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

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A Thesis Submitted in Partial Fulfillment of the Requirements
for the Degree of Master of Science in Hazardous Substance and
Environmental Management (Interdisciplinary Program)
Inter-Department of Environmental Management
GRADUATE SCHOOL
Chulalongkorn University
Academic Year 2022

ลักษณะการใช้น้ำของ *Syzygium antisepticum* และ *Adinandra integerrima* ในป่าเขตร้อนรุ่นสองในอุทยานแห่งชาติเขาใหญ่เพื่อการจัดการสิ่งแวดล้อม

นายรัชชานนท์ อัมพรพิทักษ์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
สาขาวิชาการจัดการสารอันตรายและสิ่งแวดล้อม (สหสาขาวิชา) สหสาขาวิชาการจัดการสิ่งแวดล้อม
บัณฑิตวิทยาลัย จุฬาลงกรณ์มหาวิทยาลัย
ปีการศึกษา 2565

Thesis Title	Water-use characteristics of *Syzygium antisepticum* and *Adinandra integerrima* in a secondary tropical forestin Khao Yai National Park for environmental management
By	Mr. Ratchanon Ampornpitak
Field of Study	Hazardous Substance and Environmental Management (Interdisciplinary Program)
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ป่าไม้ในเอเชียตะวันออกเฉียงใต้ได้รับผลกระทบจากการตัดไม้ทำลายป่าอย่างกว้างขวางและการเปลี่ยนแปลงการใช้ที่ดิน ดังนั้นประเทศส่วนใหญ่ในภูมิภาคนี้พยายามที่จะคืนพื้นที่ป่าด้วยการปลูกป่าทดแทน อย่างไรก็ตาม การปลูกต้นไม้อย่างมีประสิทธิภาพนั้นทำได้ยาก เนื่องจากการเปลี่ยนแปลงสภาพแวดล้อมและขนาดต้นไม้ อาจส่งผลต่อการใช้น้ำของต้นไม้ ดังนั้น ข้อมูลเกี่ยวกับลักษณะการใช้น้ำของพันธุ์ไม้ชนิดต่าง ๆ ในขนาดต้นที่แตกต่างกัน จึงมีความสำคัญต่อการคัดเลือกพันธุ์ไม้เพื่อทำการปลูกป่าทดแทน อย่างไรก็ตาม ข้อมูลที่มีอยู่เกี่ยวกับลักษณะการใช้น้ำเฉพาะของพันธุ์ไม้แต่ละชนิดนั้นยังมีอยู่อย่างกำจัด โดยเฉพาะในป่าเขตร้อนรุ่นสอง เพื่อให้ได้ข้อมูลเกี่ยวกับลักษณะการใช้น้ำเฉพาะชนิดพันธุ์ไม้ในป่ารุ่นสอง เราได้ทำการประเมิน อัตราการใช้น้ำของต้นไม้ (T) ของพันธุ์ไม้ 2 ชนิด ได้แก่ *Syzygium antisepticum* (เสม็ดแดง) และ *Adinandra integerrima* (พิกุลป่า) แทนด้วย *Sa* และ *Ai* ตามลำดับ ในป่าเขตร้อนรุ่นสอง ณ อุทยานแห่งชาติเขาใหญ่ โดยใช้ข้อมูลจากหัววัดการกระจายความร้อนที่ประดิษฐ์เอง และทำการประเมินการตอบสนองของ T ของทั้งสองชนิด ในขนาดต้นใหญ่และเล็กต่อปัจจัยทางสิ่งแวดล้อม ได้แก่ ความชื้นในดินและภาวะพร่องความดันไอ (vapor pressure deficit; VPD) ซึ่งจะเป็นตัวบ่งบอกถึงความชื้นในดินและความชื้นในบรรยากาศตามลำดับ จากการวิเคราะห์ผลพบว่า T ของ *Sa* มีค่าที่สูงกว่า *Ai* ที่ทุกช่วง VPD ผลลัพธ์ของเราชี้ให้เห็นว่า *Ai* อาจเหมาะสำหรับการปลูกป่าทดแทนในพื้นที่ที่มักเกิดภัยแล้งในระบบนิเวศปลายน้ำ เนื่องจากมีลักษณะการใช้น้ำแบบอนุรักษ์ กล่าวคือมีอัตราค่อนข้างคงที่ และอาจเป็นประโยชน์ต่อระบบนิเวศปลายน้ำด้วยการเพิ่มปริมาณน้ำที่ไหลบ่าจากป่าในช่วงฤดูแล้ง นอกจากนี้ *Ai* ยังมีลักษณะการใช้น้ำแบบอนุรักษ์โดยไม่ผันแปรตามขนาดต้นที่เปลี่ยนไป ดังนั้น *Ai* จะยังคงให้ประโยชน์เหล่านี้แก่ระบบนิเวศเมื่อพวกมันเติบโตขึ้นในอนาคต ในทางตรงกันข้าม *Sa* จะเหมาะสมในการปลูกป่าทดแทนในบริเวณที่มีน้ำท่วมบ่อย เนื่องจากมีลักษณะการใช้น้ำที่มากในช่วงที่ความชื้นในดินสูง ซึ่งอาจชะลอการไหลบ่าของน้ำจากป่าไปสู่ระบบนิเวศท้ายน้ำเมื่อเกิดพายุ อย่างไรก็ตาม การปลูกต้นไม้แบบผสมผสานน่าจะเหมาะสมสำหรับการปลูกป่าทดแทนในพื้นที่ที่ไม่เกิดภัยแล้งหรือน้ำท่วมขึ้นบ่อยนัก เพราะพันธุ์ไม้ทั้งสองชนิดนี้สามารถควบคุมการใช้น้ำที่ความชื้นในดินปานกลางได้โดยไม่เปลี่ยนแปลงตามขนาดต้นที่เปลี่ยนไป ซึ่งจะช่วยป้องกันการลดลงของน้ำในดินได้ การศึกษานี้เน้นให้เห็นว่าการตอบสนองของ T ขึ้นอยู่กับชนิดพันธุ์และขนาดของต้นไม้ ข้อมูลดังกล่าวจะเป็นประโยชน์ต่อการคัดเลือกพันธุ์ไม้สำหรับการปลูกป่าทดแทนซึ่งจะสามารถปรับตัวได้ดีกับสภาพแวดล้อม และสนับสนุนการออกแบบนโยบายเกี่ยวกับการจัดการป่าเขตร้อนและทรัพยากรธรรมชาติ อย่างไรก็ตาม ต้นไม้ทั้งสองชนิดพันธุ์นี้อาจให้ประโยชน์หรือผลเสียต่อระบบนิเวศก็ได้ ทั้งนี้ขึ้นอยู่กับวัตถุประสงค์ของการปลูกป่า

สาขาวิชา	การจัดการสารอันตรายและสิ่งแวดล้อม (สหสาขาวิชา)	ลายมือชื่อนิสิต ....
ปีการศึกษา	2565	ลายมือชื่อ อ.ที่ปรึกษาหลัก ....

6488073720 : MAJOR HAZARDOUS SUBSTANCE AND ENVIRONMENTAL MANAGEMENT (INTERDISCIPLINARY PROGRAM)

KEYWORD: tree water use, secondary forests, Syzygium antisepticum, Adinandra integerrima, tropical forests

Ratchanon Ampornpitak : Water-use characteristics of *Syzygium antisepticum* and *Adinandra integerrima* in a secondary tropical forestin Khao Yai National Park for environmental management. Advisor: Assoc. Prof. PANTANA TOR-NGERN, Ph.D.

Forests in Southeast Asia have been disrupted by widespread deforestation and land use change. Most countries in this region attempt to return the forested areas through reforestation. However, planting trees efficiently is difficult because changing environmental conditions and tree size could affect the water consumption of different tree-species under climate change. Hence, the information regarding water use characteristics of different tree-species in different tree size classes is important to the selection of tree species for reforestation. Nonetheless, available information on species-specific water-use characteristics is less investigated, especially in secondary tropical forests. To gain the information on species-specific water-use characteristics in secondary forests, we estimated tree water use (*T*) of dominant tree species including *Syzygium antisepticum* and *Adinandra integerrima,* hereafter *Sa* and *Ai*, respectively, in a secondary tropical forest at Khao Yai National Park Thailand using sap flow data from custom-made thermal dissipation probes and compare *T* of both species in different tree size classes. Specifically, we evaluated the responses of *T* of both species in large and small sizes to environmental factors including soil moisture and vapor pressure deficit (VPD) which represent soil and atmospheric humidity, respectively. Results of different soil moisture conditions in both sizes showed consistently higher *T* in *Sa* compared to *Ai* at across VPD ranges. Our results imply 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 increasing runoff from the forest during drought. 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 seem to 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. This study highlights that the response of *T* depends on species and tree 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 natural resources. Depending on reforestation purpose, *Sa* and *Ai* may provide either benefits or negative effects to the ecosystems.

Field of Study:	Hazardous Substance and Environmental Management (Interdisciplinary Program)	Student's Signature ....
Academic Year:	2022	Advisor's Signature ....

ACKNOWLEDGEMENTS

Undertaking this research has been experience for me and it would not have been possible to accomplish without the support and guidance that I received for many people. Here, I take this opportunity to acknowledge those people who contributed to this research.

First of all, I would like to say thank you to my advisor, Associate Professor Pantana Tor-ngern, Ph.D. for supporting. She always kind supported, motivated, inspired and helped me in all the time of my research. Without her guidance, this project would not have been achievable.

Besides my advisor, I would like to thank my research chairman, Professor Srilert Chotpantarat, Ph.D. and all committees including Bualuang Faiyue, Ph.D., Assistant Professor Penradee Chanpiwat, Ph.D and Assistant Professor Nisa Leksungnoen, Ph.D. for their insightful comments and suggestions.

My thank also to go the Center of Excellence on Hazardous Substance Management (HSM), Chulalongkorn University for scholarship and research funding during the study. Financial support from Thailand Graduate Institute of Science and Technology (TGIST), National Science and Technology Development Agency through a postgraduate scholarship (SCA-CO-2564-14439-TH) is gratefully acknowledged.

I would like to thank Miss Nichaphan Kasilam, Mr. Rathasart Somnuk, Miss Jutawan Moonongsang and Miss Jeerapat Thawjaturat for field assistance. Finally, I would like to express my great appreciation to my parents and my brothers for supporting me throughout my years of study. I am so grateful to receive good encouragement.

Thank you.

Ratchanon Ampornpitak

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CHAPTER 1
INTRODUCTION

In the forest water cycle, rainfall is partitioned into evapotranspiration, and runoff. Tree water use (*T*) is the major components in the water cycle because it represents 40–90% of terrestrial evapotranspiration (Deb Burman et al., 2019; Jasechko et al., 2013). Consequently, the quantity of *T* influences the precipitation that contributes to runoff which affects downstream ecosystems. Tree water use can be affected by various factors involving physiological and environmental aspects. Physiological factors that may affect *T* include tree size and leaf area (Gutierrez Lopez et al., 2021). In addition, environmental factors that may also influence *T* are air temperature, humidity, solar radiation and soil moisture (Xu & Yu, 2020). Nowadays global climate change affects *T* through changes in environmental conditions including temperature, precipitation regimes, severity of weather and climate extremes such as drought and flood (Menezes-Silva et al., 2019). Thus, the responses of *T* to environmental factors may govern outflow from forests. Evaluating such responses would provide insights for environmental management that involves water cycling, such as predicting runoff from forests which may result in floods or droughts in downstream ecosystems.

The variations of *T* are mainly related to tree size and environmental factors including soil water availability, solar radiation, and vapor pressure deficit (VPD) which represents atmospheric humidity (Gutierrez Lopez et al., 2021; Xu & Yu, 2020). Tree size may be a determinant of *T* (Jung et al., 2011; Meinzer et al., 2005). The relationship between tree diameter and *T* were found among several species of angiosperms (Meinzer et al., 2005). Zeppel and Eamus (2008) estimated daily *T* with sap flux data of *Eucalyptus crebra* (a broad-leaved species) and *Callitris glaucophylla* (a needle leaved species) in evergreen woodland in Australia, and they found that tree size influenced daily *T*. The significant correlation between tree size and *T* were also found among trees in temperate mixed-deciduous forest in South Korea (Jung et al., 2011). In addition, different tree sizes have been linked to the different responses to drought with large trees being more vulnerable to drought than small trees because of greater exposure to atmospheric demand (Bennett et al., 2015; Stovall et al., 2019).

Nevertheless, the information of effects of tree size on *T* is still lacking in secondary tropical forests. Furthermore, the effects of environmental factors on *T* are ambiguous 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 be decreased with increasing VPD during extreme drought in an Amazonian tropical rainforest. On the other hand, Spanner et al. (2022) found that sensitivity of *T* to soil moisture varied by tree species in an old-growth upland forest in central Amazon. Thus, changing environmental conditions can alter the pattern of response of *T*.

Forests in Southeast Asia are rich ecosystems that provide a range of ecosystem services with importance to many people and communities. Unfortunately, forests in this region have been disrupted by land use change and widespread deforestation (Stibig et al., 2014; Zeng et al., 2018). Land use change and widespread deforestation are transforming tropical forest to the successional forests (Curtis et al., 2018). After these areas were disrupted by human or nature, they were abandoned for several years and naturally or artificially transformed into secondary forests. Consequently, many of the forested areas in this region have been degraded and may not contribute much to improving biodiversity and mitigating climate change. Therefore, most countries in this region attempt to return the forest areas through reforestation. Reforestation projects in tropical forests emphasize the use of native species to avoid competition with other native trees, which can help restoring biodiversity and sequester carbon (Hooper et al., 2002). Nevertheless, planting trees into forests have been concerned because trees might deplete water resources (Jackson, 2005). Also, reforestation may be concern in some areas because it may reduce water supply for the existing trees and increase evapotranspiration rate (Van Kanten & Vaast, 2006). Reforestation could increase evapotranspiration rates leading to reductions in runoff (Li et al., 2014). Runoff was reduced by 44% when reforesting grass and reduced by 31% when reforesting shrubland, by a global data synthesis from many parts of the southern hemisphere and the northern hemisphere (Farley et al., 2005). Moreover, streamflow reduction was observed up to 50% under *Pinus* plantations (Buytaert et al., 2007). Thus, an appropriate tree species selection is perhaps the first options for reforestation because differences in water-use characteristics among species could affect water cycle (van Dijk & Keenan, 2007). However, available information on species-specific water-use characteristics is still limited in tropical forests, especially in secondary ones. Hence, it is important to evaluate the patterns of response of T to environmental factors in secondary tropical forests that would offer information on species-specific water-use characteristics.

Khao Yai National Park covers an area of about 200 km^2 which covered four provinces in Thailand. This national park is a UNESCO world heritage site. Khao Yai National Park vegetation is a mosaic of different stages of vegetation succession. More than 60% of tropical forests are in some stage of regeneration while the remainder are old-growth forests (Chazdon, 2008). Thus, secondary forests are important to improve biodiversity and mitigate climate change. This study was performed in a secondary tropical forest at Khao Yai National Park representing a young forest aged ~10 years. In this study site, the dominant tree species are *Syzygium antisepticum* and *Adinandra integerrima* which have naturally evolved to become dominant species in this study site. *S. 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). *A. integerrima* can be found in Thailand and other countries in tropical region such as Cambodia, China, Laos, and Vietnam (Tagane et al., 2020). Moreover, *A. integerrima* can be found as the dominant species in other secondary forests in Thailand such as Doi Inthanon National Park (Georgiadis, 2022). However, the information of water-use characteristics of both species is still lacking. Therefore, this study aims (1) to estimate T of dominant tree species including *S.* and *A. integerrima* in a secondary tropical forest in Khao Yai National Park from sap flux density (J_S) which is continuously monitored with custom-made sap flow sensors and compare T of both species in different tree size classes and (2) to evaluate the responses of T to environmental factors of both species in different tree size classes. The data will cover a period of two years (18 September 2020 to 17 November 2022) which cover a wide range of environmental conditions. The outcome from this study would provide the information of species-specific water-use characteristics in secondary forests which can support policy design on the management of tropical forests and natural resources. In addition, findings from this study may provide a recommendation for selecting appropriate tree species for forest restoration in tropical regions.

1.1 Research objectives

1.1.1 To compare tree water use of two dominant tree species, *S. antisepticum* and *A. integerrima*, in different tree size classes in a secondary forest at Khao Yai National Park.

1.1.2 To evaluate the responses of tree water use of *S. antisepticum* and *A. integerrima* to environmental factors in different tree size classes in a secondary forest at Khao Yai National Park.

1.2 Conceptual framework

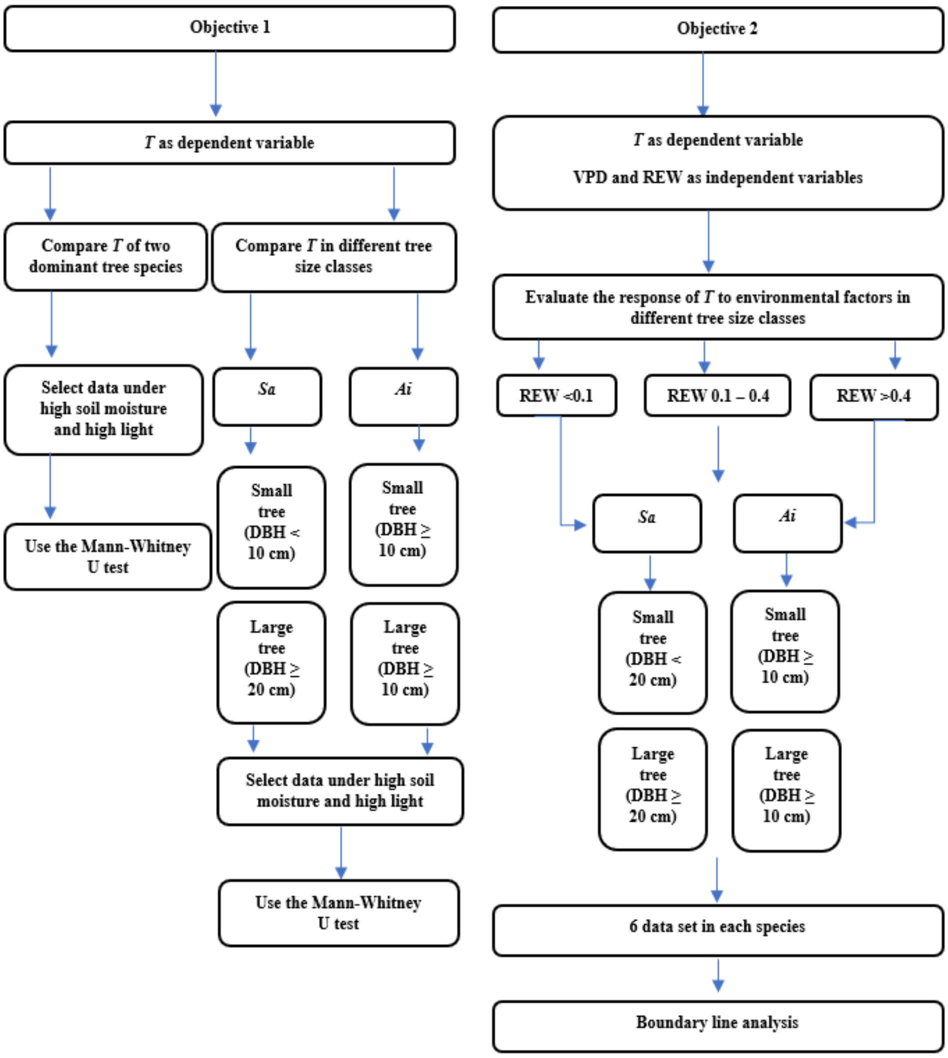


Figure 1.1 Overall framework of the study. T is tree water use (L d^{-1}), VPD is vapor pressure deficit (kPa), REW is relative extractable water, *Sa* is *S. antisepticum* and *Ai* is *A. integerrima.*

CHAPTER 2
LITERATURE REVIEW

Sap flux density (J_s, g m^{-2} s^{-1}), which is the rate of water flow per unit area of sapwood, is a critical parameter that being commonly used to calculate *T* or sap flow which refers to the amount of water that moves through a stem over a time. Many studies have continuously J_s monitored through the soil-plant-atmosphere continuum (SPAC) and scale up to *T*. The SPAC is defined as the path of movement of water from the soil, through the tree and to the atmosphere (Goldsmith, 2013).Trees uptake water via root systems. Then, water moves in xylem towards leaves. It is evaporated through stomata into the atmosphere. Consequently, the quantity of *T* influences the rainfall that contributes to runoff which affects water supply in downstream ecosystems. Because trees play an important role in the water cycle, an understanding of the processes of water transport and estimating *T* are critical to managing water resources and environments.

2.1 Water transport in trees

In trees, water can be moved by diffusion and bulk flow process. The movement of water is driven by these fundamental transport mechanisms. Diffusion is a process that causes the movement of molecules from regions of high concentration to regions of low concentration. The rate of diffusion depends on the difference in concentration of substances (Δc_s) between the distance (Δx). This relation can be written as Fick's first law:

$$J_s = -D_s \frac{\Delta c}{\Delta x} \qquad (1)$$

where J_s is the rate of water flow per unit area or the sap flux density, D_s is diffusion coefficient, Δc is the difference in concentration of substance and Δx is the distance between two points. The diffusion coefficient represents how easily substances move through medium. It depends on characteristics of the substance (larger molecules have smaller D_s) and medium. According to Fick's first law, a substance diffuses faster when the concentration gradient becomes larger or when D_s is increased. Water can move through the membrane bilayer by diffusion as shown on the left in Figure 2.1. Furthermore, water molecules can also move through a water-selective pore formed by integral membrane proteins such as aquaporins, as shown on the right in Figure 2.1.

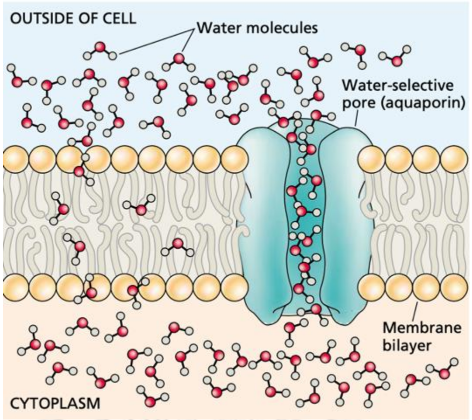


Figure 2.1 The path way for water movement across plant membranes (Taiz & E., 2002)

However, diffusion slows over long distances. The second process by which water transport is known as bulk flow. Bulk flow is the movement of groups of water, influenced by a pressure gradient. Bulk flow of water is the major process for long-distance transport of water in the xylem that water move down a pressure gradient. Moreover, water can be moved by combination of these fundamental transport mechanisms that is called osmosis. In osmosis, both types of gradient influence transport including concentration gradient and pressure gradient. The rate of water flow is determined by these two-driving force. The total driving force represents the chemical potential gradient of water. The chemical potential of water is a quantitative expression of the free energy which represents the potential for performing working. In trees, long-distance transport is driven by input of free energy into tree. Thus, plant physiologists have used a parameter called water potential (Ψ_w), defined as the chemical potential of water. Water potential is a measure of the free energy of water per unit volume (J m^{-3}). This unit is equivalent to pascal (Pa) which is commonly used for Ψ_w. Therefore, osmosis is driven by a water potential gradient.

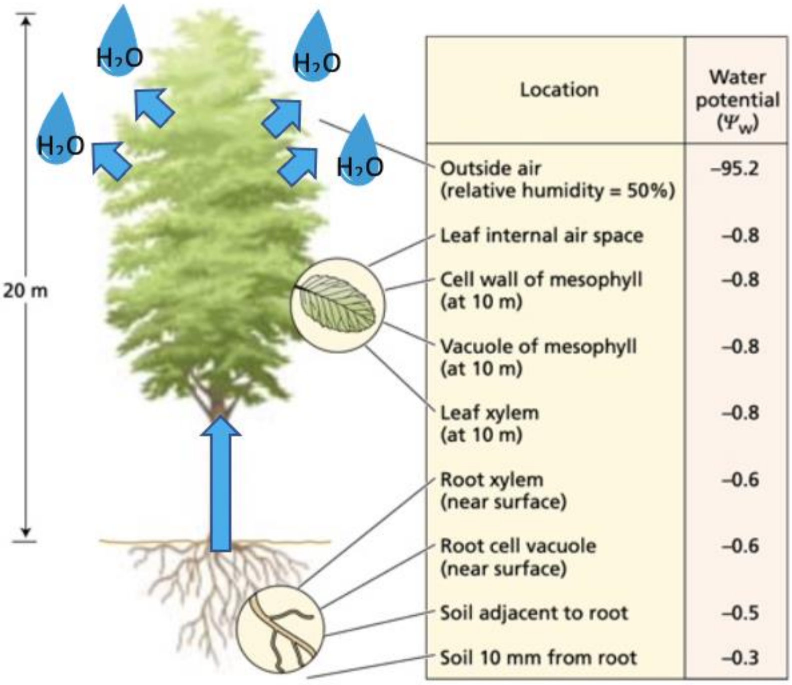
Three major factors contribute to Ψ_w in tree including concentration, pressure, and gravity, as the following:

$$\Psi_w = \Psi_s + \Psi_p + \Psi_g \quad (2)$$

where Ψ_s, Ψ_p ,Ψ_g are the effect of solutes, pressure and gravity respectively, on the free energy of water. Osmotic potential (Ψ_s) represents the effect of dissolved solutes on water potential. The free energy can be reduced by diluting the water. The mixing of solutes and water increases the disorder in the system and reduces free energy. Thus, dissolved solutes reduce the water potential of solution compared to pure water. The term Ψ_p is the hydrostatic pressure. Water potential can be increased by positive pressure. The positive hydrostatic pressure within the cells refers to turgor pressure. The Ψ_p can be negative such as in the xylem. Negative pressure outside the cells is important for moving water long distances through the tree. The Ψ_p is measured by the deviation from the ambient pressure. Moreover, gravity causes water to move downward. The Ψ_g depends on the height of water above the reference-state water, the density of water, and the acceleration due to gravity. However, the Ψ_g is omitted in water transport at cell level because it is negligible compared to Ψ_s and Ψ_p. Therefore, Equation (2) can be simplified as follows:

$$\Psi_w = \Psi_s + \Psi_p \quad (3)$$

The rate of water transport across membrane depends on Ψ_w difference across membrane. The transport of water in the SPAC is shown in Figure 2.2. When water moves through SPAC, it pass a widely variable medium (soil, plant, and atmosphere). Water moves from high water potential regions to lower water potential regions.



Location	Water potential (Ψ_w)
Outside air (relative humidity = 50%)	–95.2
Leaf internal air space	–0.8
Cell wall of mesophyll (at 10 m)	–0.8
Vacuole of mesophyll (at 10 m)	–0.8
Leaf xylem (at 10 m)	–0.8
Root xylem (near surface)	–0.6
Root cell vacuole (near surface)	–0.6
Soil adjacent to root	–0.5
Soil 10 mm from root	–0.3

Figure 2.1 Overview of water potential from the soil through the plant to the atmosphere (adapted from Taiz & Zeiger, 2002).

The transport of water from soil into root can be occurred by osmosis with water moving from high Ψ_w, which is usually soil, to low Ψ_w which is usually root. The rate of water flow from the soil into the roots depends on the size of the pressure gradient between soil and root and the hydraulic conductivity of the soil. As water is absorbed by roots, the soil recedes into small channels between the soil particles leading to it bring the soil solution into tension (more positive Ψ_p) by surface tension. When more water is absorbed by tree, more tensions are greater in soil (high Ψ_w). Moreover, soil hydraulic conductivity varies with the type of soil and water content. For example, sandy soil which has large space between particles have a large hydraulic conductivity while clay soil which is the small spaces between particles have a small hydraulic conductivity. When soil water content is decreased, the hydraulic conductivity decreases because of the replacement of water in the soil spaces by air. As more water of the soil spaces become filled by air, fewer water flows through soil into roots and the hydraulic conductivity falls. To reach the xylem when water is absorbed by root, water crosses the epidermis and then its way toward to cortex and endodermis before arriving at the xylem (Figure 2.3). From the epidermis to the endodermis of the root, there are three pathways for water movement including apoplast, sysmplast and transmembrane pathway. For symplast pathway, water flows between cells through plasmodesmata. In the transmembrane pathway, water flows across the plasma membranes with short visit to cell wall space. For the apoplast pathway, water moves through the cell wall.

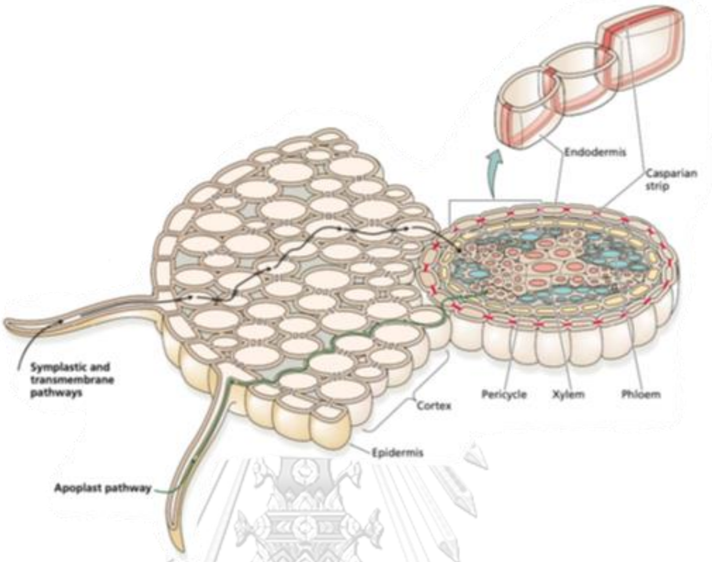


Figure 2.2 The pathways for water movement in roots (adapted from Taiz & Zeiger, 2002)

As water reaches xylem, water moves over long distances in the stems and branches. The conducting cells in the xylem have a specialized structure that allows large quantities of water transport. The xylem provides a low resistance for water transport, so reducing the pressure gradient needed to transport water from soil to the leaves. Thus, trees have trend to generate the positive pressure (high Ψ_w) at the base of tree and the negative pressure (low Ψ_w) at the top of tree. At the base of tree, root can develop positive Ψ_p when water is absorbed by roots as mentioned above which is called root pressure. However, root pressure is typically small value and disappears when transpiration rate is high. Thus, it is inadequate to move water over long distances in the stems and branches. Instead, water at the top of tree develops a large tension (a negative Ψ_w) and it pulls water up through the xylem. This mechanism is called the cohesion-tension theory of sap ascent. The cohesion-tension theory explains the ascent of sap in trees. The name of this theory comes from the ‘cohesion’ of water molecules and the capillary suction resulting from tension. The cohesion of water molecules is the property of water molecules to cling to each other through hydrogen-bonding. When water moves up through the xylem, water molecules can tight together as a result of the force of cohesion that helps water molecules great strength. This force sustains a very high degree of tension without breaking between water molecules in the xylem. In addition, it helps water transport to the canopy heights of several meters above ground. Moreover, the tension needed to pull water through the xylem results from transpiration. Tree transpiration generates a negative pressure in the xylem. The negative pressure develops at the surface of the cell wall in the leaf. Leaf direct contact with the atmosphere. As water is lost into the air, the pressure of the water within the leaf becomes more negative (more tension). Therefore, the motive force for water transport though the xylem is generated at air-water interfaces within the leaf. For water movement from the leaf to the atmosphere, water is pulled from the xylem into the cell wall of the mesophyll and then water vapor exits the leaf through the stomata (Figure 2.4).

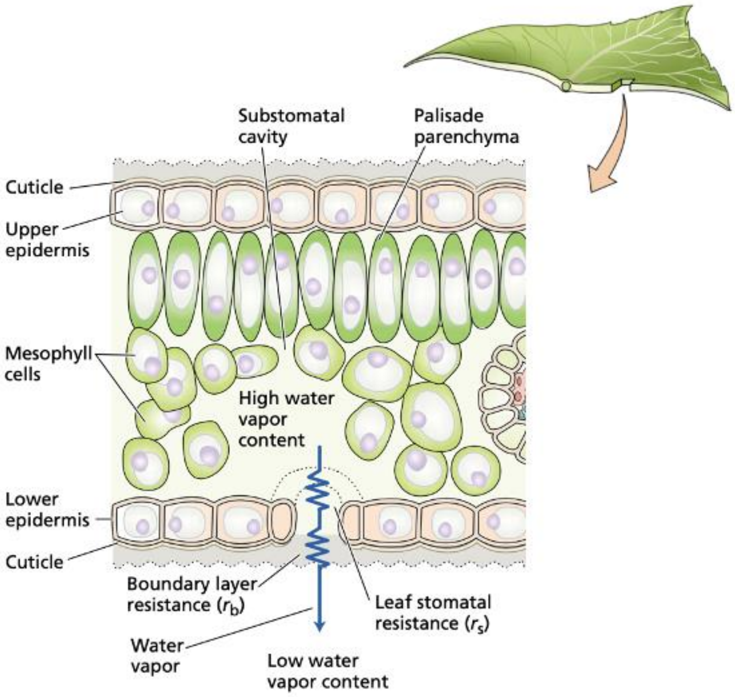


Figure 2.3 The pathway for water movement though leaf (adapted from Taiz & Zeiger, 2002)

Water transport in trees from root to atmosphere response to physical force. The mechanisms of water transport in tree include diffusion, bulk flow, and osmosis. Each of these processes is coupled to different driving forces. Water in the tree can be considered a continuous water column, connecting the water in the soil with the water vapor in the atmosphere. Water evaporation from the leaf generates large negative pressures (or tensions). These negative pressures are transmitted to the xylem, and they pull water through the xylem.

2.2 Transpiration and the water cycle in forests

The water cycle in forests, also known as the forest hydrologic cycle, involves the continuous circulation of water within the ecosystem. This cycle can be described by the water balance equation, as shown below:

$$P = I_c + E_c + E_s + R_o + Q \qquad (4)$$

P represents precipitation, which reaches the forest in the form of rainfall. The amount of precipitation varies with seasons and geographical locations. The first component of the water balance equation is interception (Ic). When rainfall occurs, a portion of it is intercepted by tree leaves in the forest canopy. However, the intercepted water that does not evaporate or evaporate from the leaves (throughfall) flows down the tree stems as stemflow. Although stemflow is typically small, it can play a role in certain situations and is considered in some water balance analyses (Oishi et al., 2010).. The second component is evapotranspiration (E_t), which represents the combined processes of evaporation from the soil surface (E_s) and transpiration by trees (E_c). Evaporation from the soil occurs when moisture on the surface evaporates into the atmosphere. Transpiration is the process by which trees release water vapor through their leaves. Evapotranspiration is a significant process in the water cycle of forest ecosystems and contributes to the movement of recycling water into the atmosphere. The remaining water that is not intercepted or returned to the atmosphere through evapotranspiration either infiltrates into the soil and contributes to groundwater recharge (Q) or flows out of the forest as surface runoff (R_o). Surface runoff is the movement of water over the land surface and can reach streams, rivers. Evapotranspiration is a major process in the forest water cycle. In tropical forests, annual evapotranspiration can be around 65% of the annual rainfall, which is approximately 1,500 mm (Kunert et al., 2017)Transpiration by trees plays a important role in the overall evapotranspiration process, representing a portion of terrestrial evapotranspiration, ranging from 40% to 90% (Deb Burman et al., 2019; Jasechko et al., 2013). The quantity of transpiration influences the amount of precipitation that ultimately contributes to runoff, thereby impacting downstream ecosystems. The water cycle of a forest ecosystem is illustrated in Figure 2.5.

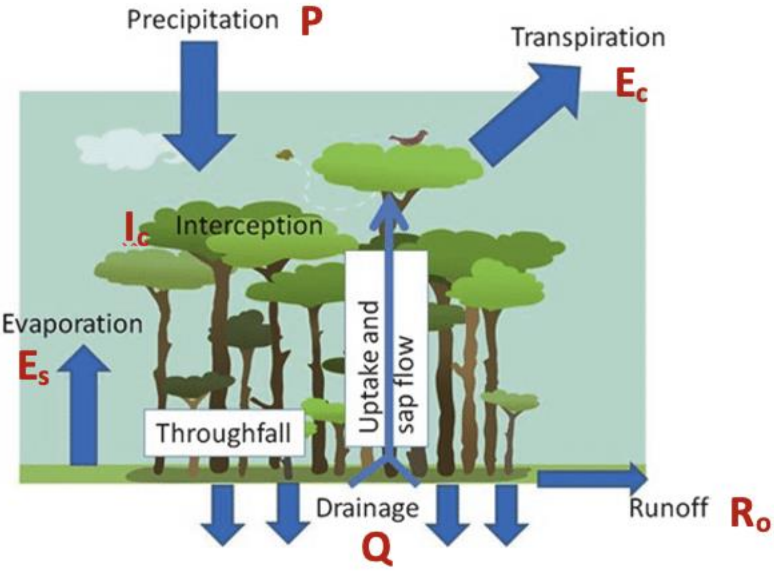


Figure 2.4 Water cycle in a forest (adapted from Centritto et al. (2010))

2.3 Sap flow method

2.3.1 Theory and designs

Sap flow methods are widely applied to determine J_s. These methods offer several advantages over other techniques. For instance, while plant chambers can be utilized to measure whole tree water use, they are often difficult and not easily portable. Additionally, plant chambers can disrupt the microclimate surrounding the tree (Goulden & B., 1994). In contrast, sap flow methods allow measurements to be taken with minimal disturbance in the site which makes them adaptable for various environments. Soil water balance is another method used to measure whole tree water use, but it tends to have low time resolution. Moreover, estimating drainage and surface runoff, which are necessary for soil water balance, often introduces uncertainties. In contrast, sap flow methods can continuous measurement of tree water use with high time resolution. Although porometers can measure stomatal conductance, which can be used to calculate transpiration rate, they are not ideal for measuring whole tree water use (Dugas et al., 1993). In contrast, sap flow methods are a preferred choice in studies of tree water use and water budgets in forests because they allow for the partitioning of evapotranspiration between tree water use and soil evaporation. These methods find applications in various fields such as agriculture, forestry, and ecology. Previous studies have utilized sap flow methods to quantify water use in areas including forest plantations (Cienciala et al., 1994; Hatton & Vertessy, 1990), natural (Köstner et al., 1992; Senock & Ham, 1995) and other specific tree species (Senock et al., 1996; Soegaard & Boegh, 1995) Consequently, Sap flow methods have been used in the studies in those fields for a long time. Thus, different designs of sap flow methods have been developed by scientists to measure the rate of water flow in stems including the stem heat balance method, the heat-pulse method, and the thermal dissipation method.

The stem heat balance method

The stem heat balance method is a technique used to measure sap flow in both woody trees (Steinberg et al., 1989) and herbaceous stems (Baker & Bavel, 1987). In this method, heat is applied to a section of the stem that is encircled by a heater. The mass flow of water within the stem can be determined by balancing the heat fluxes, ensuring that the amount of heat input into the stem equals the amount of heat output from the stem (Sakuratani, 1981), as illustrated in Figure 2.6. The heat balance of the steam can be written in an equation as follows:

$$P = q_v + q_r + q_f \tag{5}$$

where q_v is the rate of vertical heat loss by conduction in the stem, q_r is radial heat loss by conduction in the stem and q_f is heat uptake by the moving water. The value of q_f is determined by subtracting q_v and q_t from P. Finally, q_f is converted to the mass flow rate of water. However, the stem heat balance method may introduce errors due to heat storage in the stem (Groot & M., 1992). This error can become more significant with increasing stem diameter, although it is generally less problematic when determining daily sap flow (Weibel & K., 1995).

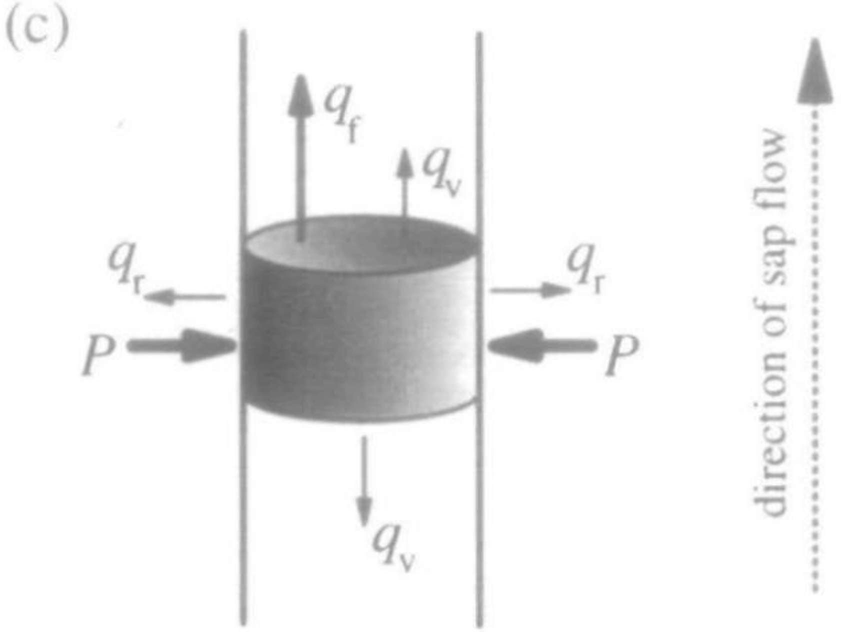


Figure 2.5 Principle of heat balance that the amount of heat transferred from the heat plate around stem (P) is equal to the heat move away from the stem in vertically and radially along with the water flow (Taken from Smith and Allen (1996)).

Heat pulse method (HPM)

The heat pulse method is another technique used to measure sap flow, specifically in woody trees. It involves determining the velocity of a short pulse of heat carried by the moving water. Heater and sensor probes are installed into the sapwood by drilling holes. A set of heat-pulse probes consists of one heater probe and two sensor probes that measure the temperature within the stem (as shown in Figure 2.7). The upstream sensor probe is placed in close proximity below the heater probe, while the downstream sensor probe is positioned above the heater probe. Short pulses of heat are emitted from the heater probe, and the sensor probes continuously monitor the velocity of each pulse as it moves with the water stream. The temperature is then calculated using the distance between the two sensor probes and the time it takes for convection to occur in the moving water stream from the upstream probe to the downstream probe. However, it is important to validate the measured temperature because the velocity of the heat pulse in the stem may not be equal to the sap flow. Thus, validation is important when applying the heat pulse technique. Additionally, the proper positioning of the heater and sensor probes, including the specific spacing between the sensor probes, is essential for accurate measurements. The heat pulse method works well for measuring sap flow in softwood species, as well as ring-porous or diffuse-porous hardwoods (Swanson, 1994; Swanson & Whitfield, 1981). However, in other hardwood species, empirical calibrations may be necessary to accurately measure sap flow using this method.

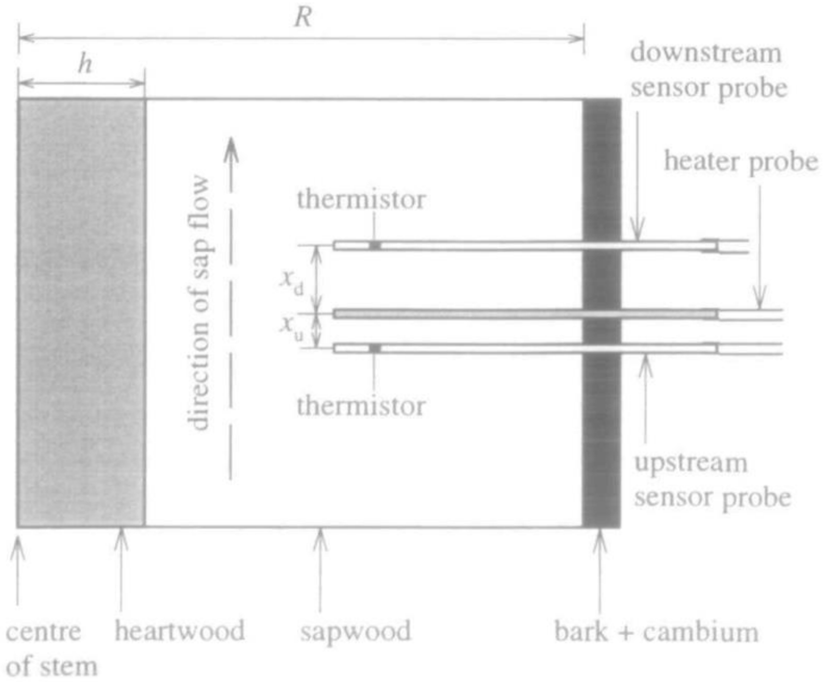


Figure 2.6 The component of heat pulse method (Taken from Smith and Allen (1996))

The thermal dissipation method

In addition to the stem heat balance method and the heat pulse method, an empirical method called the thermal dissipation method was developed by Granier (1985) for measuring sap flow rate. This method relies on the detection of temperature differences between two probes resulting from sap flow. The thermal dissipation method does not rely on the physical principles of heat transfer and heat balance like the previous methods. Instead, it is based on empirical relationships between temperature differences and sap flow rate, which are established through calibrations with actual sap flow measurements across various species. As a result, for the thermal dissipation method, it may not be necessary to calibrate the equations before installing the system. The thermal dissipation method offers several advantages, including easy installation, simple sap flow calculations, and lower costs. It has gained widespread application in ecophysiological and forest hydrological studies due to its practicality and efficiency. Furthermore, the sap flow rate measured using this method can respond to environmental factors such as air temperature, relative humidity, solar radiation, and soil moisture.

2.3.2 Granier’s thermal dissipation probe (TDP)

Granier (1985) introduced a sap flow measuring system called the Granier's thermal dissipation probe (TDP) method. This method utilizes two sensor probes: a heated probe and a reference probe (Figure 2.8). Both probes are constructed using a thermocouple composed of copper and constantan wires, which allows for the measurement of temperature difference between the two probes. the two probes are inserted into the stem, typically spaced 10-15 cm apart. The upper probe, also known as the heated probe, is continuously supplied with a 0.2 W electrical power. The lower probe, referred to as the reference probe, remains unheated and measures the ambient temperature of the surrounding wood tissue. The temperature difference between the two probes is influenced by the heat dissipation affected by sap flow. Thus, maximum temperature difference between two probes occurs when water flow is likely zero. The temperature difference between two probes is recorded by datalogger which is programmed to record data at specific times such as every 30 minutes.

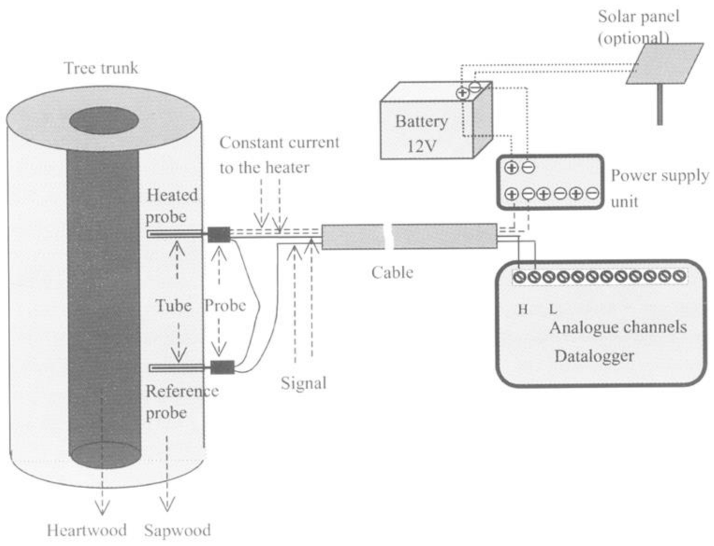


Figure 2.7 Configuration of Granier system for sap flux measurement (Taken from Lu et al. (2004))

Under the assumption of thermal equilibrium between the two probes and their surrounding environment (wood and sap), it can be inferred that the heat input to the system is equivalent to the amount of heat dissipated through convection and conduction at the surface of the probe Granier (1985). This relationship can be expressed by the following equation:

$$h\,S\left(T - T_f\right) = R\,I^2 \tag{6}$$

where h is coefficient of heat exchange (W•m^{-2}•°C^{-1})

S is exchange surface area (m^2)

T is temperature of the probe (°C)

T_f is temperature of the wood in the absence of heating (°C)

R is electrical resistance of the heating element (Ω)

I is intensity of the electric current (A)

According to Equation 6, it is assumed that the coefficient h is related to sap flux density by the following equation:

$$h = h_0\left(1 + \alpha F_d^{\beta}\right) \tag{7}$$

where h_0 is thermal exchange coefficient at zero flux,

F_d is sap flux density (m^3•m^{-2}•s^{-1}),

α, β are coefficients depending on the quantity of heat applied.

Under zero flux condition, h0 is calculated from Equation 7:

$$h_0 = \frac{RI^2}{S(T_{max} - T_f)} \tag{8}$$

where T_{max} is the temperature at zero flux

If $F_d \neq 0$ and is constant, it can be described by:

$$F_d = \left[\frac{1}{\alpha} \times \frac{h - h_0}{h_0}\right]^{1/\beta} \tag{9}$$

Combining Equations 6, 8 and 9, it can be rewritten by:

$$\begin{aligned} F_d &= \left[\frac{1}{\alpha} \times \frac{\Delta T_{max} - \Delta T}{\Delta T}\right]^{1/\beta} \\ &= \left[\frac{1}{\alpha} \times K\right]^{1/\beta} \end{aligned} \tag{10}$$

where ΔT_{max} is maximum temperature difference between the heated and reference probes at zero flux

ΔT is temperature difference between the heated and reference probes at a given F_d

K is flow index (dimensionless)

Granier (1985) experimented to find K value in Equation (10) by calibrations of the sap flow probes on several sample stems of three different tree species (*Pseudotsuga menziesii, Pinus nigra* and *Quercus pedunculata*). The result provided an experimental relationship between K and F_d. The empirical equation proposed by Granier (1985) for the relationship between K and F_d was:

$$\begin{aligned} K &= [(\Delta T_{max} - \Delta T) / \Delta T] \\ &= \alpha F_d^{\beta} \\ &= 0.0206 \times 10^{-6}\, F_d^{0.812} \end{aligned} \tag{11}$$

Equation (11) can be arranged as:

$$F_d = 118.99 \times 10^{-6}\, [(\Delta T_{max} - \Delta T) / \Delta T]^{1.231} \tag{12}$$

The Granier system directly measures the electrical potential difference (ΔV) between the two probes. However, it not necessary to convert ΔV measurements into ΔT in Equation (12) because the conversion factor from Seebeck effect. Based on Seebeck effect, the temperature difference between the conductors causes the potential difference between the conductors which is proportional with Seebeck coefficient (40 µV/°C). This coefficient will be cancelled out between the numerator and denominator in Equation (13). Thus, F_d can be directly calculated from the voltage measurements using the following equation (Lu, 1997):

$$F_d = 118.99 \times 10^{-6} [(\Delta V_{max} - \Delta V) / \Delta V]^{1.231} \quad (13)$$

where ΔV_{max} is the maximum voltage difference recorded at zero flux ($F_d = 0$), and ΔV is the voltage difference recorded at a given F_d.

2.3.3 Variations in sap flow measurement

Previous study was observed variation in sap flow measurement including radial, circumferential and axial (Cermak et al., 1992; Granier et al., 1994; Lu et al., 2000). However, it depends on tree species and sapwood pattern. Radial variation in J_s were observed in many tree species with different xylem structures (ring-porous, diffuse porous and coniferous). Sap flux density along the sapwood depth were observed with higher J_s in the outer sapwood than the inner sapwood in trees (Figure 2.9). However, trees that diffuse-porous wood without distinct annual rings tend to have sap flow rate that is relatively uniform along the radial sapwood depth (Figure 2.9f).

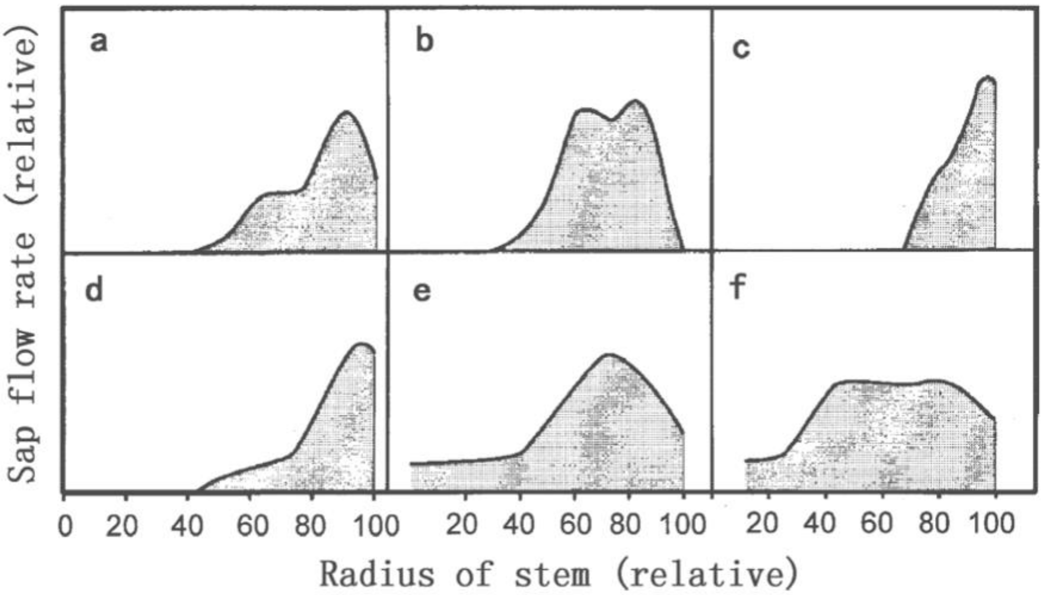


Figure 2.8 Radial pattern of relative sap flow rate in trunks of trees with different wood anatomy: (a) coniferous wood; *Populus-hybrid*, (b), summer-green deciduous tree with diffuse-porous wood; *Quercus petraea*, (c) summer-green deciduous tree with ring-porous wood; *Olea europeaea*, (d) evergreen sclerophyllous tree with

diffuse-porous wood (narrow pores); *Ficus carica*, (e) subtropical deciduous tree with diffuse-porous wood (large pores); *Shorea sumatrana* (f) tropical rainforest tree with diffuse-porous wood without distinct annual rings. This figure was adapted from (Taken from Lu et al. (2004)).

Circumferential variations in J_s were found in forest trees especially trees are in isolation (Lu et al., 2004). This variation depends on the effect of forest canopy shading. Trees may be obscured from the sunlight by canopy shading from surrounding trees leading to varying J_s along the circumference. Thus, it is recommended to install sensors along the circumference. Moreover, axial variations in J_s were observed with generally higher at higher points of the stem than at 1.3 m (Loustau et al., 1998). It is normal to measure sap flux at 1.3 m of the trunk because of the convenience of measurement. Before planning measurements and interpreting results, these variations should be determined.

2.4 Other methods of estimating tree water use

There are serval techniques for estimating tree water use not only sap flow methods but also weighing lysimeter (Edwards, 1986), large tree potometers (Roberts, 1977), ventilated chambers (Greenwood & Beresford, 1979), tritiated water (Kline et al., 1970), radioisotopes (Dye et al., 1992)

Weighing lysimeters have been used to measure *T*. It can directly measure evaporation and tree water use in a field. However, it are expensive to maintain and construct. Thus, lysimeters generally has been used to measure *T* in the crop field such as pulse crops, rice, sunflower, wheat and cotton (Wullschleger et al., 1998).

Large-tree potometers, also called ‘‘cut tree’’ experiments, have been used to measure *T*. This technique determine the magnitude of the root-soil resistance on cutting trees. However, it often induces changes in leaf water potential and stomatal conductance that may hard to interpret of data.

Ventilated chambers examine. the effects of CO_2 on the *T* and CO_2 assimilation of trees. Nonetheless, it may be concerned that that estimates of *T* by this technique are disrupted by the effects of VPD (Denmead et al., 1993).

Tritiated water was used to estimate *T*. A known volume of tritiated water was injected into holes bored into the trees. All injections went directly into the sapwood of the trees. The trees were sampled after injection till water had passed through the tree. Moreover, this method was adapted with the theory of radionuclide dynamics. The tritiated water solutions were calibrated for radioactivity like tritium.

2.5 Literature review

Dye (1996) determined the relationship between *T* and soil moisture in two field sites where soil drying in the South Africa. Site 1 was a stand of 3-year-old *Eucalyptus grandis* trees. Site 2 was 9-year-old trees. In each site, plastic sheeting was covered on the ground to prevent soil water recharge. The result shown that the trees at site 1 uptake water down to 8 m below the surface whereas trees at site 2 uptake water from depths below 8 m. These findings suggest that the soil water recharge mechanism and the water retention characteristics of the deep subsoil layers are necessary for modeling the water balance.

Eamus et al. (2000) evaluated daily and seasonal patterns of *T* in evergreen eucalypt trees growing at a wet, intermediate and dry site in a north Australian savanna. The relationship between tree size and *T* was found all species at all sites. Mean daily *T* was also correlated to DBH in wet and dry seasons. Tree water use was significantly lower in trees at the driest site. However, the significant differences in *T* between trees growing at wet and intermediate sites were not found. Among the sites, *T* was lowest at dry site. Moreover, the significant differences in *T* between seasons were not found in all site. These findings highlight that water availability in the dry season determines rates of *T* in both dry and wet season.

Dierick and Hölscher (2009) measured J_s using thermal dissipation probes in 12-year-old reforestations on Leyte Island, the Philippines. The result shown the significant differences in maximum J_s across species Moreover, they found the strong relationship between maximum of *T* and tree diameter (R^2_{adj} =0.65). This study highlight that *T* depend on species and tree size. Thus, they suggested that species selection offers opportunities to maintain *T* in reforestation site.

Dierick et al. (2010) analyzed data on J_s and *T* from 17 species in Indonesia, Panama and the Philippines. This study was performed in young forest stands (5-12 years) which were characterized by small diameter trees. The results from this study shown that *T* and the responses of *T* to solar radiation and VPD are differences across species. Moreover, they found the relationship between tree diameter and *T*. These findings suggest that species selection can be used to maintain tree water use in reforestation site.

Clulow et al. (2013) measured *T* of an evergreen overstory and understory in the peat swamp forest. Moreover, they measured *T* of tree in different heights in dune forest. The *T* of understory was more seasonal while the *T* of overstory was not influenced by seasonal rainfall variations. At the dune forest, the *T* was highest in the wetter summer due to recharge the soil water from rainfall. The result from this study shown that soil water limited 64 % on *T* at dune forest. These findings suggested that taking soil water content into account for modelling *T* would be necessary.

Chen et al. (2014) evaluated the response of *T* to environmental factors using sap flow measurement in 8 non-irrigated jujube (*Ziziphus jujuba* Mill.) Soil moisture conditions were classified into water stress ($\theta < 0.4$) and non-water stress ($\theta > 0.4$) conditions based on relative extractable water (θ). Relative sap flow (SF_R) was used to analyze the relationship between SF_R and environmental factors. The response of SF_R to environmental factors were different in soil moisture conditions. The result shown that SF_R was strongly respond to solar radiation and VPD. The sensitivity of the response of SF_R to environmental factors significantly decreased with increasing water stress. The results from this study were important for estimation tree water use. These findings suggest that it was important to concern tree water use in different soil moisture conditions.

Cavaleri et al. (2014) estimated the differences in *T* between native and invasive trees species. Moreover, they also estimated effects of invasive removal on water use in mono-dominant lowland wet tropical forest on the Island of Hawaii. They measured *T* of native and invasive tree species using thermal dissipation probes. The results shown that tree water use in the removal plots was half that of the invaded plots. The removal of invasive trees species caused a significant increasing tree water use of the remaining native trees. This study highlights that native-dominated forests without invasive species can be maintain their water use.

Yin et al. (2014) measured *T* of a willow tree, meteorological variables, soil water content, and water table depth during the growing period from mid-April to October, 2011 in the semi-arid Hailiutu River catchment, Northwest China. The diurnal pattern of *T* shown that fluctuations in sunny days and seasonal changes from 1.65 L h^{-1} in mid-April to 33 L h^{-1} in July. At daily scale, air temperature affects the dynamics of *T* significantly. Daily *T* correlates positively with net radiation and negatively with relative humidity. Moreover, *T* is strongly correlated with soil moisture and water table depth, indicating the willow tree uses both soil water and groundwater. The average *T* of the willow tree was about 13 L d^{-1} that it within range of *T* (10 to 1,180 L d^{-1}) of 93 plants from previous study. Therefore, this study suggests that willow trees seem to be suitable for reforestation purposes.

Hardanto et al. (2017) measured *T* with thermal dissipation probes and tree soil water uptake depths using a water stable isotope in mono-cultural and jungle rubber stands with a focus on the role of tree size. The results shown that *T* of rubber trees in the two cultivation systems were similar. Stand-level transpiration in jungle rubber was 27% higher than in rubber monocultures due to higher stand densities in jungle rubber stands. For tree soil water uptake, soil water uptake depths of rubber trees were different in the two cultivation systems. The main tree water uptake in the monoculture was relatively close to the soil surface, whereas rubber trees in jungle rubber stands mainly took up water from deeper soil strata. Moreover, they found a clear relationship between tree diameter and soil water uptake depth that bigger trees tended to take up soil water closer to the soil surface. These finding suggest that tree diameter and forest density regulation by thinning of big native trees may be potential management option for influencing water uptake in jungle rubber stands in favor of rubber trees.

Brum et al. (2018) characterized response of tree transpiration in different canopy strata contribution to varying environmental factors including soil, atmospheric humidity in seasonal tropical rainforest in the eastern Amazon during one of the most extreme ENSO-induced droughts. Heat pulse sap flow sensors (HPM) were installed to monitor J_s and scaled up to tree transpiration (T). The results show that canopy trees are more likely to reach deeper soil water reserves, due to their developed root system, thus allowing for T at high VPD. Deep roots provide a drought avoidance strategy in Amazon forest, increasing short-term and long-term resilience to drought. On the contrast, the extensive water loss observed by subcanopy trees may indicated a reduce ability to control transpiration. This information is critical to accurately predict changes in species composition in Amazon forest resulting from climate change and to better parametrize models forest stand transpiration

Table 2.1 Summary of water use of tropical forest trees reviewed in this proposal. 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.

Ref	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*	HPM	8.8 – 30.4	NA	16.1	August–September 1998 (Dry season)
			Eucalyptus tetrodonta		4.9 – 48.7			
			Eucalyptus latifolia		9.7 – 48.7			
			Eucalyptus Capricornia		6.1– 35.6			
			Eucalyptus spp.		6.1- 35.6		17.9	March– April 1999 (Wet season)
			Eucalyptus terminalis		9.1– 41.6			
(Dierick & D., 2009)	The Philippines (10°45′55″N, 124°47′25″E) and (10°44′10″N, 124°48′16″E)		*Shorea contorta*	TDP	18.2 ± 7	16.1 ± 3.5	18.4 ± 19.5	June to August 2006 and July to September 2007
			Parashorea malaanonan		12 ± 0.4	13.1 ± 1.6	10.6 ± 1.2	
			Hopea malibato		11.6 ± 2.4	13.3 ± 1.8	9.1 ± 8.5	
			Hopea plagata		6.6 ç 1.0	9.4 ± 1.2	4.0 ± 1.9	
			Swietenia macrophylla.		14.6 ± 1.3	14.2 ± 1.5	25.5 ± 4.1	
			Vitex parviflora		20.4 ± 5.5	12.7 ± 1.6	30.7 ± 14.6	
			Myrica javanica		22.1 ± 3.7	11.2 ± 0.6	61.7 ± 17.0	
			Sandoricum koetjape		16.3 ± 2.7	13.2 ± 1.1	32.8 ± 16.5	
			Durio zibethinus					

Ref	Location	Species	Method	DBH (cm)	Tree height (m)	T (L d^{-1})	Period
		Gmelina arborea		19.8 ± 7.3	13.8 ± 3.0	44.6 ± 18.5	
				21.9 ± 4.0	18.1 ± 2.4	27.6 ± 7.8	
(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*	TDP	18.2 ± 7	16.1 ± 3.5	18.4 ± 14.4	June to August 2006 and July to September 2007
		Parashorea malaanonan		12 ± 0.4	13.1 ± 1.6	10.6 ± 1.1	
		Hopea malibato		11.6 ± 2.4	13.3 ± 1.8	9.1 ± 6.7	
		Hopea plagata		6.6 ± 1.0	9.4 ± 1.2	4.0 ± 1.3	
		Swietenia macrophylla		14.6 ± 1.3	14.2 ± 1.5	25.5 ± 3.6	
		Vitex parviflora		20.4 ± 5.5	12.7 ± 1.6	20.7 ± 9.3	
		Myrica javanica.		22.1 ± 3.7	11.2 ± 0.6	43.2 ± 12.5	
		Sandoricum koetjape.		16.3 ± 2.7	13.2 ± 1.1	23.4 ± 12.6	
		Durio zibethinus		19.8 ± 7.3	13.8 ± 3.0	32.9 ± 14.8	
		Gmelina arborea		21.9 ± 4.0	18.1 ± 2.4	19.8 ± 6.1	
	Indonesia (1.552°S, 120.020°E)	*Theobroma cacao*	TDP	10.1 ± 1.6	4.5 ± 0.8	10.0 ± 4.5	February 2007 (Dry season)
		Gliricidia sepium		15.0 ± 2.5	10.9 ± 2.1	13.9 ± 4.1	
	Panama (9.317°N, 79.633°W)	*Luehea seemannii*	TDP	11.8 ± 1.6	8.7 ± 1.0	13.1 ± 3.6	June to September 2007 (Wet season)
		Anacardium excelsum		10.1 ± 0.6	6.4 ± 0.4	10.5 ± 2.8	
		Hura crepitans		18.0 ± 2.3	5.4 ± 1.0	14.6 ± 7.6	
		Cedrela odorata		12.0 ± 0.6	11.7 ± 1.1	9.9 ± 2.2	
		Tabebuia rosea		11.5 ± 1.3	7.4 ± 0.3	7.9 ± 0.6	
(Clulow et al., 2013)	Nkazana Peat swamp forest site (28°10.176′ S, 32°30.070′ E)	*Syzygium cordatum*	HPM	NA	22.5	30 - 45	4 September 2009 to 4 May 2011
		Shirakiopsis elliptica			6.8	2 - 12	
	Dune forest site (28°12.017′ S, 32°31.633′ E)	*Drypetes natalensis*	HPM	NA	4.5	5 - 45	
		Eugenia natalitia			7.5	2 -28	
		Mimusops caffra			7.2	1 - 4	

Ref	Location		Species	Method	DBH (cm)	Tree height (m)	T (L d^{-1})	Period
(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*	TDP	18.03 ± 0.3	14.0 ± 0.2	26.7 ± 2.2	

Ref	Location	Species	Method	DBH (cm)	Tree height (m)	T (L d^{-1})	Period
		Timonius wallichianus					
(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	

CHAPTER 3
METHODOLOGY

3.1 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^2 in Nakhon Ratchasima, Saraburi, Prachinburi and Nakhon Nayok Provinces in Thailand. This national park is a part of a UNESCO world heritage site. 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 located at Nakhon Nayok Provinces. The study site is the forest 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 1226 trees ha^{-1}. 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 were continuously monitored. Air temperature (T, °C), relative humidity (RH, %) and photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) are 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 (θ, m^3m^{-3}) at 5, 10, 15 and 30 cm depth because trees can assess 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 in each depth including 5, 10 and 15 cm. However, soil moisture at 30 cm depth was monitored by one soil moisture sensor because soil moisture at subsoil is 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 are connected to a datalogger (CR1000 series; Campbell Scientific, Logan, UT) which records 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 et al., 2013).

$$\mathrm{SVP} = 610.7 \text{ x } 10^{\frac{7.5\mathrm{T}}{237.5+\mathrm{T}}} \qquad (14)$$

$$\mathrm{VPD} = (1 - \frac{RH}{100}) \text{ x } \mathrm{SVP} \qquad (15)$$

To facilitate the cross-site comparison, soil moisture is presented by Relative Extractable Water (REW) which represent the availability of soil water in the rooting zone) calculated according to Granier et al. (2000)

$$\mathrm{REW} = \frac{\theta - \theta m}{\theta FC - \theta m} \qquad (16)$$

where θ_m is minimum volumetric soil moisture and θ_{FC} is the soil water at field capacity. In the plot where soil water at field capacity is not measured, we used maximum volumetric soil moisture during the study period as θ_{FC} for the REW calculation (Tor-ngern et al., 2018). All environmental variables have been continuously monitored in plot since 17 September 2020 until now.

3.2 Species selection and tree sampling

The dominant tree species in plot was chosen based on the relative abundance of basal area, which is calculated from the basal area of one species relative to total basal area of all species within the site (Table 3.1). Basal area is used to describe the dominance in the forest. To compare species difference in *T*, two dominant tree species with similar phenology which is evergreen leaf habit were selected for this study. Based on the available information of trees in the plot, *S. antisepticum* and *A. integerrima,* hereafter *Sa and Ai* respectively, were chosen to measure sap flow rate which is represented by sap flux density (J_s) (more details in the next section). To compare differences in *T* due to tree size, we selected trees of both species to measure J_s based on the distribution of tree diameter in this plot. We partitioned the tree size classes into 10-cm intervals. After that we had 6 size class and then sampled 3 trees in both species for each size class. Based on survey data in 2019, the distribution of tree diameter in this plot is shown in Figure 3.1. However, sap flow measurement system has limitation that selected trees for installing sap flow sensors should be within a radius of 25 m from the data logger. Thus, 4 trees of *Sa* and 5 trees of *Ai* and were selected to measure J_s (Table 3.2).

Table 3.1 Information of the selected five dominant tree species in the study site.

Species	***Phenology***	***Basal area (%)***
Cratoxylum cochinchinense	Deciduous	30.75
Syzygium antisepticum	Evergreen	26.52
Adinandra integerrima	Evergreen	12.08
Syzygium nervosum	Evergreen	11.95
Symplocos cochinchinensis.	Evergreen	3.24

Table 3.2 Information of the selected trees for sap flow measurement.

Species	**Phenology**	**Tree diameter (cm)**	**Sapwood area (cm^2)**	**Sensor location along the stem's circumference**
Adinandra integerrima	Evergreen	13.7	135.92	North and South
Adinandra integerrima	Evergreen	6.5	30.64	North
Adinandra integerrima	Evergreen	11	87.67	North and South
Adinandra integerrima	Evergreen	5.3	20.38	North
Adinandraintegerrima	Evergreen	11.3	92.51	North and South
Syzygium antisepticum	Evergreen	24.8	444.88	North and South
Syzygium antisepticum	Evergreen	22.4	363.02	North and South
Syzygium antisepticum	Evergreen	18.7	253.09	North and South
Syzygium antisepticum	Evergreen	17.8	229.34	North and South

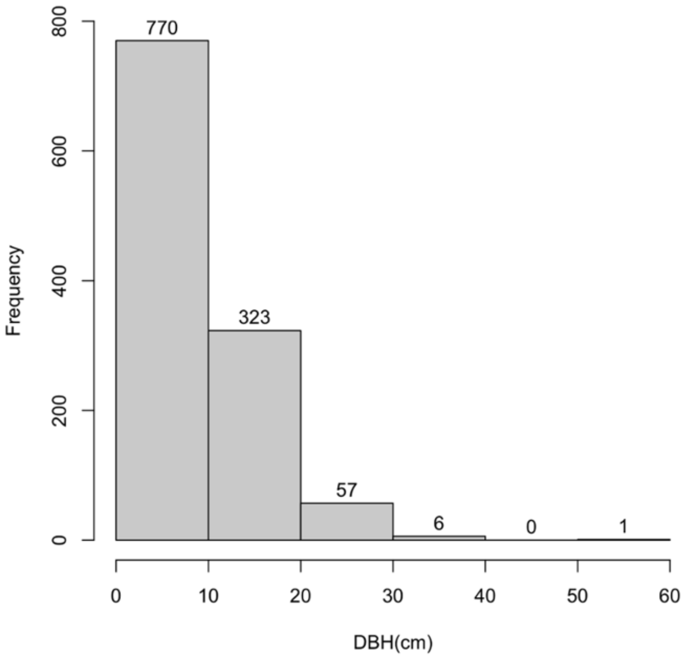


Figure 3.1 The distribution of tree diameters in plot based on data in 2019.

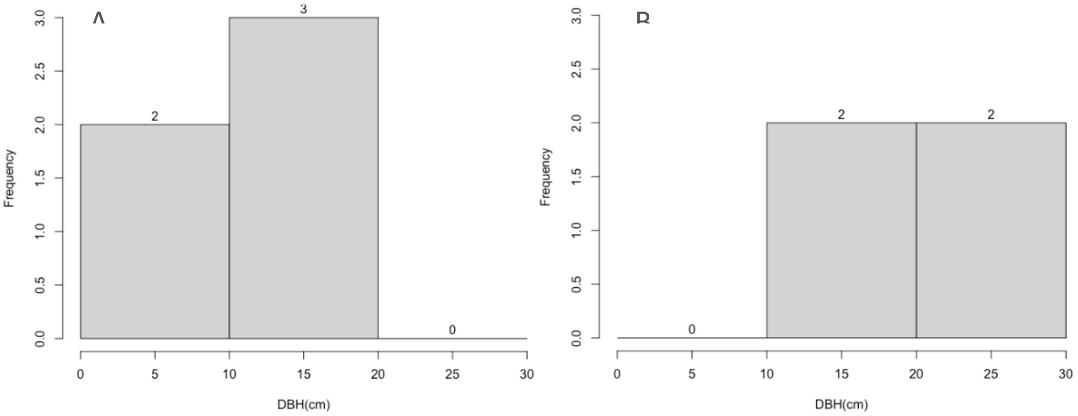


Figure 3.2 Size distribution of the sampled trees of **(A)** *A. integerrima* and **(B)** *S. antisepticum*.

3.3 Sap flow measurement and scaling to tree water use

Sap flux density (J_s, g m^{-2} s^{-1}) is measured using self-constructed thermal dissipation probes (TDPs) as shown in Figure 3.3 (Granier, 1985). TDPs contains two probes including non-heated and heated probe which supplied with a ~0.2 W electrical power. Before inserting TDPs into the trunk, 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 the inner sapwood layers in trees (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 inserted them into stem at outer sapwood to measure J_s because of the unknown pattern of sapwood area in tropical tree species (Horna et al., 2011; Salas-Acosta et al., 2022). In addition, most tropical trees have diffuse-porous wood without distinct annual rings and tend to have J_s that is relatively uniform along the radial sapwood depth (Lu et al., 2004). Therefore, we assumed that J_s is uniform along the sapwood depth of the selected trees when scaling from single-point measurements to whole tree. Therefore, TDPs were inserted in outer sapwood at 2 cm depth at breast height (~1.3 m above ground). The upper probe is heated at constant ~ 0.2 W electrical power and dipped in the thermal paste for better heat conduction while lower probe, which not be heated, measure the ambient temperature of xylem as reference. The difference of temperature between two probes provides the heat dissipation effect of sap flow. Each TPD was shielded with aluminum foil to provide thermal insulation. Azimuthal variation of J_s may produce variation when scaling up from J_s to *T* (Lu et al., 2000). This variation depends on the effect of forest canopy shading. Trees may be obscured from the sunlight by canopy shading from surrounding trees leading to varying J_s along the circumference. To determine this variation, we sampled trees that may be potentially influenced by canopy shading from surrounding trees to install TPDs in difference azimuthal directions. Based on our observation, 8 and 6 sensors were distributed at two azimuthal directions (north and south, as shown in Table 3.2) which being potentially affected by canopy shading, in *Sa* and *Ai* respectively. Data from TDPs have been recorded as 30-minute means of voltage difference between the probes (ΔV, mV) by the same data logger (CR1000, Campbell Scientific, Logan, UT, USA) which also records environmental data. For the analysis, the voltage difference was converted to J_s using an empirical equation (Granier, 1985)

$$J_s = 118.99 \text{ x } 10^{-6} \text{ x } \left(\frac{\Delta V_m - \Delta V}{\Delta V}\right)^{1.231} \quad (17)$$

where ΔV_m is the maximum voltage difference which may be occur at night or when VPD is low. The Baseliner program version 4.0 was used to select ΔV_m to calculate J_s (Oishi et al., 2016). The program automatically determines maximum daily ΔV to represent ΔV_m. Maximum voltage difference may occur at night if air humidity is 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 (Phillips & Oren, 1998). Thus, no universal rule for identifying ΔV_m. The Baseliner software was used to identify ΔV_m by identifying points in time where water flow is likely zero and permitting the user to modify those points. Sap flux density has been continuously monitored in the plot since 17 September 2020 until now. The information of installed TPDs and the selected trees for measuring J_s is shown in Table 3.2.

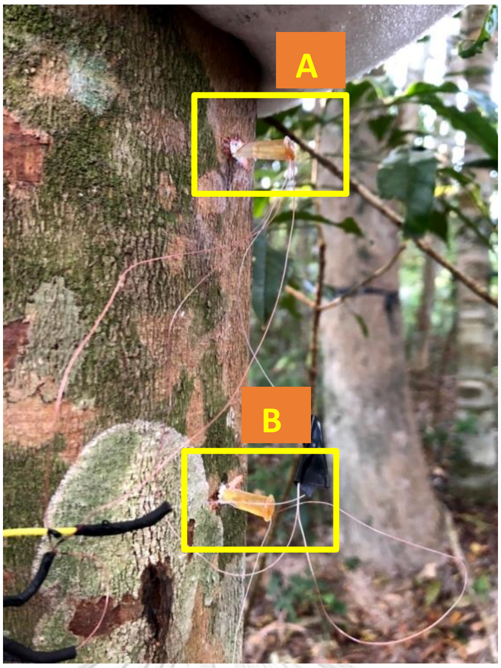


Figure 3.3 Self-constructed thermal dissipation probes (TDPs) contain (A) heated probe and (B) non-heated probe or reference probe.

To scale up from J_s to *T*, we employed the following approach. Daily sum J_s (g $m^{-2}{}_{sapwood}$ 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 & Oren, 1998). When nighttime recharge increases with decreasing soil moisture, the proportions of sap flow at night relative to sap flow during the day become larger. This problem can be avoided when calculating *T* as daily sum (Phillips & Oren, 1998). To test variation of daily sum J_s with azimuthal directions in each species, we performed analysis under non limiting soil moisture and high light conditions. The criteria for selecting daily sum J_s in different azimuthal directions under non limiting soil moisture and high light conditions was derived by: (1) partitioning daily sum J_s data of each day into North and South direction, (2) selecting the days under rain-free condition to avoid wet canopy condition issue that may inhibit *T* when leaf surface is covered with water droplets (Aparecido et al., 2016), (3) selecting the days that have REW values falling above the mean plus two standard deviation of each group of REW data and then selecting the days with PAR values falling above the mean plus two standard deviation of each group of PAR data. After the steps of data selection, we had 2 subset data with different azimuthal directions under non limiting soil moisture and high light conditions in each species. An independent t-test was used to compare the selected data from the north and south directions and thus testing variation of daily sum J_s with azimuthal directions in each species. Although marginally significant variation of daily sum J_s with azimuthal directions in *Ai* and *Sa* ($p = 0.01$ and 0.002 respectively) was found in our data, many studied reported that ignoring the azimuthal variation in J_s caused small errors in the estimation of T in 12.6 % in Korean pine (*Pinus koraiensis*) (Moon et al., 2015) and 16.1 % in a Japanese cedar (*Cryptomeria japonica* D. Don.) forest (Shinohara et al., 2013). Thus, daily sum J_s in each direction was averaged to a mean daily J_s (J_{mean}) for individual tree. To obtain individual T, we multiplied the sapwood area by J_{mean} using the following equation

$$T = 1800 \text{ x } 10^{-7} \text{ x } J_{mean} \text{ x } A_s \qquad (18)$$

where T is daily tree water use (L d^{-1}) which is the quantity of water uptake from the soil by the tree per day, J_{mean} is mean daily sum J_s (g m^{-2} day $^{-1}$) and A_s is sapwood area (cm^2). In both species, A_s was estimated based on an allometric equation derived from 13 dominant species in old growth and secondary forests at Khao Yai National Park as follows (Yaemphum et al., 2022).

$$y = 0.728x^{1.998} \qquad (19)$$

where y is sapwood area (cm^2), x is tree diameter (DBH, cm).

3.4 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 effect 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 in this study. To compare T of two dominant tree species, *Sa* and *Ai*, we analyzed the difference of T of each species using the Mann-Whitney U test by selecting T under non limiting soil moisture and high light condition. The criteria for selected *T* under non limiting soil moisture and high light conditions of both species was derived by: (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 deviation of each group of REW data which refer to non limiting soil moisture and then selecting the days with PAR values falling above the mean plus two standard deviation of each group of PAR data which refer to high light condition. After the steps of data selection, we had 2 subset data with different species under non limiting soil moisture and high light conditions. To test for the difference in *T* between both tree species, the Mann-Whitney U test was used to compare the selected data from the *Sa* and *Ai* because our data of *Sa* and *Ai* is not normally distributed (Shapiro Wilk's test, p = 0.001 and 0.004 respectively).

To compare *T* in different tree size classes, trees were categorized into two size classes based on the size distribution of sampled tree in each species into large trees (DBH ≥ 10 cm for *Ai* and DBH ≥ 20 cm for *Sa*) and small trees (DBH < 10 cm for *Ai* and DBH < 20 cm for *Sa*) as shown in Figure 3.2. We analyzed the difference of *T* of each species in different tree size classes using the Mann-Whitney U test by selecting *T* under non-limiting soil moisture and high light condition. The criteria for selected *T* under non limiting soil moisture and high light conditions of both species in different tree size classes was derived by: (1) selecting the day falling above the mean plus two standard deviations of REW which refer to non limiting soil moisture and then (2) selecting the day falling above the mean plus two standard deviations of PAR which refer to high light condition. After this step, we had 2 subset data in each species with different tree size classes under non limiting soil moisture and high light conditions. The Mann-Whitney U test was used to test the difference of tree water use 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 optimal conditions. Trees in both species were categorized into two size classes based on the size distribution of sampled trees into large trees and small trees as mentioned above. After that, T from all trees in the same category was averaged to mean T (T_{mean}) in each day. Tree water use varies with VPD, REW and PAR (Phillips & 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 (REW <0.1), intermediate soil moisture (REW 0.1-0.4) and high soil moisture (REW >0.4) as shown in Figure 3.4. With two classes of tree size (large and small), we had six subset data in both species. Each subset was subjected to the boundary line, designed to select data representing maximum T_{mean} for each tree size in each REW class along the range of VPD. The upper boundary line was derived by: (1) partitioning T_{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_{mean} in each interval, (3) removing outliers using Dixon's test (Sokal & Rohlf, 2013), (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_{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 vapor pressure deficit in all REW classes). All statistical tests were considered at 95% significance level. Data management and analysis were performed with Rstudio, version 1.3.1073 (The R Foundation for Statistical Computing, http://www. R- project.org).

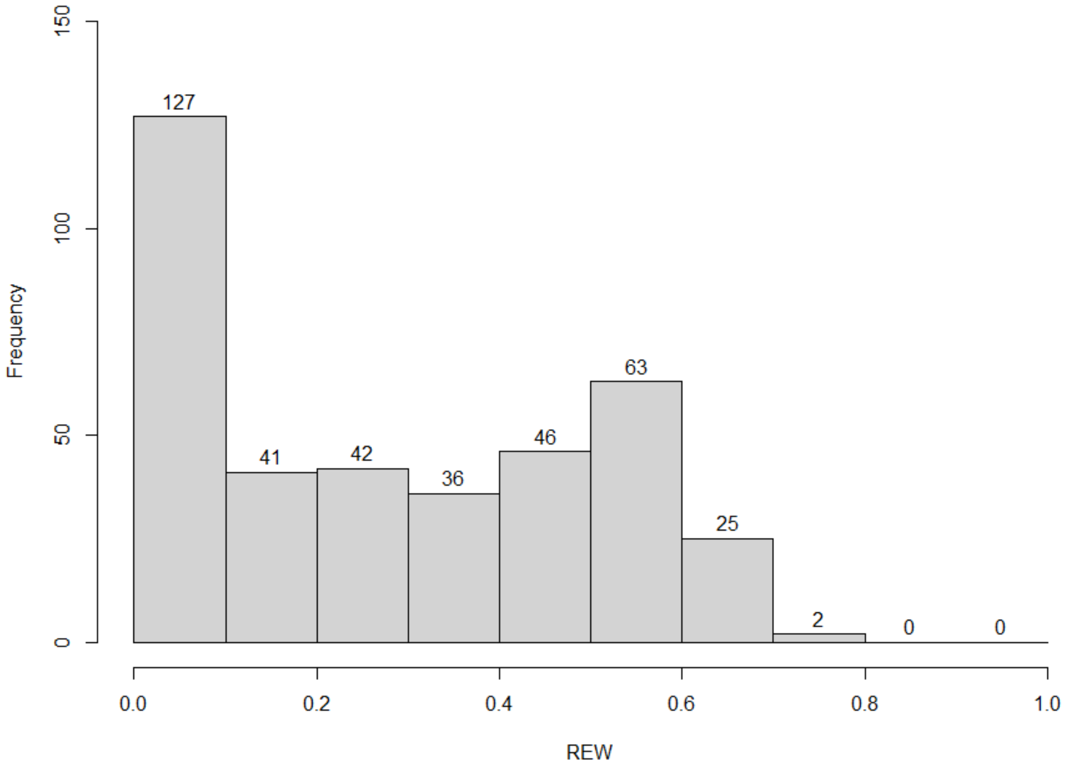


Figure 3.4 REW distribution under rain-free conditions during the study period.

CHAPTER 4
RESULTS AND DISCUSSION

4.1 Environmental conditions in the study site

Environmental conditions that influence *T* including air temperature, relative humidity (RH) photosynthetically active radiation (PAR), soil moisture and rainfall were continuously monitored in the study site during the study period (18 September 2020 to 26 November 2022). The mean of volumetric of soil moisture (θ) was 0.10 ± 0.04 (one standard deviation), 0.12 ± 0.04, 0.12 ± 0.05 and 0.10 m^3m^{-3} at 5, 10, 15 and 30 cm depth, respectively. Volumetric of soil moisture in each depth were averaged into the $\theta_{average}$. The maximum and minimum of $\theta_{average}$ during the study period were 0.2 and 0.04 $m^3 m^{-3}$, respectively. Figure 4.1 shows θ in each depth throughout the study period.

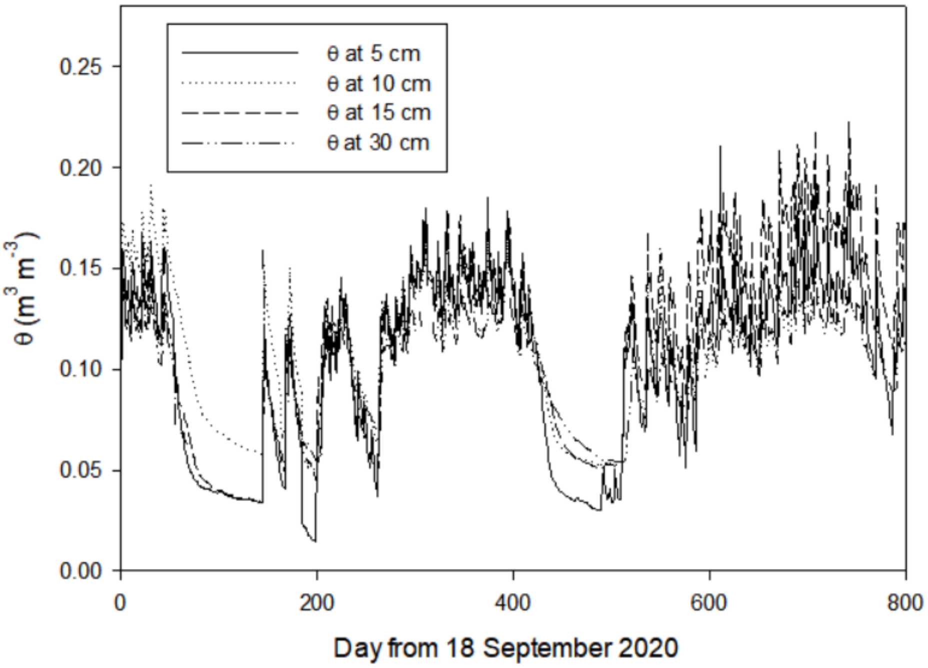


Figure 4.1 Volumetric soil moisture (θ) at 5, 10, 15 and 30 cm depth during the study period.

The $\theta_{average}$ was used to calculate REW which represent the availability of soil water in the rooting zone to facilitate the cross-site comparison. The average REW was 0.44 ± 0.25. 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 of average PAR during study period were 575 and 57.3 µmol m^{-2} s^{-1}, respectively, with a mean of 345.76 ± 103.47 µmol m^{-2} s^{-1}. The average daily VPD was 0.34 ± 0.23 kPa. Based on our data during the study period, VPD and PAR were highly correlated ($r = 0.79$, $p = <0.001$). Overall, environmental data in the study site during the study period represents a wide range of environmental conditions which allowed the evaluation of responses in the analysis. Figure 4.2 summarizes the environmental conditions during the study period.

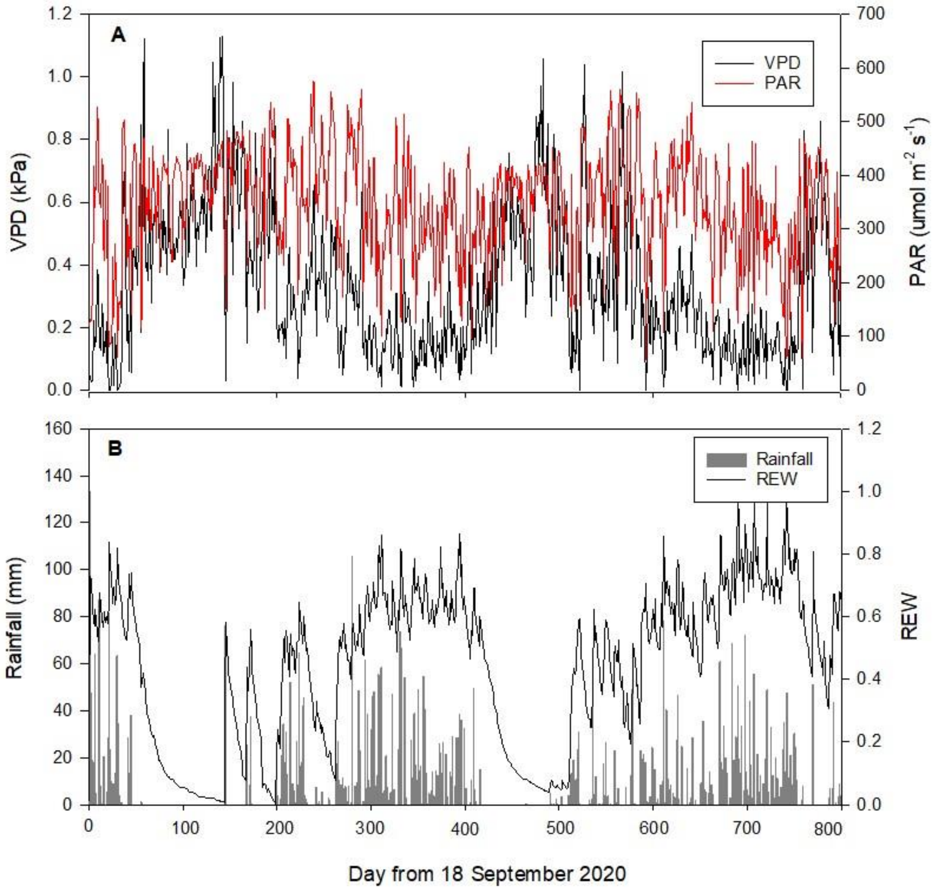


Figure 4.2 Environmental conditions during the study period including (**A**) vapor pressure deficit (VPD in kPa; red line) and photosynthetically active radiation (PAR

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

4.2 Tree water use of *Syzygium antisepticum* and *Adinandra integerrima*

Scaled up from J_{mean} to *T*, the values of *T* of both species during the study period are shown in Figure 4.3. The average values of *T* with one standard deviation of *Sa* and *Ai* during the study period were 21.48 ± 7.73 and 10.01 ± 4.04 L d^{-1}, respectively. The maximum *T* of *Sa* in our data (47.5 L d^{-1}) was found higher than the ranges that were found in Clulow et al. (2013) who measured *T* of *Syzygium cordatum* in a peat swamp forest in south Africa, a species of the same genus as *Sa*. They reported that the maximum *T* values of *S. cordatum* ranged from approximately 30 L d^{-1} in the winter to 45 L d^{-1} in the summer. Moreover, the same study also reported the *T* value of *Eugenia natalitia*, which is the same family with *Sa*, between 2 to 28 L d^{-1} and that *T* of *Sa* in our study is within the same range. Although we did not find the studies that reported *T* values of *Ai* or similar genus, the *T* of *Ai* was within the range of *T* (10 to 1,180 L d^{-1}) found in 93 tree species from Wullschleger et al. (1998) which reviewed 52 studies that estimated of whole-plant water use for trees growing in natural forests or plantations. They indicated 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 France to 1,180 L d^{-1} for an overstory tree, *Euperua purpurea* Bth., growing in the Amazonian rainforest. Overall, *T* values in both species in this study were within the ranges found in previous studies. Focusing on *T* in different species (Figure 4.4), *T* of *Sa* was significantly higher than *Ai* under non limiting soil moisture and high light conditions ($p < 0.0001$). Comparing *T* of both species in different tree size classes under non limiting soil moisture and high light conditions (Figure 4.5), *T* of large tree size was significantly higher than small size in *Sa* and *Ai* ($p < 0.0001$ for both) which may be related to relatively lower sapwood area in small size. Tree water use is calculated from J_s and sapwood area. Previous studies showed that the variation of J_s among trees of different ages and sizes is relatively low (Jaskierniak et al., 2016; Kumagai et al., 2007); thus, sapwood area may be a major determinant of *T*. However, based on our data, J_s of trees in different tree size classes was marginally low in *Sa* and *Ai* (p =

0.01 and 0.02, respectively). The result from this study was similar to the result found in a previous study which determined water use by *Acer saccharum Marsh*. (sugar maple) in different sizes (Dawson, 1996). They found that small trees can use only shallow soil water whereas large trees can access water from deeper soil, thereby permitting greater water use in large trees. Moreover, other research in tropical forests reported that large trees consume much more water relative to small trees and found positive relationship between water consumption and tree size (Aparecido et al., 2016; Horna et al., 2011; Meinzer et al., 2001; O'Grady et al., 1999)

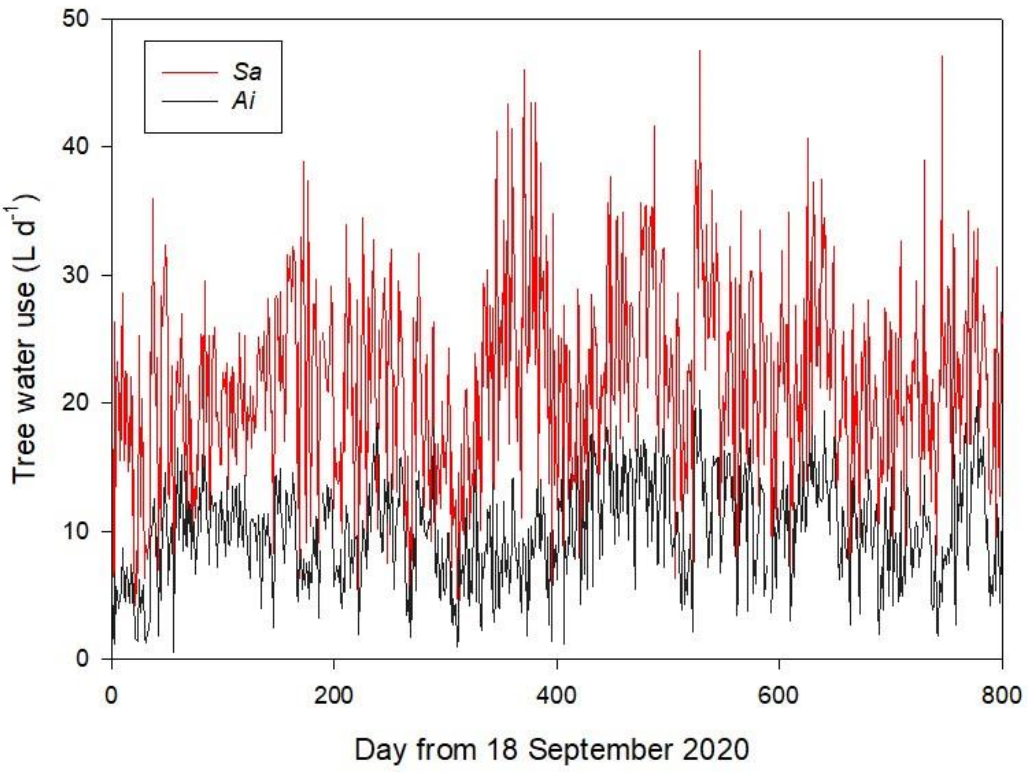


Figure 4.3 Tree water use throughout the study period of *S. antisepticum* (red line) and *A. integerrima* (black line).

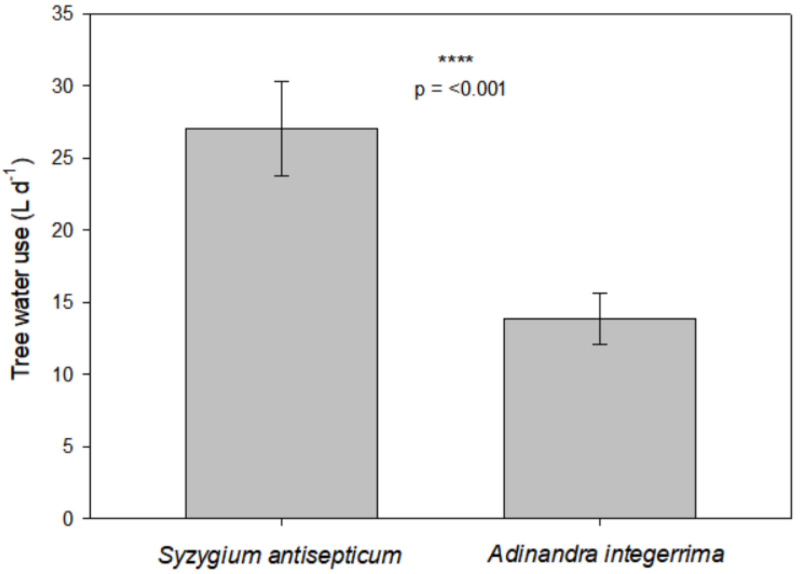


Figure 4.4 Average tree water use (*T;* L d^{-1}) under non limiting soil moisture and high light conditions during the study period of *S. antisepticum* and *A. integerrima*.

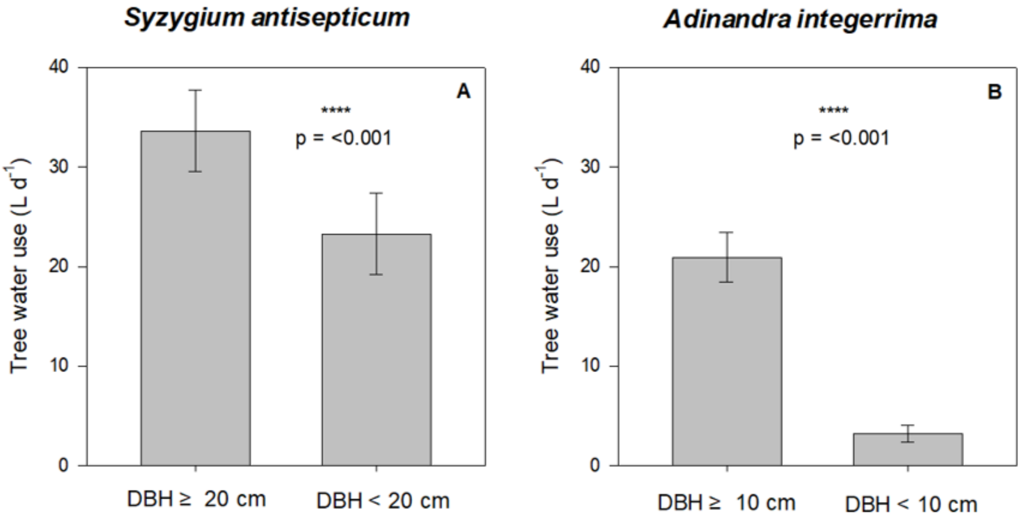


Figure 4.5 Average tree water use (T; L d^{-1}) under non limiting soil moisture and high light conditions during the study period of **(A)** *S. antisepticum* and **(B)** *A. integerrima* in different tree size classes.

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

Results of different soil moisture conditions in both sizes showed consistently higher *T* in *Sa* compared to *Ai* across VPD ranges (Figure 4.6, 4.7 and 4.8). The result from small size classes showed that *T* of *Ai* did not respond to VPD under low soil moisture (REW<0.1) (Figure 4.6D). In contrast, *T* of *Sa* in small size increased at low VPD and then gradually saturated at high VPD, probably to save water which can prevent it from losing water through stomata under low soil moisture (Figure 4.6C). This pattern of response shared similar pattern to the results from analysis of 26 studies in 54 pine forests worldwide (Tor-ngern et al., 2017). Moreover, it shared similar pattern to the result in other studies from tropical forest such as lowland tropical forest of Central and northern South America (Meinzer et al., 1993), primary lowland tropical forest in eastern Amazon (Brum et al., 2018) and perhumid tropical forest of Central Sulawesi in Indonesia (Horna et al., 2011). These results indicate that *Sa* was more sensitive to increasing VPD than *Ai* in small size while *Ai* can maintain their water use regardless of change in VPD under low soil moisture. Focusing on *T* of both species in large size under low soil moisture (Figure 4.6A and B), they had similar pattern from results in small tree size classes of both species. This implies that *Ai* may be more tolerant to drought than *Sa* and has strong control over their water use under low soil moisture regardless of tree size which can prevent it from negative effect from droughts. Comparing our results with a previous study that investigated drought tolerance of both species in this site (Unawong et al., 2022), we found similar results that *Ai* have more tolerance to drought than *Sa* with higher ability to resist xylem embolism. They reported that the xylem pressure at 50% loss of hydraulic conductivity (P_{50}) of *Ai* and *Sa* were −5.97 and −4.71 MPa respectively. The presence of species with lower P_{50} could imply the adaptive importance of embolism resistance in response to the environments where water stress is occurred more frequently (Maherali et al., 2004). When comparing *T* in different tree size classes of *Sa* (Figure 4.6A and C), it was less sensitive to rising VPD at lower VPD when size becomes larger under low soil moisture. The less sensitivity of large trees to rising VPD lead to slower decrease in water consumption rate to save water than small tree resulting in it may be greater vulnerability to hydraulic failure during drought. A previous study synthesized data on tree growth and mortality collected during 40 drought events in forests worldwide to see whether there was size-dependent sensitivity to drought (Bennett et al., 2015). They found that droughts consistently had a more impact on the growth and mortality rates of larger trees. Greater vulnerability of large trees to drought could be affected by the higher exposure to radiation and atmospheric demand as a result of increasing tree height (Nepstad et al., 2007; Roberts et al., 1990). Moreover, large trees have to transport water to greater height which is against the effects of gravity and thus face greater hydraulic failure (Ryan et al., 2006). Thus, large *Sa* may be at higher risk to hydraulic failure when drought is more pronounced leading to increasing mortality rates (Choat et al., 2018).

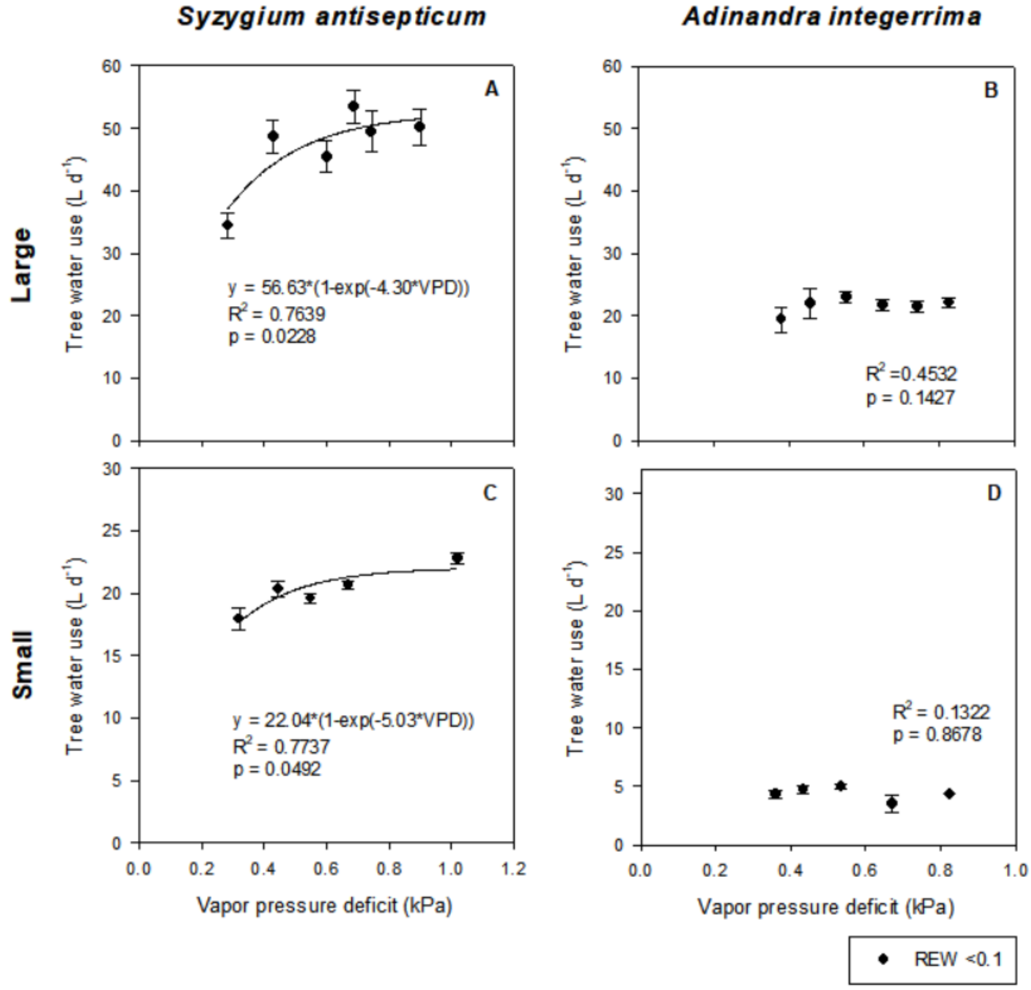


Figure 4.6 Relationship between tree water use (T; L d^{-1}) and vapor pressure deficit (VPD; kPa) of *S. antisepticum* in (**A**) large and (**C**) small size classes and *A.*

integerrima in (**B**) large and (**D**) small size classes under low soil moisture condition (REW <0.1).

Under intermediate soil moisture condition (REW 0.1-0.4), *T* of both species in both sizes did not respond to VPD (Figure 4.7). These results imply that both species can maintain their tree water use at moderate soil moisture regardless of tree size.

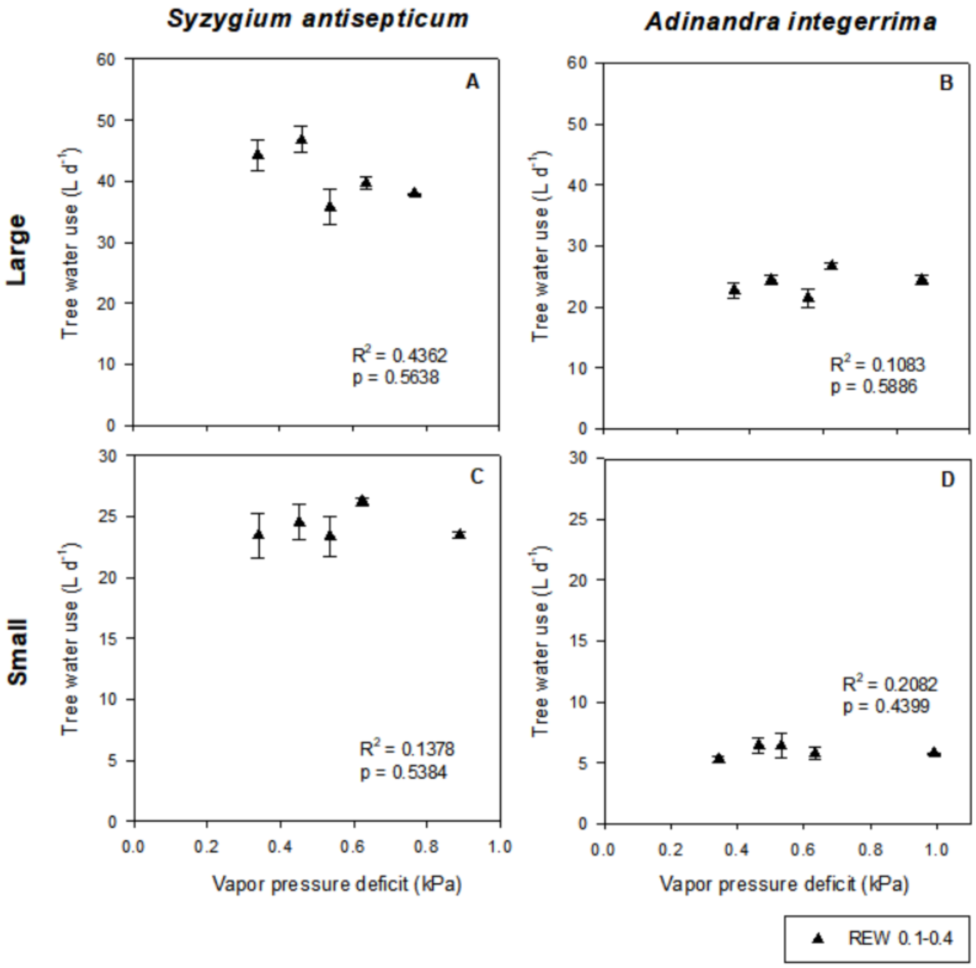


Figure 4.7 Relationship between tree water use (*T*; L d^{-1}) and vapor pressure deficit (VPD; kPa) of *S. antisepticum* in (**A**) large and (**C**) small size classes and *A. integerrima* in (**B**) large and (**D**) small size classes under intermediate soil moisture condition (REW 0.1-0.4).

Under high soil moisture (Figure 4.8), *T* of both species in both sizes increased with rising VPD at low VPD. Then, *T* of both species saturated at high VPD. In addition, *T* of both species in large size was less sensitive to rising VPD than small tree leading to higher water use at high VPD. When the air is drier, small trees decrease water consumption rate faster to save water than large trees. This may be partly due to that fact that small trees use shallow soil water whereas large trees can access water from deeper soil (Brum et al., 2018). Thus, this allows large trees to be less sensitive to rising VPD and consume more water than small trees at high VPD level. These results imply that *Sa* may consume more water under high soil moisture condition, but it may slow down runoff from forest into downstream ecosystems when storms come.

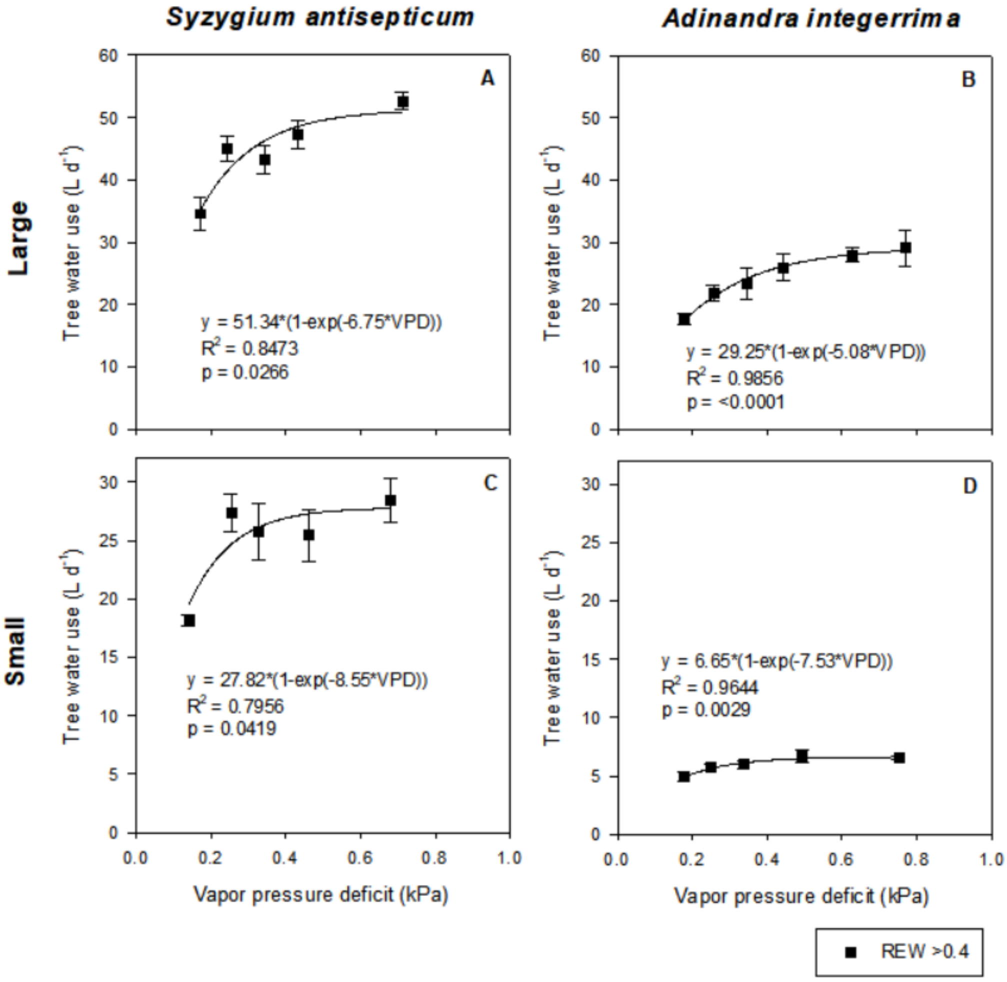


Figure 4.8 Relationship between tree water use (*T*; L d^{-1}) and vapor pressure deficit (VPD; kPa) of *S. antisepticum* in (**A**) large and (**C**) small size classes and *A. integerrima* in (**B**) large and (**D**) small size classes under high soil moisture condition (REW >0.4).

4.4 Implications for environmental management

The results from this study imply that *Sa* may provide ecosystem disservice with high water-use in dry areas but may slow down runoff when storms come. In contrast, *Ai* may provide ecosystem benefits by conservatively using water under drought but may increase runoff when storms come. Our results suggest that *Ai* may be suitable for reforestation in the area that droughts frequently occur in the downstream ecosystem through its conservative water-use behavior and may benefit downstream ecosystems with increasing runoff from the forest during drought. 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* may be 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. Nevertheless, mixed planting species seem to 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 addition, mixed planting species could reduce the competition for limited water resources because the differences in structure of plant roots of different 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). This study highlights that the response of *T* depends on species and tree 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 natural resources. Depending on reforestation purpose, *Sa* and *Ai* may provide either benefits or negative effects to the ecosystems.

Table 4.1summary 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 a significance level of 0.05. n/a indicates no significant relationship was found.

Species	**Size classes**	**REW classes**	**Relationships**	**r^2**	**p**
Syzygium antisepticum	Small (DBH < 20 cm)	< 0.1	T = 22.04*(1-exp(-5.03*VPD))	0.7737	0.0492
		0.1 – 0.4	n/a	0.1378	0.5384
		> 0.4	T = 27.82*(1-exp(-8.55*VPD))	0.7956	0.0419
	Large (DBH ≥ 20 cm)	< 0.1	T = 56.63*(1-exp(-4.30*VPD))	0.7639	0.0228
		0.1 – 0.4	n/a	0.4362	0.5638
		> 0.4	T = 51.34*(1-exp(-6.75*VPD))	0.8473	0.0266
Adinandra integerrima	Small (DBH < 10 cm)	< 0.1	n/a	0.1322	0.8678
		0.1 – 0.4	n/a	0.2082	0.4399
		> 0.4	T = 6.65*(1-exp(-7.53*VPD))	0.9644	0.0029
	Large (DBH ≥ 10 cm)	< 0.1	n/a	0.4532	0.1427
		0.1 - 0.4	n/a	0.1083	0.5886
		> 0.4	T = 29.25*(1-exp(-5.08*VPD))	0.9856	<0.0001

CHAPTER 5
CONCLUSIONS

We estimated tree water use (*T*) of dominant tree species including *S. antisepticum* (*Sa*) and *A. integerrima* (*Ai*) in a secondary tropical forest in Khao Yai National Park from sap flux density (J_S) which is 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* under non limiting soil moisture and high light. Comparing *T* in different tree size classes, *T* of large size was significantly higher than small size in both species which may be related to relatively lower sapwood area in small size. Further analysis on the pattern of response 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 more tolerant to drought than *Sa* and has strong control over their water use under low soil moisture regardless of tree size which can prevent it from negative effect from droughts. Under intermediate soil moisture, both species can maintain their tree water use regardless of tree size. When soil moisture becomes higher, *T* of both species in both sizes increased with rising VPD at low VPD and then saturated at high VPD under high soil moisture. Nevertheless, *T* of both species in large size was less sensitive to rising VPD than small size because large trees can access water from deeper soil leading to higher water use at high VPD. 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 increasing runoff from the forest during drought. 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 seem to 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. This study highlights that the response of *T* depends on species and tree size. Thus, species-specific allometric equations should be derived in different tree size classes. 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 natural resources. Depending on reforestation purpose, *Sa* and *Ai* may provide either benefits or negative effects to the ecosystems. Nevertheless, this study focused on the effect of tree size and environmental factors to *T*. In the further study, other physiological factors and environmental factors that influence on *T* should be studied to improve the understanding of the response of *T* in different species.

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AWARD RECEIVED	1. Outstanding undergaduate research project of faculty of science, Chulalongkorn Unviversity, Bronze prize in Young rising stras of science 2021 2. Best presentation (Silver prize) in The Hitachi Trophy 2021 Competition