under no flow conditions which usually occurs at

222   night and when VPD is low. The Baseliner program version 4.0 was used to select ΔV_m to

223   calculate J_s (Oishi et al. 2016). The program automatically determines the maximum daily ΔV to

224   represent ΔV_m. Maximum voltage difference may occur every night if air humidity is very high,

225   or VPD reaches 0 kPa, resulting in potentially zero water flow. However, this assumption is not

226   valid for many ecosystems due to nighttime transpiration (e.g. Caird et al. 2007; Forster 2014;

227   Dayer et al. 2020) or recharge of stem water (Phillips and Oren 1998). For these reasons, no

228   universal rule exists for identifying ΔV_m. The Baseliner software takes an approach to ΔV_m

229   estimation by first identifying points in time where flow is likely zero and allowing the user to

230   visually inspect and modify those points.

231   To scale up from J_s to T, we employed the following approach. Daily sum J_s (g m^{-2} day^{-1})

232   was considered in the analysis to avoid issues related to the nighttime recharge of stem water that

233   may increase as soil moisture becomes more depleted (Phillips and Oren 1998). When nighttime

234   recharge increases with decreasing soil moisture, the proportions of sap flux at night relative to

235   sap flux during the day become larger. This problem can be avoided when calculating T as a

236   daily sum (Phillips and Oren 1998). For trees with sensors in the north and the south direction,

237   daily sum J_s from both sensors were averaged to a mean daily J_s (J_{mean}) for each of them (Kunert
238   et al. 2012). The following equation was used to estimate T
239                                    $T = 1800 \times 10^{-7} \times J_{mean} \times A_S$ (5)
240   where T is daily tree water use (L d^{-1}), J_{mean} is mean daily sum J_s (g m^{-2} day $^{-1}$) and A_S is
241   sapwood area (cm^2). In both species, A_S was estimated based on an allometric equation which
242   was derived from 13 dominant species in an old growth and a secondary forest (the same plot as
243   this study site) at Khao Yai National Park as follows (Yaemphum et al. 2022)
244                                    $y = 0.728x^{1.998}$ (6)
245   where y is sapwood area (cm^2), x is diameter at breast height (cm).
246   ***Data analysis***
247   For the analysis, we used the environmental data and T between 18 September 2020 to 26
248   November 2022. The data covered two years which represents a wide range of environmental
249   conditions. To avoid the potential effects of wet canopy conditions that may inhibit T when the
250   leaf surface is covered with water droplets (Aparecido et al. 2016), we selected the days under
251   rain-free conditions to perform the analysis.
252   To evaluate the responses of T to environmental factors including VPD and REW, we
253   performed a boundary line analysis (Schäfer et al. 2000) to obtain the response of T to
254   environmental factors under non-limiting conditions. Trees were categorized based on the size
255   distribution of each species as presented in Table 1 into large trees (DBH $\geq$ 10 cm for *Ai* and
256   DBH $\geq$ 20 cm for *Sa*) and small trees (DBH < 10 cm for *Ai* and DBH < 20 cm for *Sa*). This
257   results in 2 trees for both species in the small class, and 3 *Ai* trees and 2 *Sa* trees in the large
258   class. After that, T from all trees in the same category was averaged to mean T (T_{mean}) for each
259   day. Tree water use varies with VPD, REW and PAR (Phillips and Oren 2001). Based on our
260   data during the study period, VPD and PAR were highly correlated (r = 0.79, p = <0.001),
261   therefore we focused on VPD and REW as environmental driving variables. We performed
262   boundary line analysis after partitioning data into three REW classes based on the REW
263   distribution including low soil moisture (REW <0.1), intermediate soil moisture (REW 0.1-0.4),
264   and high soil moisture (REW >0.4). With two classes of tree size (large and small), we had six
265   subsets of data in both species. Each subset was subjected to the boundary line, designed to
266   select data representing the maximum T_{mean} for each tree size in each REW class along the range
267   of VPD. The upper boundary line was derived by (1) partitioning T_{mean} data of each REW class
268   into at least five VPD intervals for appropriate number of data points in regression analysis (at
269   least five data points per analysis), (2) calculating the mean and standard deviation of T_{mean} in
270   each interval, (3) removing outliers using Dixon's test, (4) selecting the data falling above the
271   mean plus one standard deviation and (5) averaging the selected data for each VPD interval. For
272   each tree size and REW class, the mean T_{mean} values of all VPD intervals obtained in step (5)
273   were analyzed by regression analysis. All regression analyses were performed in SigmaPlot
274   version 12.0 (Systat Software, Inc., San Jose, CA USA). Data management and analysis were
275   performed with Rstudio, version 1.3.1073 (The R Foundation for Statistical Computing,
276   http://www. R- project.org).

277

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 μmol m^{-2} s^{-1}, respectively, with an average of 345.76 $\pm$ 103.47 μmol m^{-2} s^{-1}. The average daily VPD was 0.34 $\pm$ 0.23 kPa. Volumetric soil moisture of all depths was averaged into $\theta_{average}$. The maximum and minimum $\theta_{average}$ during the study period were 0.2 and 0.04 m^3 m^{-3}, respectively. The $\theta_{average}$ was then used to calculate REW with an 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 integerrima

Tree water uses 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 L d^{-1}, respectively. Comparing T between both species, we found that the T of Sa was significantly higher than that of Ai under high soil moisture and high light conditions (p <0.0001).

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

Figure 3 summarizes the results of the responses of T to VPD under various REW ranges, with the regression statistics in Table 2. At low soil moisture (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 conditions (REW 0.1-0.4, gray squares), the T of both species in both sizes did not respond to VPD. Under high soil moisture (REW>0.4, red triangles), the 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 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 L d^{-1} in the winter to 45 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 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 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 L d^{-1} for trees in a 32-year-old plantation of $Quercus$ $petraea$ L. ex Liebl. in eastern

317   France to 1,180 L d^{-1} for an overstory tree, *Euperua purpurea* Bth., growing in the Amazonian
318   rainforest. Overall, the *T* values of both species in this study were within the wide ranges found
319   in previous studies in tropical settings (Table 3).
320   Previous studies showed that the variation of J$_s$ among trees of different ages and sizes is
321   relatively low (Kumagai et al. 2007; Jaskierniak et al. 2016); thus, sapwood area may be a major
322   determinant of *T* in this study. Based on our data, J$_s$ of trees was similar between both species (p
323   = 0.278), suggesting the greater contribution of sapwood area or tree size to the significant
324   difference in *T*. Additionally, higher water use in large trees may imply their deeper access to
325   groundwater whereas small trees may only consume water from shallow soil as previously
326   shown in a study investigating water use by *Acer saccharum Marsh.* in different sizes (Dawson
327   1996). Moreover, other research in tropical forests reported that large trees consume much more
328   water relative to small trees as indicated by the positive relationship between water consumption
329   and tree size (O'Grady et al. 1999; Meinzer et al. 2001; Horna et al. 2011; Aparecido et al.
330   2016).
331   The response pattern of saturating exponential function of *T* with VPD found in this study
332   is similar to the one observed in various tree species in a wide range of tropical forests, including
333   a lowland tropical forest of Central and northern South America (Meinzer et al. 1993), a primary
334   lowland tropical forest in eastern Amazon (Brum et al. 2018) and a per-humid tropical forest of
335   Central Sulawesi in Indonesia (Horna et al. 2011). A previous study showed that tree
336   transpiration strongly increases with rising VPD under high soil water availability; however,
337   such response may become weaker or disappear when soil moisture is lower, depending on tree
338   species (Butz et al. 2018). In general, we observed similar responses of *T* to VPD under wet and
339   dry conditions with stronger responses in the former; whereas no responses were detected when
340   trees experienced moderate soil moisture. Under dry conditions, our results indicate that *Sa* was
341   sensitive to increasing VPD while *Ai* can maintain their water use rate regardless of changes in
342   VPD, regardless of tree size. This implies that *Ai* may be more tolerant to drought than *Sa* and
343   may have strong control over their water use under low soil moisture, regardless of tree size,
344   which can prevent it from negative effects from droughts. This result agreed with a previous
345   study that investigated the drought tolerance of both species in this site (Unawong et al. 2022).
346   Based on tree hydraulic measurement, the study reported that xylem pressure at 50% loss of
347   hydraulic conductivity (P$_{50}$) of *Ai* and *Sa* were −5.97 and −4.71 MPa, respectively. It is implied
348   that species with lower P$_{50}$ have greater resistance to embolisms, thus allowing better adaptation
349   to environments where water stress frequently occurs (Maherali et al. 2004). When comparing *T*
350   in different size classes of *Sa*, large trees were less sensitive to rising VPD at lower VPD ranges.
351   The less sensitivity of large trees to rising VPD leads to a slower decrease in water consumption
352   rate to save water than small trees, resulting in potentially greater vulnerability to hydraulic
353   failure during drought in large trees. Previous studies have shown size-dependent sensitivity to
354   droughts in many ecosystems. A synthetic study using data on tree growth and mortality, which
355   were collected during 40 drought events in forests worldwide, showed that droughts consistently
356   exerted negative impacts on the growth and mortality rates of larger trees (Bennett et al. 2015).

357   Greater vulnerability of large trees to drought could be affected by the higher exposure to
358   radiation and atmospheric demand because of increasing tree height (Roberts et al. 1990;
359   Nepstad et al. 2007). Moreover, large trees have to transport water to greater heights, which is
360   against the effects of gravity, thus facing greater hydraulic failure (Ryan et al. 2006; Zhang et al.
361   2009). Thus, large *Sa* may be at higher risk of hydraulic failure when drought is more
362   pronounced, plausibly leading to increasing mortality rates (Choat et al. 2018). At moderate soil
363   water, the results indicated that both species could maintain their tree water use, regardless of
364   tree size. Under high soil moisture conditions, the *T* of both species in both sizes also followed
365   the saturating exponential pattern as in the case of low soil moisture conditions. However, the
366   sensitivity of increasing *T* at low VPD was different between sizes. In both species, *T* of large
367   sizes was less sensitive to rising VPD than small ones. In other words, when the air becomes dry,
368   small trees may decrease water consumption rate faster to save water than large trees. This may
369   be partly because small trees mainly use shallow soil water whereas large trees can access water
370   from deeper soil (Brum et al. 2018), allowing less sensitivity to droughts in large trees.
371   Nevertheless, further studies that investigate water-source partitioning of different tree species in
372   the same forest (e.g., Hasselquist et al. 2010; Wang et al. 2020), tracing isotopic signals of water
373   from various soil layers to the stems, may be performed to confirm these results.
374

375   ***Implications for environmental management***
376   The results from this study imply that *Sa* may provide ecosystem disservice in dry areas due to
377   its high water consumption which results in low water supply for the downstream community,
378   but it may slow down runoff in the region that experiences heavy precipitation. In contrast, *Ai*
379   may provide ecosystem benefits by conservatively using water, even under drought conditions,
380   but may increase runoff when storms come with high rainfall. Another implication is that *Ai* may
381   be suitable for reforestation in the area where droughts frequently occur in downstream
382   ecosystems through its conservative water-use behavior, thus maintaining runoff from the forests
383   during drought. Moreover, because *Ai* showed relatively constant water use regardless of tree
384   size, the species would still provide such benefits to the ecosystems even when it grows larger in
385   the future. In contrast, *Sa* may be appropriate for reforestation in the area with frequent floods
386   because it has high water consumption during high water availability which may decelerate
387   runoff from forests into downstream ecosystems. This would benefit the downstream ecosystems
388   when storms occur. Regardless, mixed planting species seem to be suitable for reforestation in
389   the areas where extreme events do not frequently occur because both species can maintain their
390   water use at moderate soil moisture regardless of tree size, therefore preventing the depletion of
391   soil water availability. In addition, mixed planting species could reduce the competition for
392   limited water resources because the differences in root structures of different tree species lead to
393   less competition for water (Schwendenmann et al. 2015). Nevertheless, reforestation projects
394   should emphasize the use of native species to avoid competition with other native trees on the
395   site (Hooper et al. 2002).
396

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 of 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 the negative effects of 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, the T of both species in both sizes increases with rising VPD and then saturated at high VPD. Nevertheless, T of both species in large size was less sensitive to rising VPD than in 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 areas where extreme events do not frequently occur because both species can maintain their water use at moderate soil moisture regardless of tree size which prevents 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 the physiological parameters of trees, such as root depth, is needed to support the proposed findings.

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References

441 Aparecido LMT, Miller GR, Cahill AT, Moore GW (2016) Comparison of tree transpiration
442   under wet and dry canopy conditions in a Costa Rican premontane tropical forest. Hydrol
443   Process 30(26): 5000–5011. https://doi.org/10.1002/hyp.10960

444 Bennett AC, Mcdowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most
445   during drought in forests worldwide. Nat Plants 1: 15139.
446   https://doi.org/10.1038/nplants.2015.139

447 Brockelman WY, Nathalang A, Maxwell JF (2017) *Mo Singto plot: Flora and*
448   *ecology*. Bangkok, Thailand: National Science and Technology Development Agency
449   and Department of National Parks, Wildlife and Plant Conservation.

450 Brum M, López, Gutierrez Lopez J, Asbjornsen H, Licata J, Pypker T, Sanchez G, Oiveira RS
451   (2018) ENSO effects on the transpiration of eastern Amazon trees. Philos Trans R Soc B:
452   Biol Sci 373: 1760. https://doi.org/10.1098/rstb.2018.0085

453 Bunyavejchewin S (1999) Structure and dynamics in seasonal dry evergreen forest in
454   northeastern Thailand. J Veg Sci 10(6): 787–792. https://doi.org/10.2307/3237303

455 Butz P, Hölscher D, Cueva E, Graefe S (2018) Tree water use patterns as influenced by
456   phenology in a dry forest of Southern Ecuador. Front Plant Sci 9: 945.
457   https://doi.org/10.3389/fpls.2018.00945

458 Caird MA, Richards JH, Donovan LA (2007) Nighttime stomatal conductance and transpiration
459   in C3 and C4 plants. Plant Physiol 143: 4-10. https://www.jstor.org/stable/40065208

460 Cavaleri MA, Ostertag R, Cordell S, Sack L (2014) Native trees show conservative water use
461   relative to invasive trees: results from a removal experiment in a Hawaiian wet forest.
462   Conserv Physiol 2(1): cou016. https://doi.org/10.1093/conphys/cou016

463 Chanthorn W, Ratanapongsai Y, Brockelman WY, Allen MA, Favier C, Dubois MA (2016)
464   Viewing tropical forest succession as a three-dimensional dynamical system. Theor Ecol
465   9: 163-172. https://doi.org/10.1007/s12080-015-0278-4

466 Chanthorn W, Hartig F, Brockelman WY (2017) Structure and community composition in a
467   tropical forest suggests a change of ecological processes during stand development. For
468   Ecol Manag 404: 100–107. https://doi.org/10.1016/j.foreco.2017.08.001

469 Chen D, Wang Y, Liu S, Wei X, Wang X (2014) Response of relative sap flow to meteorological
470   factors under different soil moisture conditions in rainfed jujube (*Ziziphus jujuba* Mill.)
471   plantations in semiarid Northwest China. Agric Water Manag 136: 23-33.
472   https://doi.org/10.1016/j.agwat.2014.01.001

473 Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE (2018) Triggers of
474   tree mortality under drought. Nature 558: 531-339. https://doi.org/10.1038/s41586-018-
475   0240-x

476 Clausnitzer F, Köstner B, Schwärzel K, Bernhofer C (2011) Relationships between canopy
477   transpiration, atmospheric conditions and soil water availability—Analyses of long-term
478   sap-flow measurements in an old Norway spruce forest at the Ore Mountains/Germany.
479   Agric For Meteorol 151(8): 1023-1034. https://doi.org/10.1016/j.agrformet.2011.04.007
480 Clulow AD, Everson CS, Price JS, Jewitt GPW, Scott-Shaw BC (2013) Water-use dynamics of a
481   peat swamp forest and a dune forest in Maputaland, South Africa. Hydrol Earth Syst Sci
482   17(5): 2053-2067. https://doi.org/10.5194/hess-17-2053-2013
483 Curtis PG, Slay CM, Harris N., Tyukavina A, Hansen MC (2018) Classifying drivers of global
484   forest loss. Science 361 (6407): 1108–1111. https://doi.org/10.1126/science.aau3445
485 Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and
486   transpiration analyses: The roles of tree size and hydraulic lift. Tree Physiol 16(1–2):
487   263-272. https://doi.org/10.1093/treephys/16.1-2.263
488 Dayer S, Herrera JC, Dai Z, Burlett R, Lamarque LJ, Delzon S, Bortolami G, Cochard H,
489   Gambetta GA (2020) Nighttime transpiration represents a negligible part of water loss
490   and does not increase the risk of water stress in grapevine. Plant Cell Environ 44(2): 387-
491   398. https://doi.org/10.1111/pce.13923
492 Deb Burman PK, Sarma D, Morrison R, Karipot A, Chakraborty S (2019) Seasonal variation of
493   evapotranspiration and its effect on the surface energy budget closure at a tropical forest
494   over north-east India. J Earth Syst Sci 128: 127. https://doi.org/10.1007/s12040-019-
495   1158-x
496 Dierick D, Hölscher D (2009) Species-specific tree water use characteristics in reforestation
497   stands in the Philippines. Agric For Meteorol 149: 1317-1326.
498   http://dx.doi.org/10.1016/j.agrformet.2009.03.003
499 Dierick D, Kunert N, Köhler M, Schwendenmann L, Hölscher D (2010) Comparison of tree
500   water use characteristics in reforestation and agroforestry stands across the tropics. In
501   Tscharntke T, Leuschner C, Veldkamp E, Faust H, Guhardja E, Bidin A (eds) Tropical
502   Rainforests and Agroforests under Global Change. Environmental Science and
503   Engineering. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-00493-
504   3_13
505 Dye PJ (1996) Response of Eucalyptus grandis trees to soil water deficits. Tree Physiol 16: 233-
506   238. https://doi.org/10.1093/treephys/16.1-2.233
507 Eamus D, O'Grady APO, Hutley L (2000) Dry season conditions determine wet season water
508   use in the wet-tropical savannas of northern Australia. Tree Physiol 20(18): 1219-1226.
509   https://doi.org/10.1093/treephys/20.18.1219
510 Ford CR, McGuire MA, Mitchell RJ, Teskey RO (2004) Assessing variation in the radial profile
511   of sap flux density in *Pinus* species and its effect on daily water use. Tree Physiol 24(3):
512   241-249. https://doi.org/10.1093/treephys/24.3.241
513 Forster MA (2014) How significant is nocturnal sap flow? Tree Physiol 34: 757-765.
514   https://doi.org/10.1093/treephys/tpu051

515   Georgiadis P (2022) Ethnobotanical knowledge against the combined biodiversity, poverty and
516   climate crisis: A case study from a Karen community in Northern Thailand. Plants People
517   Planet 4(4): 382–391. https://doi.org/10.1002/ppp3.10259

518   Granier A (1985) *Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des*
519   *arbres*. Ann For Sci 42(4) : 193-200. https://doi.org/10.1051/forest:19850204

520   Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow
521   measurements. Tree Physiol 3: 309– 320. https://doi.org/10.1093/treephys/3.4.309

522   Granier A, Loustau D, Bréda N (2000) A generic model of forest canopy conductance dependent
523   on climate, soil water availability and leaf area index. Ann For Sci 8: 755–765.
524   https://doi.org/10.1051/forest:2000158ï

525   Gutierrez Lopez J, Tor-ngern P, Oren R, Kozii N, Laudon H, Hasselquist NJ (2021) How tree
526   species, tree size, and topographical location influenced tree transpiration in northern
527   boreal forests during the historic 2018 drought. Glob Change Biol 27(13): 3066-3078.
528   https://doi.org/10.1111/gcb.15601

529   Hardanto A, Röll A, Niu F, Meijide A, Hendrayato, Hölscher D (2017) Oil palm and rubber tree
530   water use patterns: effects of topography and flooding. Front Plant Sci 8: 2017.
531   https://doi.org/10.3389/fpls.2017.00452

532   Hasselquist N, Allen MF, Santiago LS (2010) Water relations of evergreen and drought-
533   deciduous trees along a seasonally dry tropical forest chronosequence. Oecologia 164:
534   881-890. https://doi.org/10.1007/s00442-010-1725-y

535   Hooper E, Condit R, Legendre P (2002) Responses of 20 Native Tree Species to Reforestation
536   Strategies for Abandoned Farmland in Panama. Ecol App 12(6): 1626-1641.
537   https://doi.org/10.2307/3099927

538   Horna V, Schuldt B, Brix S, Leuschner C (2011) Environment and tree size controlling stem sap
539   flux in a perhumid tropical forest of Central Sulawesi, Indonesia. Ann For Sci 68(5):
540   1027–1038. https://doi.org/10.1007/s13595-011-0110-2

541   Jackson RB, Jobbágy EG, Avissar R, Roy SB, Barrett DJ, Cook CW, Farley KA, Maitre DC,
542   McCarl BA, Murray BC (2005) Trading water for carbon with biological carbon
543   sequestration. Science 310(5756): 1944-1947. https://doi.org/10.1126/science.1119282

544   James SA, Clearwater MJ, Meinzer FC, Goldstein G (2002) Heat dissipation sensors of variable
545   length for the measurement of sap flow in trees with deep sapwood. Tree Physiol 22(4):
546   277-283. https://doi.org/10.1093/treephys/22.4.277

547   Jasechko S, Sharp ZD, Gibson JJ, Birks SJ, Yi Y, Fawcett PJ (2013) Terrestrial water fluxes
548   dominated by transpiration. Nature 496: 347–350 https://doi.org/10.1038/nature11983

549   Jaskierniak D, Kuczera G, Benyon RG, Lucieer A (2016) Estimating tree and stand sapwood
550   area in spatially heterogeneous southeastern Australian forests. J Plant Ecol 9(3): 272-
551   284. https://doi.org/10.1093/jpe/rtv056

552   Jung EY, Otieno D, Lee B, Lim JH, Kang SK, Schmidt MWT, Tenhunen J (2011) Up-scaling to
553   stand transpiration of an Asian temperate mixed-deciduous forest from single tree

554   sapflow measurements. Plant Ecol 212(3): 383–395. https://doi.org/10.1007/s11258-010-
555   9829-3
556   Kumagai T, Aoki S, Shimizu T, Otsuki K (2007) Sap flow estimates of stand transpiration at two
557   slope positions in a Japanese cedar forest watershed. Tree Physiol 27(2): 161-168.
558   https://doi.org/10.1093/treephys/27.2.161
559   Kunert N, Schwendenmann L, Potvin C, Hölscher D (2012) Tree diversity enhances tree
560   transpiration in a Panamanian forest plantation. J App Ecol 49(1): 135-144.
561   https://doi.org/10.1111/j.1365-2664.2011.02065.x
562   Li S, Xu M, Sun B (2014) Long-term hydrological response to reforestation in a large watershed
563   in southeastern China. Hydrol Process 28(22): 5573-5582.
564   https://doi.org/10.1002/hyp.10018
565   Lu P, Müller WJ, Chacko EK (2000) Spatial variations in xylem sap flux density in the trunk of
566   orchard-grown, mature mango trees under changing soil water conditions. Tree Physiol
567   20(10): 683-692. https://doi.org/10.1093/treephys/20.10.683
568   Lu P, Urban L, Ping Z (2004) Granier's Thermal Dissipation Probe (TDP) method for measuring
569   sap flow in trees: theory and practice. Acta Bot Sin 46(6): 631-646.
570   Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody
571   plants to xylem cavitation. Ecology, 85(8): 2184-2199. https://doi.org/10.1890/02-0538
572   Marod D, Sungkaew S, Mizunaga H, Thinkampheang S, Thongsawi J (2020) Woody plant
573   community and distribution in a tropical coastal sand dune in southern Thailand. J Coast
574   Conserv 24: 44. https://doi.org/10.1007/s11852-020-00761-9
575   Meinzer FC, Goldstein G, Holbrook NM, Jackson P, Cavelier J (1993) Stomatal and
576   environmental control of transpiration in a lowland tropical forest tree. Plant Cell Environ
577   16(4): 429–436. https://doi.org/10.1111/j.1365-3040.1993.tb00889.x
578   Meinzer FC, Goldstein G, Andrade JL (2001) Regulation of water flux through tropical forest
579   canopy trees: Do universal rules apply? Tree Physiol 21(1): 19-26.
580   https://doi.org/10.1093/treephys/21.1.19
581   Meinzer FC, Bond BJ, Warren JM, Woodruff DR (2005) Does water transport scale universally
582   with tree size? Funct Ecol 19(4): 558–565. https://doi.org/10.1111/j.1365-
583   2435.2005.01017.x
584   Menezes-Silva PE, Loram-Lourenço L, Alves RDFB, Sousa LF, Almeida SE da S, Farnese FS
585   (2019) Different ways to die in a changing world: Consequences of climate change for
586   tree species performance and survival through an ecophysiological perspective. Ecol Evol
587   9(20): 11979-11999. https://doi.org/10.1002/ece3.5663
588   Monteith JL, Unsworth MH (1990) Principles of environmental physics. Butterworth-
589   Heinemann, London, p 287.
590   Nepstad DC, Tohver IM, David R, Moutinho P, Cardinot G (2007) Mortality of large trees and
591   lianas following experimental drought in an amazon forest. Ecology 88(9): 2259-2269.
592   https://doi.org/10.1890/06-1046.1

593 Noguchi H, Suwa R, Adélia C, de Souza S, Kajimoto T, Ishizuka M (2014) Examination of
594   vertical distribution of fine root biomass in a tropical moist forest of the Central Amazon,
595   Brazil. Japan Agric Res Q 48: 231-235.
596 O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season:
597   Patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiol
598   19(9): 591-597. https://doi.org/10.1093/treephys/19.9.591
599 Oishi AC, Oren R, Stoy PC (2008) Estimating components of forest evapotranspiration: A
600   footprint approach for scaling sap flux measurements. Agric For Meteorol 148(11):
601   1719–1732. https://doi.org/10.1016/j.agrformet.2008.06.013
602 Oishi AC, Hawthorne DA, Oren R (2016) Baseliner: An open-source, interactive tool for
603   processing sap flux data from thermal dissipation probes. SoftwareX 5: 139–143.
604   https://doi.org/10.1016/j.softx.2016.07.003
605 Phillips N, Oren R (1998) A comparison of daily representations of canopy conductance based
606   on two conditional time-averaging methods and the dependence of daily conductance on
607   environmental factors. Ann For Sci 55(1-2): 217-235.
608   https://doi.org/10.1051/forest:19980113
609 Phillips N, Oren R (2001) Intra- and inter-annual variation in transpiration of a pine forest. Ecol
610   App 11(2): 385-396. https://doi.org/10.2307/3060896
611 Raquel Salas-Acosta E, Luis Andrade J, Adrián Perera-Burgos J, Us-Santamaría R, Figueroa-
612   Espinoza B, Uuh-Sonda JM, Cejudo E (2022) Transpiration of a Tropical Dry Deciduous
613   Forest in Yucatan, Mexico. Atmosphere 13(2): 271.
614   https://doi.org/10.3390/atmos13020271
615 Roberts J, Cabral OMR, Aguiar LF De (1990) Stomatal and boundary-layer conductances in an
616   Amazonian terra firme rain forest. J App Ecol 27(1): 336-353.
617   https://doi.org/10.2307/2403590
618 Rodtassana C, Unawong W, Yaemphum S, Chanthorn W, Chawchai S, Nathalang A,
619   Brockelman WY, Tor-ngern P (2021) Different responses of soil respiration to
620   environmental factors across forest stages in a Southeast Asian forest. Ecol Evol 00: 1-
621   14. https://doi.org/10.1002/ece3.8248
622 Rong L, Duan X, Feng D, Zhang G (2017) Soil moisture variation in a farmed dry-hot valley
623   catchment evaluated by a redundancy analysis approach. Water 9(2): 92.
624   https://doi.org/10.3390/w9020092
625 Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant Cell
626   Environ 29(3): 367-381. https://doi.org/10.1111/j.1365-3040.2005.01478.x
627 Spanner GC, Gimenez BO, Wright CL, Menezes VS, Newman BD, Collins AD, Jardine KJ,
628   Negron-Juarez RI, Nogueira Lima AJ, Rodrigues JR, Chambers JQ, Higuchi N, Warren
629   JM (2022) Dry Season Transpiration and Soil Water Dynamics in the Central Amazon.
630   Front Plant Sci 13:2022. https://doi.org/10.3389/fpls.2022.825097

631 Schäfer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal
632   conductance. Plant Cell Environ 23(4): 365 - 375. http://dx.doi.org/10.1046/j.1365-
633   3040.2000.00553.x
634 Schwendenmann L, Pendall E, Sanchez-Bragado R, Kunert N, Hölscher D (2015) Tree water
635   uptake in a tropical plantation varying in tree diversity: Interspecific differences, seasonal
636   shifts and complementarity. Ecohydrol 8(1): 1-12. https://doi.org/10.1002/eco.1479
637 Stibig HJ, Achard F, Carboni S, Rasi R, Miettinen J (2014) Change in tropical forest cover of
638   Southeast Asia from 1990 to 2010. Biogeosci 11: 247-258. https://doi.org/10.5194/bg-11-
639   247-2014
640 Stovall AEL, Shugart H, Yang X (2019) Tree height explains mortality risk during an intense
641   drought. Nat Commun 10: 4385. https://doi.org/10.1038/s41467-019-12380-6
642 Tagane S, Souladeth P, Nagahama A, Suyama Y, Ishii N, Tanaka N, Yahara T (2020) Twenty-
643   five new species records in the flora of Laos. Nat Hist Bull Siam Soc 64(1): 25-41.
644 Tateishi M, Kumagai T, Utsumi Y, Umebayashi T, Shiiba Y, Inoue K, Kaji K, Cho K, Otsuki K
645   (2008) Spatial variations in xylem sap flux density in evergreen oak trees with radial-
646   porous wood: comparisons with anatomical observations. Trees 23: 23-30.
647   https://doi.org/10.1007/s00468-007-0165-8
648 Theilade I, Schmidt L, Chhang P, McDonald JA (2011) Evergreen swamp forest in Cambodia:
649   Floristic composition, ecological characteristics, and conservation status. Nord J Bot
650   29(1): 71–80. https://doi.org/10.1111/j.1756-1051.2010.01003.x
651 Tor-ngern P, Oren R, Palmroth S, Novick K, Oishi A, Linder S, Ottosson-Löfvenius M, Näsholm
652   T (2018) Water balance of pine forests: Synthesis of new and published results. Agric For
653   Meteorol 259: 107–117. https://doi.org/10.1016/j.agrformet.2018.04.021
654 Unawong W, Yaemphum S, Nathalang A, Chen Y, Domec JC, Tor-ngern P (2022) Variations in
655   leaf water status and drought tolerance of dominant tree species growing in multi-aged
656   tropical forests in Thailand. Sci Rep 12: 6882. https://doi.org/10.1038/s41598-022-
657   10988-1
658 van Dijk AIJM, Keenan RJ (2007) Planted forests and water in perspective. For Ecol Manag
659   251(1-2):1-9. https://doi.org/10.1016/j.foreco.2007.06.010
660 Van Kanten R, Vaast P (2006) Transpiration of arabica coffee and associated shade tree species
661   in sub-optimal, low-altitude conditions of Costa Rica. Agroforest Syst 67(2): 187-202.
662   https://doi.org/10.1007/s10457-005-3744-y
663 Wang D, Tang Y (2014) A one-parameter Budyko model for water balance captures emergent
664   behavior in darwinian hydrologic models. Geophys Res Lett 41: 4569-4577.
665   https://doi:10.1002/2014GL060509
666 Wang J, Fu B, Lu N, Wang S, Zhang L (2019) Water use characteristics of native and exotic
667   shrub species in the semi-arid Loess Plateau using an isotope technique. Agric Ecosyst
668   Environ 276: 55-63. https://doi.org/10.1016/j.agee.2019.02.015

669   Wang J, Fu B, Wang L, Lu N, Li J (2020) Water use characteristics of the common tree species
670   in different plantation types in the Loess Plateau of China. Agric For Meteorol 288-289:
671   108020. https://doi.org/10.1016/j.agrformet.2020.108020
672   Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in
673   trees. Tree Physiol 18(8–9): 499-512. https://doi.org/10.1093/treephys/18.8-9.499
674   Xu S, Yu Z (2020) Environmental control on transpiration: A case study of a desert ecosystem in
675   northwest china. Water 12(4): 1211. https://doi.org/10.3390/W12041211
676   Yaemphum S, Unawong W, Tor-Ngern P (2022) Sapwood area~DBH allometries for 14
677   common tree species in a successional tropical forest in Thailand. Forestry 95(4): 562–
678   571. https://doi.org/10.1093/forestry/cpab054
679   Zeng Z, Estes L, Ziegler AD, Chen A, Searchinger T, Hua F, Guan K, Jintrawet A, Wood EF
680   (2018) Highland cropland expansion and forest loss in Southeast Asia in the twenty-first
681   century. Nat Geosci 11: 556–562. https://doi.org/10.1038/s41561-018-0166-9
682   Zeppel M, Eamus D (2008) Coordination of leaf area, sapwood area and canopy conductance
683   leads to species convergence of tree water use in a remnant evergreen woodland. Austr J
684   Bot 56(2): 97–108. https://doi.org/10.1071/BT07091
685   Zhang YJ, Meinzer FC, Hao GY, Scholz FG, Bucci SJ, Takahashi FSC, Villalobos-Vega R,
686   Giraldo J P, Cao KF, Hoffmann WA, Goldstein G (2009) Size-dependent mortality in a
687   Neotropical savanna tree: The role of height-related adjustments in hydraulic architecture
688   and carbon allocation. Plant Cell Environ 32(10): 1456-1466.
689   https://doi.org/10.1111/j.1365-3040.2009.02012.x

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 µmol m^{-2} s^{-1}; red line) and (**B**) rainfall (mm; gray bar) and relative extractable water (REW; red line).
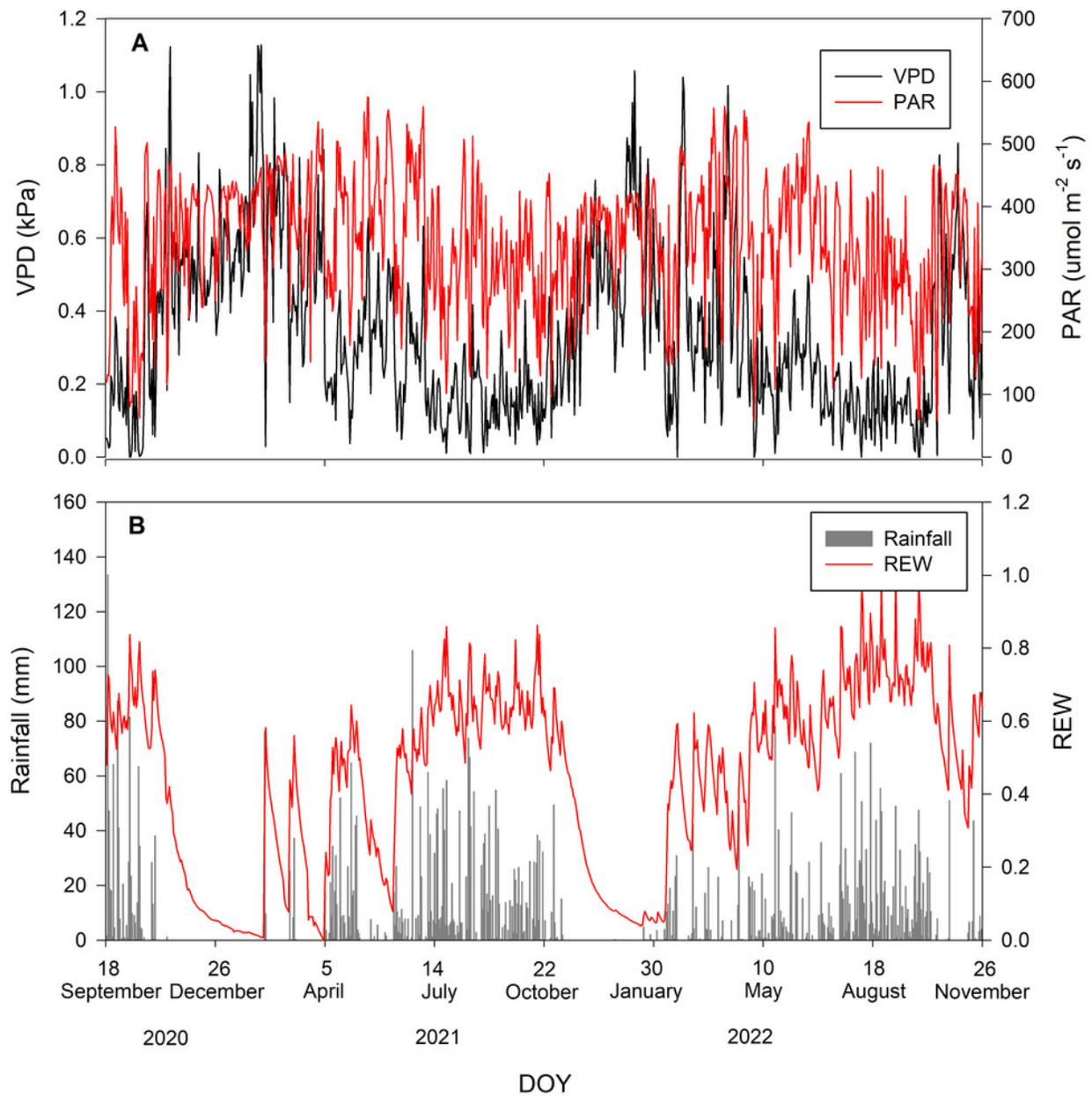
Figure 2

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), averaged across all trees for each species, throughout the study period from 18 September 2020 to 26 November 2022.
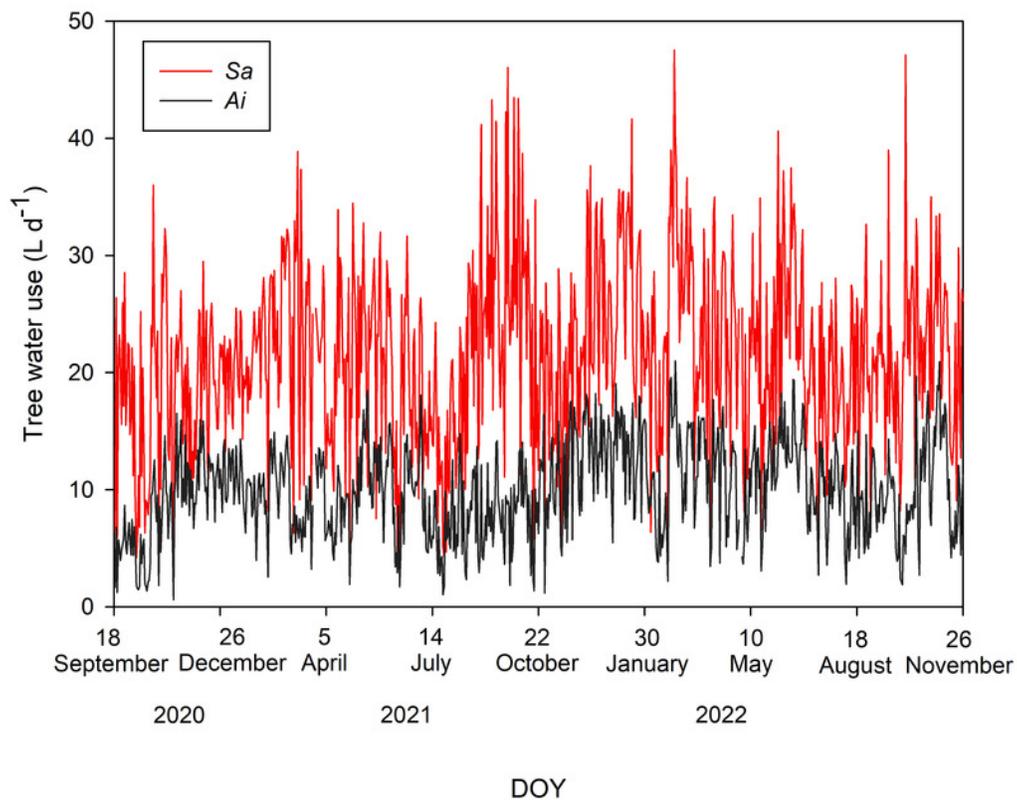
Figure 3

Figure 3 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).
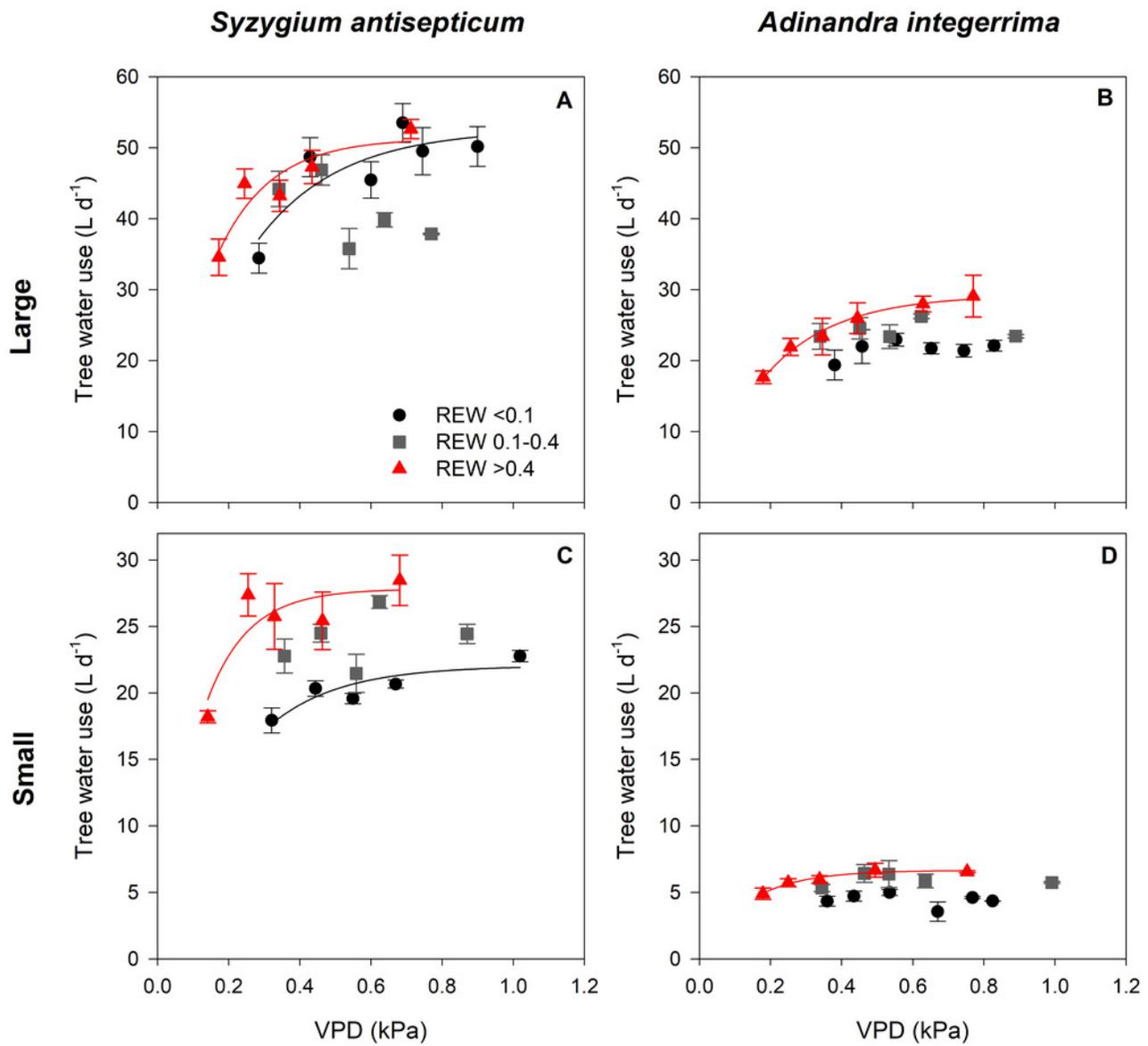
Table 1 Information of the selected study trees. DBH refers to the diameter at breast height in cm. Sapwood area (in cm^2) was estimated using an allometric equation derived from dominant species in the study site (Yaemphum et al. 2022).

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

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.

Species	Size classes	REW classes	Relationships	r^2	p
Syzygium antisepticum (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
Adinandra integerrima (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 Summary of water use of tropical forest trees reviewed in this study.

Mean values (± SD if available) are presented. The abbreviations are DBH, diameter at breast height (~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⁻¹)	Period
Dye 1996	Frankfort State Forest in South Africa (24°49′ S, 30°43′ E)	Site 1 (3-year-old trees)	*Eucalyptus grandis*	HPM	14.7 ± 1.17	14.7 ± 1.01	45.8	July 1993
		Site 2 (9-year-old trees)	*Eucalyptus grandis*	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)		*Eucalyptus miniate* *Eucalyptus tetrodonta* *Eucalyptus latifolia* *Eucalyptus Capricornia* *Eucalyptus spp.* *Eucalyptus terminalis*	HPM	8.8 – 30.4 4.9 – 48.7 9.7 – 48.7 6.1– 35.6 6.1- 35.6 9.1– 41.6	NA	16.1	August–September 1998 (Dry season)
							17.9	March–April 1999 (Wet season)
Dierick and Hölscher 2009	The Philippines (10°45′55″N, 124°47′25″E) and (10°44′10″N, 124°48′16″E)		*Shorea contorta* *Parashorea malaanonan* *Hopea malibato* *Hopea plagata* *Swietenia macrophylla.* *Vitex parviflora* *Myrica javanica* *Sandoricum koetjape*	TDP	18.2 ± 7 12 ± 0.4 11.6 ± 2.4 6.6 ç 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

		Durio zibethinus *Gmelina arborea*					
Dierick et al. 2010	The Philippines (10°45′55″N, 124°47′25″E) and (10°44′10″N, 124°48′16″E)	*Shorea contorta* *Parashorea malaanonan* *Hopea malibato* *Hopea plagata* *Swietenia macrophylla* *Vitex parviflora* *Myrica javanica.* *Sandoricum koetjape.* *Durio zibethinus* *Gmelina arborea*	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)	*Theobroma cacao* *Gliricidia sepium*	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)	*Luehea seemannii* *Anacardium excelsum* *Hura crepitans* *Cedrela odorata* *Tabebuia rosea*	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)

Reference	Site	Subsite	Species	Method				Study period
Clulow et al. 2013	Nkazana Peat swamp forest site (28°10.176′ S, 32°30.070′ E)		*Syzygium cordatum* *Shirakiopsis elliptica*	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)		*Drypetes natalensis* *Eugenia natalitia* *Mimusops caffra*	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)		*Ziziphus jujuba*	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	*Metrosideros polymorpha* *Cecropia obtusifolia* *Macaranga mappa* *Melastoma septemnervium*	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	*Metrosideros polymorpha*	TDP	9.0 - 42.0	NA	5 - 43	
Hardanto et al. 2017	rubber monoculture		**Rubber trees** *Hevea brasiliensis*	TDP	20.3 ± 0.6	13.4 ± 0.4	25.6 ± 3.7	June to August 2013
	jungle rubber		**Rubber trees** *Hevea brasiliensis*	TDP	17.8 ± 0.5	140. ± 0.5	24.1 ± 4.2	

		Admixed native trees *Cratoxylum sumatranum* *Callerya atropurpurea* *Ixonanthes petiolaris* *Santiria griffithii* *Macaranga cf. sumatrana* *Artocarpus nitidus* *Alstonia angustifolia* *Streblus elongates* *Artocarpus integer* *Porterandia anisophylla* *Timonius wallichianus*	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	