Assessments of hydraulic responses to climate variability of dominant trees in successional forests in Khao Yai National Park for environmental management

Mr. Weerapong Unawong

A Thesis Submitted in Partial Fulfillment of the Requirements
for the Degree of Master of Science in Hazardous Substance and
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การประเมินการตอบสนองเชิงไฮดรอลิคต่อความแปรปรวนของภูมิอากาศของพันธุ์ไม้เด่นในป่าหลายขั้นการทดแทนในอุทยานแห่งชาติเขาใหญ่เพื่อการจัดการด้านสิ่งแวดล้อม

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วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
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ป่าเขตร้อนในบริเวณเอเชียตะวันออกเฉียงใต้ถูกคุกคามเพิ่มมากขึ้น ทั้งจากการกระทำของมนุษย์ และการเปลี่ยนแปลงของธรรมชาติ โดยเฉพาะการเปลี่ยนแปลงของสภาพภูมิอากาศในสภาวะขาดน้ำ อย่างไรก็ตาม ป่าในแต่ละพื้นที่อาจตอบสนองต่อการเปลี่ยนแปลงต่อสภาวะขาดน้ำที่แตกต่างกัน จึงเป็นที่มาในการศึกษาเกี่ยวกับค่าชลศักย์ของน้ำในใบที่เปลี่ยนไปตามฤดูกาลและสมบัติในการเคลื่อนย้ายน้ำของชนิดเด่นในป่าหลายขั้นทดแทน ณ อุทยานแห่งชาติเขาใหญ่ โดยศึกษา ค่าชลศักย์ของน้ำในใบช่วงเที่ยงวัน (Ψ_{md}) ในฤดูฝนและฤดูแล้ง และค่าการสูญเสียการลำเลียงน้ำที่ร้อยละ 50 ในกิ่งไม้ (P_{50}) จากชนิดเด่นในป่าที่มีช่วงอายุแตกต่างกัน รวมไปถึงการตรวจสอบความสัมพันธ์ระหว่าง P_{50} กับค่าการลำเลียงน้ำในท่อลำเลียงสูงสุด (K_{smax}) และค่าความยาวของท่อลำเลียงสูงสุด (MVL) นอกจากนี้ ยังมีการคำนวณสัดส่วนของการสูญเสียน้ำอันเนื่องมาจาก Ψ_{md} ในฤดูแล้ง (PLC_{dry}) ผลการศึกษาพบว่า ค่า Ψ_{md} ของป่าที่มีอายุน้อยจะมีค่าต่ำกว่าป่าที่มีอายุมากทั้งในฤดูฝนและฤดูแล้ง และเมื่อเปรียบเทียบความแตกต่างของค่า Ψ_{md} ต่อการเปลี่ยนแปลงของฤดูกาล พบว่า ค่าที่ได้ในพื้นที่ป่าอายุน้อยมีความแตกต่างอย่างมีนัยสำคัญกับพื้นที่ป่าในช่วงอายุอื่น อาจเป็นเพราะการปรับตัวเพื่อเอื้อต่อการสังเคราะห์ด้วยแสงและการเจริญเติบโต แม้จะมีความเสี่ยงต่อการเกิดฟองอากาศและอุดตันในท่อลำเลียง ต่อมา ในกลุ่มพื้นที่ป่าที่มีช่วงอายุแตกต่างกัน พบว่า ค่า MVL, K_{smax}, และ P_{50} ที่ได้ ไม่มีรูปแบบที่ชัดเจน และพบความสัมพันธ์ระหว่างค่า P_{50} กับ K_{smax} บ่งชี้ว่า ความสามารถในการทนแล้ง แปรผกผันต่อความสามารถในการลำเลียงน้ำ ทั้งนี้ ไม่พบความสัมพันธ์ระหว่างค่า P_{50} กับ MVL นอกจากนี้ ยังพบว่า ค่า Ψ_{md} ช่วงฤดูแล้งของทุกชนิด ส่งผลให้เกิดการสูญเสียความสามารถในการลำเลียงน้ำ (PLC_{dry}) ในสัดส่วนที่แตกต่างกัน และชนิดที่มีความสามารถในการทนแล้งได้ดีกว่า จะมีค่า PLC_{dry} ที่ต่ำกว่า ยิ่งไปกว่านั้น ผลการศึกษายังบ่งชี้ว่า คุณสมบัติของชนิดที่มีความทนทานต่อการเกิดฟองอากาศในท่อลำเลียง สามารถบ่งบอกถึงความเสี่ยงของการลำเลียงน้ำที่มีปัญหาในสภาวะขาดน้ำของชนิดนั้นได้ องค์ความรู้เรื่องการตอบสนองของชนิดต่อสภาวะขาดน้ำในพื้นที่ป่าหลายขั้นทดแทนที่แตกต่างกันนี้ สามารถนำมาวางแผนกลยุทธ์ต่อการจัดการพื้นที่ป่าได้อย่างเหมาะสม กับสภาพภูมิอากาศที่เปลี่ยนแปลงในอนาคตที่คาดการณ์ว่าจะมีอุณหภูมิเพิ่มสูงขึ้น

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Weerapong Unawong : Assessments of hydraulic responses to climate variability of dominant trees in successional forests in Khao Yai National Park for environmental management. Advisor: Assoc. Prof. PANTANA TOR-NGERN, Ph.D.

In Southeast Asia, tropical forests have been increasingly threatened by human disturbances and climate change-induced water stress. However, uncertainty remains as to how these forests would respond to environmental changes under water deficit conditions. Here, we conducted a study of seasonal variation in leaf water status and hydraulic properties of dominant tree species across forest successional stages in Khao Yai National Park, Thailand. Specifically, we measured midday leaf water potential (Ψ_{md}) during the wet and dry season, and assessed branch xylem vulnerability at which 50% is lost (P_{50}). The associations between P_{50} and maximum xylem hydraulic conductivity (K_{smax}) and maximum vessel length (MVL) were examined. We also calculated percentage loss of hydraulic conductivity corresponding to Ψ_{md} during the dry season (PLC_{dry}). Our results showed that, lower Ψ_{md} during the wet and dry season and greater variation in Ψ_{md} resulted from seasonal changes were observed in drier sites. This could be an adaptive strategy to optimize photosynthesis and growth, but at higher risk of hydraulic failure. Substantial within-site variation in MVL, K_{smax}, and P_{50} were observed in this study, leading to unclear variations across the successions. P_{50} was correlated with K_{smax}, supporting the hydraulic efficiency-safety tradeoff, but not with MVL. Additionally, all studied tree species from each succession experienced changes in Ψ_{md} during the dry season that could lead to PLC_{dry} in different degrees. Species with more resistant to xylem cavitation exhibited lower PLC_{dry} than species with higher xylem vulnerability. This observation highlights the significance of cavitation resistance for determining species' risk of hydraulic dysfunction during low water availability. Therefore, knowing responses to water stress of different tree species and different forest successions would be beneficial for selecting ones that could be well adapted to specific environments, thus improving the strategies for managing forests in different successions under a warmer future.

Field of Study:	Hazardous Substance and Environmental Management	Student's Signature ....
Academic Year:	2020	Advisor's Signature ....

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CHAPTER 1

INTRODUCTION

Anthropogenic impacts on tropical forests have received a considerable amount of attention due to their significant consequences on climate, food, energy, and ecological systems (Crist et al., 2017; Lawrence & Vandecar, 2015; Wilcove et al., 2013; Zeng et al., 2017). Tropical forests provide numerous ecosystem functions and services that are imperative for sustaining terrestrial ecosystems and beneficial for human society. They are considered as a key component in global water cycling (Avissar & Werth, 2005) and the global epicenter of terrestrial biodiversity containing more than 60,000 different tree species (FAO & UNEP, 2020). Tropical forests also supply many goods and services needed for agricultural, livestock, forestry, and fishery production (Reed et al., 2017), which improve people’s livelihoods around the globe. Due to their numerous benefits, tropical forests have been overexploited over the centuries to meet the needs of increasing human population and economic growth. As a result, a drastic loss of forested area and extensive forest conversion have occurred from anthropogenic disturbances (Popradit et al., 2015; Ryan et al., 2017). Even worse, tropical forests have also been severely affected by extreme events from human-induced climate change, including droughts, warmer temperature, heat waves and fires (Allen et al., 2010). Among these adverse impacts, droughts may have the greatest effect on forested areas worldwide (Reichstein et al., 2013). In particular, the ongoing effect from an increase in frequency, duration, and intensity of droughts is threatening the productivity and survival of forests (Barbeta et al., 2015). With this regard, droughts have been defined as an important contributing factor affecting forest physiological responses in many regions (Allen et al., 2010; Mueller et al., 2005), potentially accelerating the rates of tree decline and mortality of forests (Carnicer et al., 2011; Shaw et al., 2005). Therefore, the combination of the impacts from anthropogenic disturbances and severe droughts will surely be exacerbated. Such impacts may contribute to the degradation of ecosystem functions and services mentioned earlier (Anderegg et al., 2013; Choat et al., 2012; Morin et al., 2018; Pan et al., 2011; Ryan et al., 2010)

Tropical forests have been substantially converted for other forms of land use. Over the past decades, the rate of forest clearance in Southeast Asia has been ranked among the highest in the tropics, losing approximately 1.6 million ha yr^{-1} between 1990 and 2010 (Stibig et al., 2014). Most of the land conversion is attributed to a number of human activities, including commercial logging (Wilcove et al., 2013), intensive cultivation (Zeng et al., 2018), and food production (Imai et al., 2018). These areas are typically abandoned after several years of operation and transformed into secondary forests, whether by natural succession or human plantation. This regeneration distinguishes the stage of forest succession in Southeast Asia into primary forests and different phases of secondary forests. Clearly, the forest structure and species composition in secondary forest are different compared to primary forest (Lebrija-Trejos et al., 2011). Different vegetation structures, such as canopy coverage, differentiate microclimate and soil properties among successional stages (Lee et al., 2006), and thus affecting location, duration, and distribution of tree species being able to regenerate within each stage (Lebrija-Trejos et al., 2010). Moreover, differences in canopy openness, tree density, vertical stratification, and the amount of plant litter strongly influence the variation of temperature, atmospheric humidity, and soil water availability along successional stages in the forests (Heithecker & Halpern, 2007; Marthews et al., 2008), creating warmer and drier environment in secondary forest in comparison to primary forest (Pineda-Garcia et al., 2013). Given these differences, the attempts to study physiological mechanisms across forest succession have emerged in temperate and tropical ecosystems (Matheny et al., 2017; Pineda-Garcia et al., 2016; Powell et al., 2017; Ruiz-Benito et al., 2017), but rarely in Southeast Asia. Besides, differences in species composition of the primary and secondary forests can also complicate our understanding on how forests will respond to water stress. Since trees establishing in different successional stages may respond differently to droughts (Bretfeld et al., 2018), this knowledge gap could be crucial for the restoration of forests along successional gradients. Outcome from studies addressing physiological variation among forest stages will provide more definitive recommendations for selecting appropriate tree species for forest restoration in tropical regions, especially in Southeast Asia.

Knowing the response of forests to changing environment depends on the understanding of drought-induced physiological mechanisms of dominant trees at the species level (Choat et al., 2012). Instead of carbon starvation from reduction in photosynthesis, it has been revealed that deterioration of the water transport system, also known as hydraulic failure, is the main driver of plant mortality triggering tree death from drought in tropical areas (Rowland et al., 2015). Since water is necessary for plant in many processes, its limitation could lead to many dysfunctions in terrestrial plants. One method to study the response of trees to drought-induced hydraulic dysfunction is by quantifying their responses to water supply. Apart from various key variables in plant functioning, plant water potential is a measurable indicator of tree water status and represents the overall plant health because plant growth, productivity, and recovery are all dependent on plant water status (Taiz & Zeiger, 2003). Plant water potential is the main driving force controlling water movement from roots to leaves (González & Reigosa Roger, 2001) and also describes how hydrated a plant is (Perez-Harguindeguy et al., 2016), providing a relative index of water stress that the plant is exposed to. In plant physiological study, water potential can be used to see how trees generally respond to changes in their surroundings and to quantitatively compare water status among tree species (Steppe, 2018; Teskey & Hinckley, 1986). The measurement of plant water potential, thus, offers the information regarding trees' responses to the changing environment, which is very crucial for the understanding of how plants survive during water stress (McDowell et al., 2008). Another method to assist in characterizing the sensitivity of plants to drought stress is by measuring how well water can transport from roots to leaves (soil-plant-atmosphere continuum) through xylem tissue. The xylem elements supply water for all aspects of plant functioning, such as growth, maintenance, and reproduction. However, insufficient water availability during drought events may induce the formation of bubble in xylem conduits, affecting the continuous water column in xylem network. This hydraulic dysfunction in xylem tissue is called cavitation (Taiz & Zeiger, 2003), which could interrupt water transport to tree crowns and eventually lead to tree death (Adams et al., 2017). One index that plays an important role in defining performance of water transport in trees during droughts is xylem vulnerability to cavitation, which is considered as the key trait responsible for setting the drought tolerance of any species (Skelton et al., 2015). It has been indicated that the xylem vulnerability strongly relates to the capability of woody trees to resist and retrieve from periods of prolonged drought (Domec et al., 2015). Nevertheless, this trait varies among species and is largely determined by difference in xylem structure

(Delzon et al., 2010; Maherali et al., 2004). Investigating the response of trees to drought-induced hydraulic failure and their xylem vulnerabilities will, therefore, offer a fundamental aspect representing an important property for stating the limits of drought tolerance for woody tree species and determining trends in drought-induced forest mortality of forests in different successional stages.

With these regards, this study aims to evaluate seasonal variation of tree hydraulics through plant water potential and to assess xylem vulnerability of dominant tree species in Khao Yai National Park, a seasonal evergreen forest in north-eastern Thailand. This national park is a UNESCO world heritage site. Measurements and analyses will be performed in both wet (May–October) and dry (November–April) seasons across three forest stands representing an old-growth forest (OF, >200 years), an intermediate forest (IF, ~45 years), and a young forest (YF, ~5 years). The outcome from this study will fulfill the knowledge gaps on physiological responses of tropical forests to seasonal changes, as well as offer knowledge on species-specific responses along the forest successional stages. This knowledge will provide useful insights to support policy decisions on tropical forest management, especially for species selection to restore forests, particularly in highly deforested and degraded region in Southeast Asia.

1.1 Research objectives

1.1.1 To determine seasonal variation in leaf water status of dominant tree species across forest succession in Khao Yai National Park

1.1.2 To characterize drought tolerance of dominant tree species across forest successional stages

1.2 Research schedule

The study period starts from July 2019 to August 2021. Key tasks are listed below at 2-month intervals.

Table 1.1 The study period

Task	2019			2020						2021			
	July - Aug	Sep - Oct	Nov - Dec	Jan - Feb	Mar - Arp	May - June	July - Aug	Sep - Oct	Nov - Dec	Jan - Feb	Mar - Arp	May - June	July - Aug
1. Design the study	■	■											
2. Review literature	■	■	■	■	■	■	■	■	■	■	■	■	■
3. Survey study plots and design the experiment		■	■										
4. Collect samples for tree hydraulic measurement (Ψ_{md})			■	■	■	■	■	■					
5. Collect sample for xylem vulnerability to cavitation analysis (P_{50} and PLC_{dry})											■	■	
6. Analyze and interpret results						■	■	■	■	■	■	■	■
7. Prepare and submit thesis												■	■

1.3 Expected outcome

7.1 This study will enhance the understanding on physiological responses of forest trees from different successional stages to seasonal variation.

7.2 This study will provide a measurable index describing the capacity of woody tree species from different successional forests to tolerate water stress.

7.3 Results from this study can be used in forest management projects, especially for species selection to increase the likelihood of success in forest restoration.

CHAPTER 2

LITERATURE REVIEW

A major trade-off when uptaking carbon dioxide (CO_2) from the atmosphere for photosynthetic process is the loss of water through plant stomata. Water is vital for plant development and considered as a key determinant of vegetation distribution across ecosystems. In this sense, limited water availability is predicted to be a major environmental constraint in forest ecosystems owing to climate change predictions (IPCC, 2019). Several studies have evaluated the physiological responses of plants to water stress (Adams et al., 2017; Allen et al., 2010; Martinez-Vilalta et al., 2019; McDowell et al., 2008; Sevanto et al., 2014), with the aim of developing reliable indicators for plant mortality risk. Among these responses, plant hydraulic efficiency involved in water transport has been acknowledged to play a crucial role in plant response and adaptation to water stress. Nevertheless, plant responses resulted from water stress could be dependent on site and/or species (Ryan et al., 2010; Vilagrosa et al., 2012), in which, however, facing similar exposure to stress or damage during the periods of water-limited conditions (Choat et al., 2012). This emphasizes the need for a better understanding of water stress impacts on different tree species and ecosystems, in order to provide useful and relevant information for forest management and protection.

2.1 Status and succession in Southeast Asian tropical forests

Southeast Asia (SEA) is home to approximately 7% of the world’s forest area (FAO, 2020), and roughly 15% of the world’s tropical forests (Stibig et al., 2014) (Fig 2.1). The tropical forest in SEA plays a crucial role for biodiversity hotspots (Slik et al., 2015), as well as socio-economy and the livelihoods for forest-dependent people. This region, however, is being lost through successive waves of anthropogenic disturbances, including colonization, cultivation, and abandonment, and also exacerbated by the impacts of climate change. As a result, secondary (regrowth) forests are replacing as patches in the primary (old-growth) forests, leading to equal or larger areas of regrowth forests than that of mature forests in the SEA regions (Estoque et al., 2019).

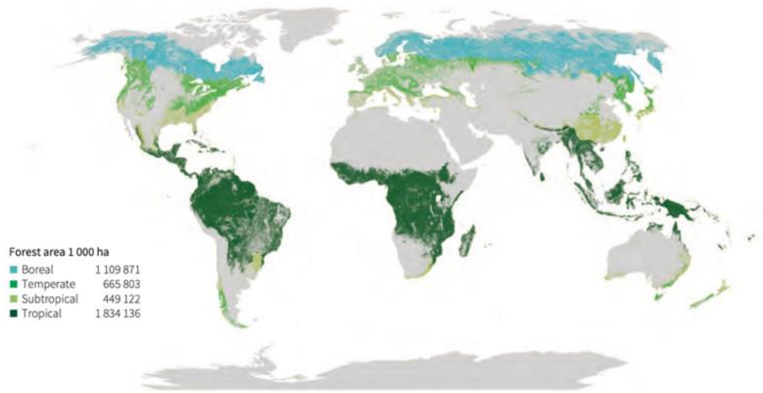

Figure 2.1 The distribution of global forest area categized by climatic domain[1]

SEA is facing irregular climate events due to the combination of various pattern of climate associated with El Niño events (Islam et al., 2018). Specifically, in Thailand, the combination of these interactions results in changing in amplitude and variability of climate behaviors, which consequently lead to more frequent and broader hydrological disasters, such as droughts (Power et al., 2020). Kaewthongrach et al. (2019) studied the impacts of severe drought during the strong 2015/2016 El Niño event in a secondary dry dipterocarp forest in Thailand, with the aim of evaluating how this forest would respond to extreme climatic events. The results showed that the amount of rainfall during the El Niño decreased to 30% of the total rainfall in normal years, and subsequently reduced soil moisture to around 5% for 5–6 consecutive months rather than 3 months during typical dry seasons. Lower water availability during the El Niño event induced xylem embolism in the crown, leading to the increase of the forest dieback and mortality up to 50% compared to non-El Niño events. This study serves as a pioneer assessment for potential impacts of climate change on the secondary forests in Thailand, which is rare and remains poorly understood. Thus, it is of paramount importance to not only protect the remaining areas of primary forest and conserve the regrowth ones, but also to understand their responses to changing environment, as a prerequisite to ameliorate the strategies dealing with managing forests in different areas and generations.

Dividing forest dynamics into distinct successional phases is a useful method for comparative studies and ecological research that focus on transitions in forest

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[1] Taken from FAO. (2020). Global forest resources assessment 2020: Main report.

structure, species composition, and ecosystem properties (Chazdon, 2013). The boundary between stages of succession is vague, but these stages generally follow the order of time. As shown in Table 2.1, the vegetation structure in each successional stage changes depending on temporal sequence. In the stand initiation stage, pioneer species starts colonizing the disturbed lands, herbaceous species declines, and shade-tolerant species establishes as seedlings. The next stage is generally referred to as the stem exclusion or dense structure, as all space of the land is occupied by fast growing species and thus the canopy becomes closure. This results in suppression of shade-intolerant species, while shade-tolerant species continue to establish and recruit in the canopy. During understory reinitiation stage, canopy gaps are formed due to the mortality of long-lived pioneer trees, which decreases the homogeneity of light availability. This process allows a vegetative understory to develop, turning over the species in the understory back to the land again. The last stage, old-growth stage, begins with the mortality of pioneer trees establishing during the stem initiation stage. It is the most diverse stage for trees and epiphytes and is categorized by high functional diversity and large spatial heterogeneity.

Table 2.1 Vegetation dynamic processes related to stages of forest succession and time since disturbances[2]

Successional stages	**Vegetation dynamic processes**
0-15 years Stand initiation	• Germination of seeds in seed bank (i.e., in soil) • Resprouting of remaining trees • Colonization of short- and long-lived pioneer trees • Rapid height and diameter growth of woody species • High mortality of herbaceous species (i.e., grasses, flowers etc.)
15-50 years Stem exclusion	• Canopy Closure • Recruitment of shade-tolerant seedling, saplings, and trees • Growth suppression of shade-intolerant trees in understory • High mortality of short-lived-pioneer trees • Dominance of long-lived pioneer trees
30-200 years Understory reinitiation	• Mortality of canopy trees • Formation of small canopy gaps • Reproductive maturity of early-colonizing species • Increase heterogeneity in understory light availability • Tree recruitment of early-establishing shade-tolerant species

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[2] Adapted from Chazdon, R. (2013). Tropical Forest Regeneration. In (pp. 277-286).

Successional stages	Vegetation dynamic processes
> 200 years Old-growth	• Range of gap sizes • Recruitment of shade-tolerant and gap canopy species • Spatial heterogeneity in biomass and microtopography • Large woody debris • Maximum diversification of trees and epiphytes (i.e., lichens, ferns etc.)

Focusing on the study area, Khao Yai National Park comprises a mosaic of patches in various forest succession covering three out of the four stages described earlier (Chanthorn et al., 2016). The national park was officially founded in 1962 and considered as Thailand’s first official national park. It is a forest ecosystem surrounded by traditional upland farming from Thai Tha Dan people since the end of the nineteenth century. The old-growth stage has existed over a few hundred to a thousand years and there is no evidence of human disturbance (Figure 2.2A). The canopy height within this stage is around 20–35 meters with some of the large trees (emergents), notably the Dipterocarpaceae family, reaching over 50 meters. Within this stage, a forest dynamics plot, Mo Singto, was created in 1996, covering 30 ha in area and containing nearly 700 species of plants (Brockelman et al., 2017). The next stage is called young smooth forest, which is characterized as in stem exclusion stage (Figure 2.2B). This site is a re-growth forest from abandoned agricultural lands when the park was founded. Being categorized as stand initiation stage, the next forest succession is called very young forest (Figure 2.2C). It was cleared and used in military purposes until 1975, then left for regeneration. The last stage within Khao Yai National Park is naturally afforesting grassland (Figure 2.2D), regenerated since 2001 from a former golf course. Clumps of trees can be seen scatteringly within this stage.

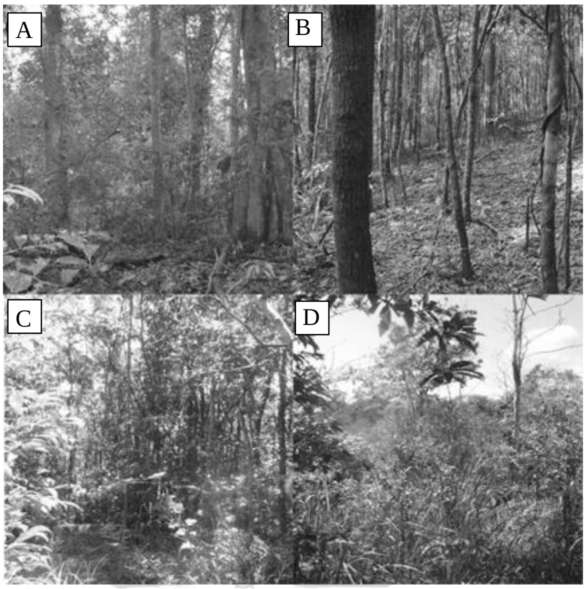

Figure 2.2 Different forest successions in Khao Yai National Park[3]
A. Old-growth forest, B. Young smooth forest, C. Very young forest, and
D. Naturally afforested grassland

2.2 Hydraulic architecture and water transport in plants

Since plants started to colonize on land, uptaking and transporting water to distal organs have been the challenge that plants are dealing with against the gravitational force. Large amounts of water are required for plants to live and grow. To perform photosynthesis, carbon dioxide (CO_2) is absorbed by plants through pores on the leaf surface called stomata. It takes one molecule of water for one molecule of CO_2 to be synthesized in this essential process. However, when stomata open, hundred times of water molecules are lost in comparison to the small amount of CO_2 absorbed (Ruggiero et al., 2017). Such amount of water evaporating from plants across ecosystems returns approximately 40% of terrestrial rainfall globally (Schlesinger & Jasechko, 2014), and thus is an important factor driving water cycle at the global scale.

2.2.1 Plant water relation

Generally, water taken up by terrestrial plants is entered to roots from the soil by osmosis (Taiz & Zeiger, 2003). A root system comprises of a complex network of roots

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[3] Taken from Chanthorn, W., Ratanapongsai, Y., Brockelman, W., Allen, M., Favier, C., & Dubois, M.-A. (2016). Viewing tropical forest succession as a three-dimensional dynamical system. *Theoretical Ecology*, *9*.

in different diameter sizes along their length. Roots growing at the tips are thinner and smaller lateral roots, which are called fine roots and have the greatest capability to absorb water in the root system (McCully, 1999). During the absorption, water enters the epidermis and then moves inwards crossing cortex, endodermis, and pericycle before it reaches water-conducting tissues, or xylem (Figure 2.3, Figure 2.6J).

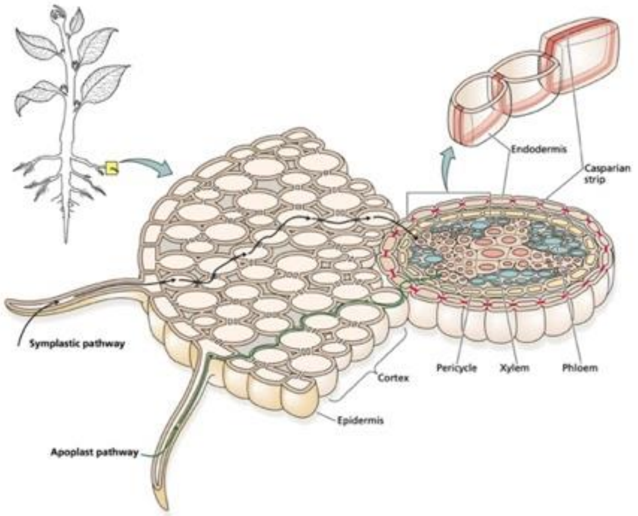

Figure 2.3 The pathways for water movement in roots[4]

To reach the xylem, water can travel through the spaces between cell walls (apoplast pathway) or move through the inside of cells (symplastic pathway). At the endodermis, the cell walls are impermeable at the casparian strip, forcing water movement in the route of apoplast to enter another layer via symplastic pathway instead. The casparian strip in plant roots is a paracellular barrier that regulates the water and solutes movement from the soil to the water-conducting elements (Grebe, 2011). Generally, roots closely contact to soil, which provides nutrients, water, and other substances that may be lethal to plants. To control the uptake of substances from the soil, evolving the paracellular barrier inside the root enables plants to perceive and select things before passing them to the vascular system (Geldner, 2013).

Once in the water-conducting tissues, water moves freely over long distances in open pipelines in the stems and branches. These conducting elements have a specialized formation, allowing them to transport water with great efficiency (Jung et

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[4] Adapted from Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany, 91.*

al., 2008). There are two kinds of tracheary elements in the xylem: tracheids and vessels (Figure 2.4). Tracheids can be found in all vascular plants but mostly in gymnosperms, including conifers and ferns, whereas vessels are presented only in angiosperms (Mencuccini, 2003). The xylem elements originate with living cells, but dead at maturity (Taiz & Zeiger, 2003). These conducting elements undergo an adjustment where they scarify their organelles and form hollow tubes to decrease resistance while transporting water. Structurally, tracheids are lengthened with spindle-shaped cells and usually smaller than vessels in diameter (Figure 2.4A). Comparing to tracheids, vessels are likely to be shorter and wider and contain the end walls that assemble a perforation plate (Figure 2.4A). The perforated end walls enable vessels to stack their ends to form continuous open tubes, providing a very efficient and low resistant pathway for water movement. Along with the tracheary elements, xylem also contains parenchyma cells that help store and transport water and carbohydrates within conduits, as well as fibers that provide structural support (Secchi et al., 2017).

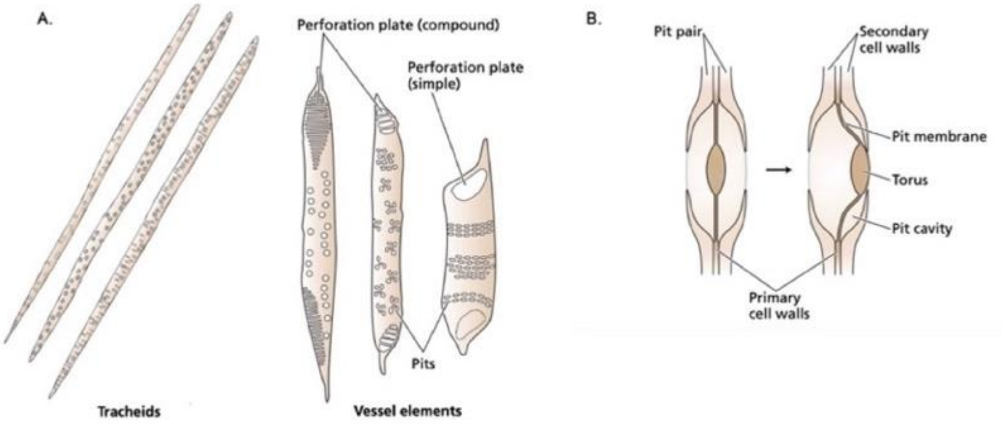

Figure 2.4 Xylem elements and their interconnections[5]
A. Tracheids and vessel elements, and
B. A bordered pit with a torus (a special characteristic of pit membranes mostly found in gymnosperms) either centered or resided to one side in the pit cavity

Xylem elements are bordered by pit membranes, where water has to pass to move from one conduit to a neighboring one (Figure 2.4B; Figure 2.6I). Pit membranes are cavities and discontinuities in the secondary cell walls. Comprising of a degraded

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[5] Adapted from Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany, 91.*

primary cell wall and middle lamella, pit membranes play a significant role in higher evolution of vascular plants by allowing the transport of water while preventing the entry of air and microbes between the adjacent conduits (Choat et al., 2008). The pit membranes, thus, function as safety faucets in the water transport system of plants.

After taken up from roots and transported to stems and branches, water enters leaves though the xylem in a petiole, a stalk that attaches the leaf to the branch. The petiole bridges the xylem connection into the midrib (also called midvein) which then branches off into a very fine and complex network of veins throughout the leaf (Figure 2.5A). Once water leaves the xylem, water is drawn from the bundle sheath cells to the cell wall surfaces of mesophyll cell, where it diffuses into the internal air spaces. In response to the concentration gradient, water vapor exits the leaf through stomata and passes through the still-air layer adjacent to the leaf surface (Figure 2.5B). The process in which water moves from the xylem and evaporates out of the leaves is called transpiration.

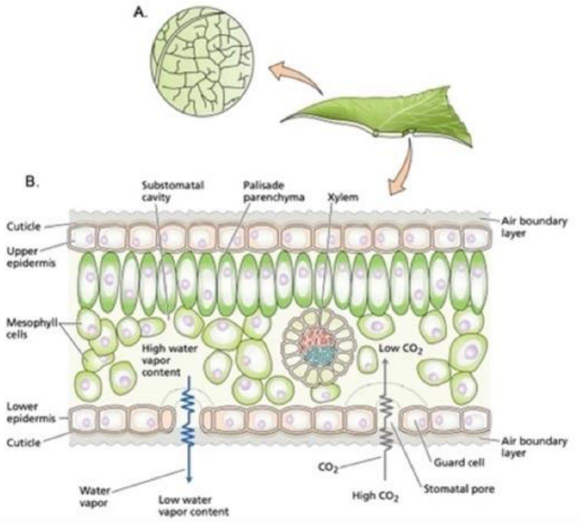

Figure 2.5 A leaf diagram[6] presenting A. Venation of a leaf showing ramification of the midrib into smaller veins., and B. The pathway for water movement in a leaf.

2.2.2 The mechanisms driving the ascent of water in plants

The ascent of water in plants is generally a passive process driven by water potential gradient. Water moves by bulk flow towards regions of lower water potential. The

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[6] Adapted from Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany, 91.*

mechanism driving the transport of water in plants can be referred to as the "cohesion-tension" mechanism (Dixon & Joly, 1895; Taiz & Zeiger, 2003; Tyree & Zimmermann, 2002; Venturas et al., 2017). The name comes from the 'cohesion' of hydrogen-bonding property of water and the capillary suction resulted from the pulling action, or 'tension', generated by transpiration (Figure 2.6). Water is a polar molecule and has a strong cohesive force, allowing for the formation of hydrogen bonds with other molecules. These hydrogen bonds pull the water molecules tightly together, which enable water columns in plants to withstand a very high tension without disconnecting and help explain the capability of water transport to the canopy heights of several meters above ground. In the plant xylem, the tension exists because of transpiration, leading to a tug-of-war process that pulls a continuous stream of water in root-to-leaf pathway (Figure 2.6A). This tension is a negative hydrostatic pressure ($P_x < 0$) that is conventionally signified to water potential (Ψ). The increasing negative on Ψ, the greater tension imposes on the water column. As pointed out before, plant transpiration occurs when water evaporates from mesophyll cell walls surrounded by the air spaces inside the leaves (Figure 2.6B). Water menisci occur at this air-water boundary where the water in apoplast is exposed to the air (Figure 2.6C). Because transpiration is predominantly driven by sunlight, water molecules are broken down by solar energy and evaporate from the meniscus (Figure 2.6E). The evaporation creates tension in the xylem that exerts the capillary suction on the meniscus within the cell walls. This suction results in the replacement of evaporated water molecules by others in the continuous stream of water. The tension occurred in this interface is also propagated along the water column, causing the water potential gradient along the roots and the leaves (Figure 2.7).

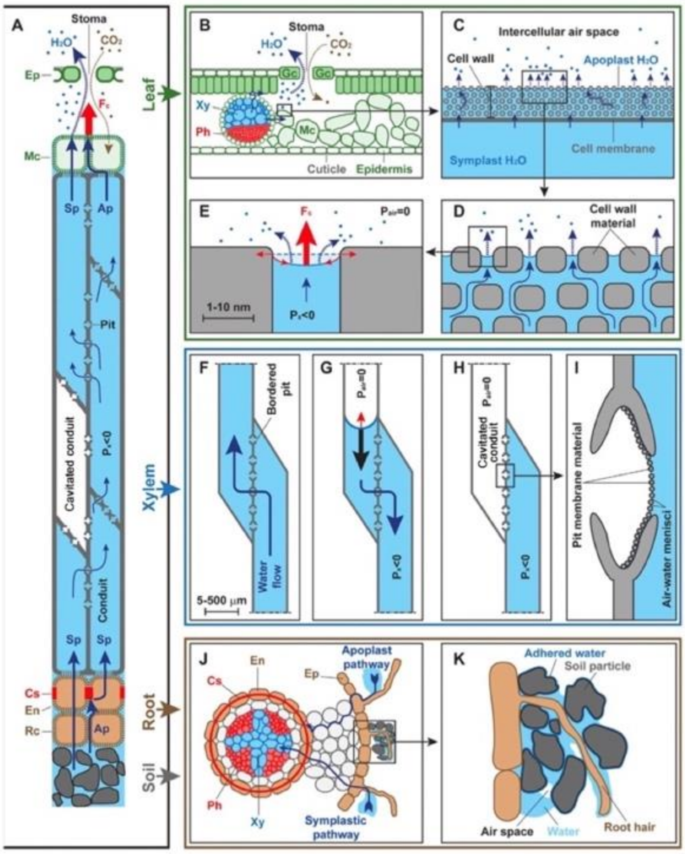

Figure 2.6 The cohesion-tension mechanism of water transport in plants[7]

A. Diagram of water column from soil to leaf cells. The bulk of water is drawn (blue arrows) from soil to leaf surface by negative pressure, or tension, ($P_x < 0$) and capillary suction (red F_c arrow). From the bottom up, water moves from roots (Rc) in the soil to the xylem (Xy) via symplastic (Sp) and apoplastic (Ap) pathways. The water movement is controlled at the endodermis (En) due to casparian strip (Cs) that blocks the Ap pathway. Water moves inwards to water-filled xylem tissues in the stem (no gas bubbles or cavitation). The capillary suction moves water out of the mesophyll (Mc) by diffusion from the leaf as the epidermis (Ep) and stomata regulate the loss of water (dotted blue arrow) and the uptake of carbon dioxide (dotted brown arrow)., B. Leaf cross section illustrating transpiration and photosynthesis processes which are mainly governed by stomatal aperture (Gc)., C. The cell wall surfaces of mesophyll cell surrounding by the air space., D. The air-water interface on the mesophyll cell wall., E. A single meniscus showing the capillary suction (F_c) and diffusion of water (dotted blue arrows). As water evaporates, the surface water forms meniscus, the tension is generated ($P_x < 0$), and F_c is exerted in the cell wall. The tension is transmitted through the water stream in A taking water up from the soil., F. The water-conducting tissues are linked through pit membranes functioning as safety faucets in water transport pathway., G. If air spreads into the xylem elements, capillary suction alone cannot retain the continuous column of water due to large diameter of xylem conduits., H. Water is drained to the neighboring conduit and leaves the previous tissue to become empty., I. Pit membranes help prevent the entry of air from the adjacent conduit., J. Root cross section presenting the ways for water being absorbed by the root., and K. A root hair that makes direct contact with soil and water adsorbing to the surface of soil particles.

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[7] Adapted from Venturas, M. D., Sperry, J. S., & Hacke, U. G. (2017). Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, *59*(6), 356-389.

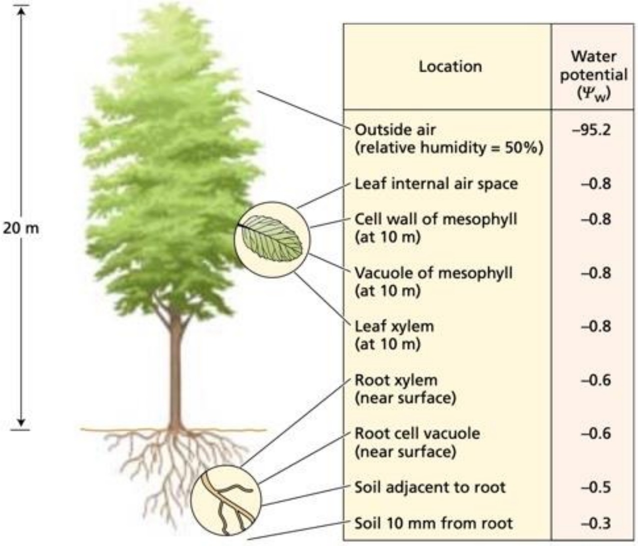

Figure 2.7 An example of water potential at various points along the water transport pathway[8]

2.2.3 The initiation of xylem cavitation

As mentioned earlier, water in plants is drawn under tension (negative pressure) corresponding with cohesion-tension mechanism. When the tension inside xylem becomes too high (more negative), the water stream breaks and disconnects the continuous column of water molecules–a phenomenon known as cavitation (Tyree & Zimmermann, 2002) (Figure 2.6F-H). A number of mechanisms have been proposed for the establishment of air in the water-conducting conduits, but the most acknowledged one is air-seeding mechanism (Tyree & Zimmermann, 2002; Venturas et al., 2017; Vilagrosa et al., 2012). In the xylem network, there is a threshold for the cavitation to occur in the xylem elements. It is when the tension becomes higher than the pressure needed to tug an air bubble from a cavitated tissue into a water-filled one through pit membranes–a process known as air seeding (Figure 2.8). Once inside the water-filled tissue, the tension causes the air bubble to enlarge and fill the entire tissue. In accordance to water stress conditions, this phenomenon can propagate through the xylem network and decrease the efficiency of xylem to conduct water, leading to the reduction or cessation of water uptake from roots to distal organs in plants

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[8] Adapted from Taiz, L., and Zeiger, E. 2003. Plant physiology. 3rd ed.

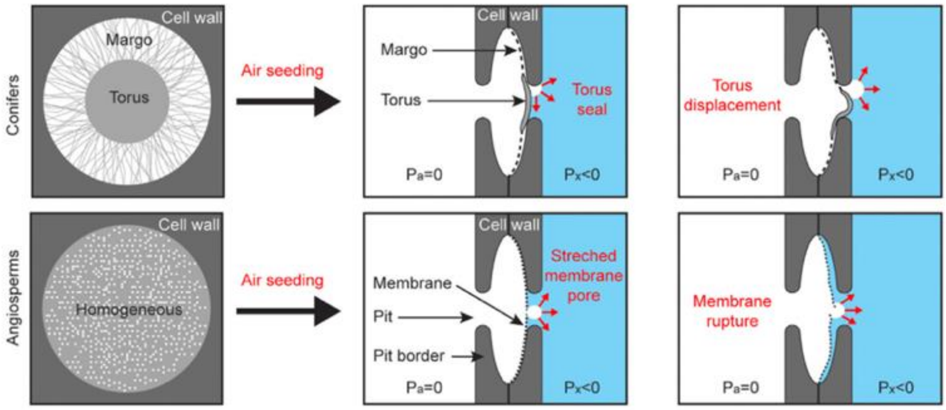

Figure 2.8 Air-seeding process under water-limited condition for gymnosperms and angiosperms[9]. The pressure difference (ΔP) between the cavitated conduit (P_a=0) and the adjacent water-filled conduit (P_x<0) leads to the deflection of pit membranes against the pit border. Air is seeded into the conduit filled with water when ΔP reaches the threshold pressure (i.e., critical plant water potential (Ψ_{crit})). For example, in gymnosperms, air seeding occurs when ΔP exceeds the threshold that efficiently maintain the torus or when ΔP is too high causing the displacement of the torus from the sealing position. In angiosperms, air is begun to spread into the water-filled conduit when ΔP causes the capillary failure at pit membranes or when the membranes are ruptured.

2.2.4 Xylem cavitation as a limiting factor for plant survival in the water-limited condition

During water-limited condition or drought event, a reduction in rainfall results in decreases of soil water availability, which are usually coincided with higher temperature and evaporative demand. The combination of these influences induces water stress in plants, which results in a greater tension (more negative) in the xylem network. Water stress in plants can be measured through plant water potential (Ψ), an index that controls water movement from roots to leaves (González & Reigosa Roger, 2001) and becomes markedly low during drought (Farooq et al., 2012). As plants dehydrate, the subsequent decrease in turgor pressure results in stomatal closure, reducing plant desiccation and the declining rate of Ψ. Recent studies reveal that stomata in plants are likely to close despite their negative consequences before reaching a critical plant water potential threshold (Ψ_{crit}), which potentially triggers xylem cavitation in the stem (Li et al., 2018; Martin-StPaul et al., 2017) (Figure 2.9). In a short time scale, the costs associated with stomatal closure include a restriction in

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[9] Taken from Venturas, M. D., Sperry, J. S., & Hacke, U. G. (2017). Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, *59*(6), 356-389.

photosynthesis, reduction in CO_2 uptake, and loss of evaporative cooling from canopy transpiration (Lambers et al., 1998). For a longer time scale, the onset of low photosynthetic rate resulted from stomatal closure initiates the lower availability of stored carbohydrate in all organs (Mitchell et al., 2013) as well as the production of compounds used to defense biotic agents and plant diseases (McDowell et al., 2011). In spite of these consequences, stomatal closure before the incidence of cavitation emphases the significance of plants to avoid xylem cavitation for long-term survival (Rowland et al., 2015).

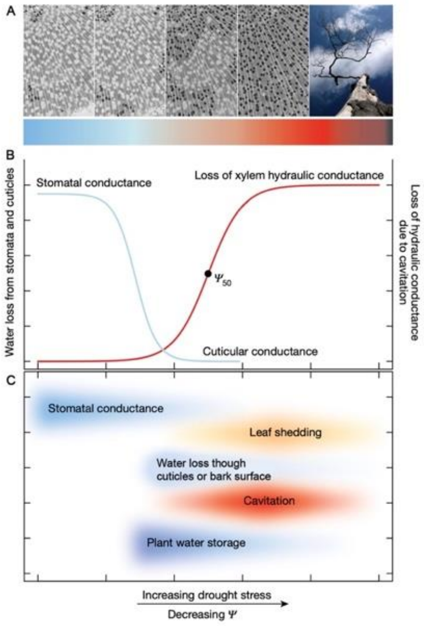

Figure 2.9 Periods of drought stress and general responses of plants[10]
A. Time series of transverse slices of water-conducting tissues showing the spread of cavitation with increasing drought stress (left to right). Vessels filled with water are in bright circles, while dark circles represent cavitated vessels. A severe prolonged drought can lead to hydraulic failure that causes mortality of the whole plant (right).,
B. Changes in water loss though stomata or cuticles (blue line) and xylem hydraulic conductance due to cavitation (red line) with increasing drought stress. Ψ_{50} indicates the plant water potential at which 50% hydraulic conductivity is lost., and
C. Common patterns for the extent and time of plant responses during drought stress.

Once closing the stomata, Ψ continues to drop as water can also be lost through cuticular transpiration (Kerstiens, 1996), or bark surface (Oren & Pataki, 2001). Water loss during these processes are generally low compared to fully opened stomata periods. During this phase, decreases in Ψ are maintained by the release of plant water storage (Borchert & Pockman, 2005). If drought is prolonged, Ψ_{crit} will eventually be reached, and the cavitation will subsequently occur in the xylem. This process can be found throughout the hydraulic pathway from roots to leaves (Brodribb et al., 2016; Choat et al., 2015; Choat et al., 2018) (Figure 2.10). The ability to resist xylem cavitation has

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[10] Adapted from Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., Lopez, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531-539.

emerged as a key trait representing the capacity of plant to tolerate drought and is generally determined as the xylem pressure causing 50% loss of hydraulic conductivity (Choat et al., 2012). Since cavitation reduces the efficiency of xylem to conduct water, this hydraulic impairment can lead to loss of leaves and death of branches (Rood et al., 2000). During intense drought, cavitation can propagate through the xylem network, involving systemic failure of the hydraulic system. In case that drought persists with longer duration and higher intensity, disastrous malfunction of plant water transport system can occur, after which plants may die through desiccation and dehydration (Brodribb & Cochard, 2009; Urli et al., 2013).

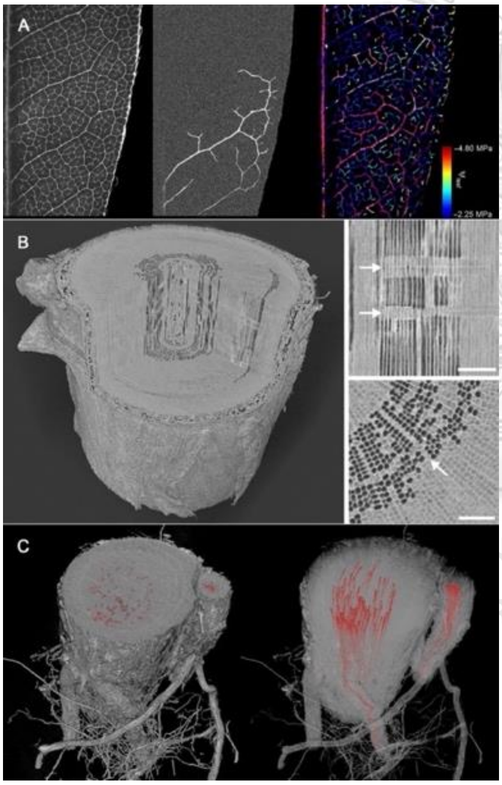

Figure 2.10 Noninvasive imaging techniques showing xylem cavitation through the hydraulic pathway

A. A series of images showing the expansion of cavitation in leaf vein networks with transmitted light[11]. Left, transmitted light images highlighting the majority of the vein network. Middle, a single cavitation event from the midrib into the venation. Right, a color map of all cavitation events recorded during dehydration.,

B. X-ray micro-computed tomography showing three-dimensional, radial longitudinal, and transverse images of xylem tissue of a pine stem[12]. Gas-filled and water-filled tracheids can be seen in black and grey, respectively. White arrows indicate parenchyma cells within the stem and white bars indicate 100 µm scale., and

C. Cavitated xylem vessels in a root system (red) taken from a micro-computed tomograph[13]. Lateral roots during dehydration and the pathway of cavitated vessels are illustrated in left and right, respectively.

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[11] Taken from Brodribb, T. J., Skelton, R. P., McAdam, S. A. M., Bienaime, D., Lucani, C. J., & Marmottant, P. (2016). Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New Phytologist*, *209*(4), 1403-1409.

[12] Taken from Choat, B., Brodersen, C. R., & McElrone, A. J. (2015). Synchrotron X-ray microtomography of xylem embolism in Sequoia sempervirens saplings during cycles of drought and recovery. *New Phytologist*, *205*(3), 1095-1105.

[13] Taken from Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., Lopez, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531-539.

2.3 Measurements on hydraulic thresholds to tree mortality

2.3.1 Measuring plant water status though plant water potential

All living organisms need a constant input of free energy (the energy available to perform work) for maintaining and repairing their structures, as well as for growth and reproduction (Taiz & Zeiger, 2003). Processes such as accumulation of solutes, biochemical reactions, and the ascent of water are all exerted by an input of free energy to the plant. Due to their continuous biochemical activity, plants never reach to the actual equilibrium point (Passioura, 2010). However, they are close enough for describing their water status in term of equilibrium thermodynamics (González & Reigosa Roger, 2001; Taiz & Zeiger, 2003). The chemical potential of water is a measurable index of the free energy related to water. It has the unit of energy per mole of substance (J mol^{-1}). Due to the importance of pressure in plant processes, plant physiologists have chosen to use a related parameter called "water potential", designated by Ψ (the Greek letter 'psi'), that is chemical potential divided by the volume of one mole of water (energy/volume; J m^{-3}). The unit of water potential is expressed in that of pressure, Pascal (Pa), which has the dimensions of force/area. This unit is, therefore, the common unit for water potential.

The idea of water potential is able to be implemented to any sample of water; inside a cell, cell wall, or water-conducting elements, and often represented as an index of the water status in plants. Water potential can be formalized by considering the components contributing to the water potential. The major components include solutes, pressure, and gravity (Boyer & Kramer, 1995; González & Reigosa Roger, 2001; Taiz & Zeiger, 2003);

$$\Psi = \Psi_s + \Psi_p + \Psi_g \qquad \text{Eq 2.1}$$

where Ψ is water potential and the terms Ψ_s, Ψ_p, and Ψ_g signify the effects of solutes, pressure, and gravity, respectively. Each component refers to the same point in the solution, and is additive according to either it increases (positive) or decreases (negative) the Ψ at that point. The state of pure water at ambient pressure and temperature is used for the reference state to determine total Ψ.

Each component affects Ψ in specific ways. The term Ψ_s, solute potential or osmotic potential, characterizes the influence of dissolved solutes on water potential.

Solutes lowers the free energy of water by diluting the water, and thus decreases Ψ. The term Ψ_p represents hydrostatic pressure of the solution. It links to the turgor pressure and expresses as positive hydrostatic pressure within cells. The value of Ψ_p can also be negative in the water-conducting elements or in the walls between cells, in which a tension or negative hydrostatic pressure can proceed. The last term, Ψ_g, is the potential for water movement due to gravity. When dealing with water transport in plants, the Ψ_g component will be ignored because it is insignificant in comparison to Ψ_s and Ψ_p. In this case, Eq 2.1 reduces to:

$$\Psi = \Psi_s + \Psi_p \qquad \text{Eq 2.2}$$

where the combination of Ψ_s and Ψ_p results in negative Ψ because water in plant has Ψ_s that is always negative when compared to pure water at the same state, and is exerted by negative hydrostatic pressure (Ψ_p) due to transpiration.

Given the importance of water for plant survival, the use of simple, reliable, and accurate methods for determining plant water status would be beneficial for determining physiological condition in plants. Generally, two main methods have been performed to quantify Ψ. The first method is thermocouple psychrometry (Boyer & Knipling, 1965; Nonami et al., 1987), which is considered to be one of the most broadly used and versatile approaches for measuring water status in plants. Psychrometer employs the principle that water vapor pressure is reduced when its water potential is decreased. It can be performed to quantify the water vapor pressure of a solution or a piece of plant tissue based on the fact that water evaporation from a surface decreases temperature at the surface. To make a measurement, a plant sample is placed inside a chamber that has a temperature sensor contacting with a small droplet of a known concentration solution (known Ψ) (Figure 2.11). If the sample has lower water potential than the solution, water evaporates from the solution, disperses to the air, and is absorbed by the plant sample. The evaporation occurring here lowers the surface temperature of the solution. On the other hand, if the solution has lower water potential as opposed to the sample, water diffuses from the sample to the solution, leading to warmer temperature of the solution. Repeating the measurement with several solutions of known Ψ until the water movement between the solution and the plant sample becomes zero (no temperature changes) will eventually indicate the Ψ of the sample, in which is similar to that of the solution. Despite its popularity and versatility for measuring plant water status, psychrometer requires a good deal of care while applying. A main difficulty of this technique is the sensitivity to temperature variations. Making a measurement with psychrometer is, thus, possible only in laboratory with constant temperature conditions.

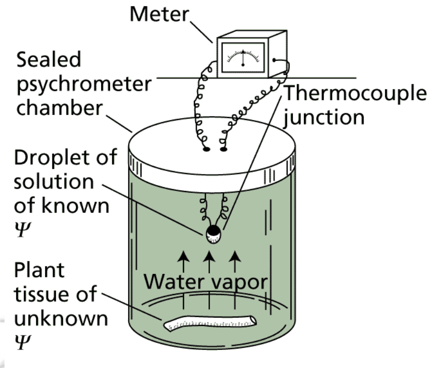

Figure 2.11 The use of thermocouple psychrometer to measure the water potential of a plant tissue[14]

The second method is by the use of pressure chamber (Boyer & Kramer, 1995; Turner, 1988). It is considered to be a relatively rapid and sturdy method for measuring the water potential of plant samples (i.e., leaves, shoots, branches etc.). Before the measurement, a plant sample is cut from the plant and partially put in a pressure chamber (Figure 2.12). Due to the transpiration process, the continuous water stream in the xylem is under tension (negative hydrostatic pressure) before cutting (Figure 2.12A). When the stream is disconnected (by cutting), water in the xylem recedes into the adjacent cells, causing the cut surface to be dry (Figure 2.12B). By applying pressure in the chamber with compressed gas (usually nitrogen), water is forced to return to its initial state and eventually appears at the cut surface when the applied pressure fully counters the tension when the sample is still intact (Figure 2.12C). The pressure needed to force the water back to its original state is called the balance pressure. Though measuring by this technique is often referred to the tension in the xylem (Ψ_p), fortunately Ψ_s of the xylem is usually insignificant compared to typical midday tensions ($\Psi_s \sim -0.1$ MPa while $\Psi_p \sim -1$ to -2 MPa). In addition to its speed and

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[14] Taken from Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany*, *91*.

simplicity of operation, pressure chamber has been widely used under field conditions for measuring total water potential of plant samples.

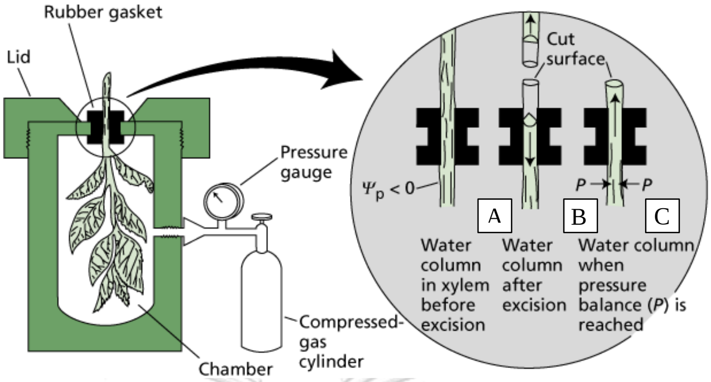

Figure 2.12 Measuring plant water potential by pressure chamber[15]

A. The xylem is uncut and under tension. B. The xylem is cut, resulting in a receding of water away from the cut surface resulted from the tension in the xylem., and C. The chamber is pressurized, forcing the water to be back to the cut surface.

2.3.2 Defining the risk of hydraulic failure in plants by assessing their xylem vulnerability

Over the past decades, scientists have dedicated a huge amount of work to develop accurate and reliable methods to measure xylem vulnerability in plants. By constructing curves showing the risk of hydraulic failure in plants, the vulnerability curves can be generated as the percentage loss of xylem water conductivity (y axis) at given xylem pressures (x axis). The techniques for measuring xylem vulnerability are various and diverse, mainly in how cavitation is detected or induced (Cochard et al., 2013). There are three main techniques extensively used to induce cavitation to the plant sample: bench dehydration, air injection, and centrifugation.

Bench dehydration (Sperry et al., 1988): This technique is considered to be the most straightforward technique to induce cavitation to plant samples. Bench dehydration involves evaluating cavitation after an excised branch with multiple branched sections is dehydrated freely and naturally to different xylem pressures (P_x). The P_x is measured periodically from leaves attached to the segment with a pressure chamber or psychrometer. When a targeted P_x is reached, conductance of a segment is measured. Then, the segment is flushed with water to displace cavitated xylem vessels,

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[15] Taken from Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany*, *91*..

and measured the conductance again for the maximum water conductivity of the segment. This offers a value for the percentage loss of hydraulic conductivity with a target P_x. Excessive samples and time are required to complete the xylem vulnerability curve. However, this method best simulates actual water stress and is often performed as a reference technique to validate the others (Martin-StPaul et al., 2014).

Air injection (Sperry & Saliendra, 1994): According to the air seeding mechanism, an air bubble is pulled from a cavitated cell to the next water-filled one when the pressure difference (P_{air} - P_x) exceeds a critical value (Figure 2.8). Therefore, increasing or decreasing either P_{air} or P_x would induce cavitation to the sample if the difference is large enough to reach the threshold. In other words, decreasing P_x by dehydration under normal atmospheric pressure (P_{air} = 0) or increasing P_{air} while maintaining P_x close to zero would have the similar effect on cavitation induction. In general, cavitation is induced by pushing air pressure into a xylem segment inside a specially designed chamber, after which the conductance is simultaneously measured and calculated. Unlike bench dehydration, air injection technique can be applied to various plant organs, including small stems, branches, twigs, and roots. Moreover, this technique enables the completion of xylem vulnerability curve on only one sample, since several pressures can be applied on the same sample with great accuracy of pressure control and less time is required (Cochard et al., 2013).

Centrifugation (Pockman et al., 1995): The centrifugal force has been used by physicists to introduce water to negative pressures (Briggs, 1950), until Pockman et al. (1995) employed this technique to induce cavitation in plant samples. The principle of centrifugation technique is to generate negative xylem pressures in the middle part of sample during rotation due to the centrifugal force. It takes only a few minutes to induce cavitation in xylem before the determination of percentage loss of conductivity is made. The centrifugation has several advantages similar to air injection, such as less time consuming and plant samples. However, centrifugation can only be applied to the plant samples with specific size (to be able to put them in the centrifuge rotor) and poses to some potential artifacts (Cochard et al., 2010; Li et al., 2008).

2.4 Gap knowledge on tree hydraulic study

Study on plant hydraulics is still a relatively new aspect in science, and the challenges facing the understanding of its essential role in water stress-induced mortality remain numerous (McDowell et al., 2019). The first challenge is dealing with the observation suggesting that all forest ecosystems is equally susceptible to malfunction of hydraulic system resulted from anthropogenic climate change, even in the habitats that are not considered water deficit (Choat et al., 2012). Unfortunately, current studies of forest responses and mortality risk are insufficient to determine if one forest ecosystem is emerging in part due to the lack of a reliable, up-to-date, and consistent assessment. Particularly in Thailand, there have been lower than 10 publications relevant to this subject from 1990 to 2021 (the result from searching using keywords that include ‘forest’, ‘vulnerability’, ‘water stress’, and ‘Southeast Asia’ in the article from Google Scholar, ScienceDirect, and Web of Science). The next challenge arises the need to determine the role of regeneration dynamics to changes in plant vulnerability to water stress. This will improve the knowledge of vegetation shifts and the ecosystem-level implications in a landscape that comprises of forest fragments at different successional stages (Martinez-Vilalta & Lloret, 2016). Since many forest ecosystems are dictated by how water stress interacts with plant functions, only knowledge armed with detailed understandings in plant hydraulics will enable us to confidently interpret and predict plant responses during low water availability conditions.

2.5 Literature review

Rowland et al. (2015) tested either carbon starvation or dysfunction of water transport pathways in plants trigger tree mortality by synthesizing data from the world’s longest experimental drought study in tropical forest–the Brazilian Amazon. The study site was located in the Caxiuana National Forest in the eastern Amazon, where a drought experiment plot (throughfall exclusion–TFE), and a corresponding control plot were implemented since 2002. The data used in this study included non-structural carbohydrate (NSC) concentration measured by enzymatic method and xylem vulnerability measured by air injection technique. The results showed that, NSC concentrations were not significantly depleted in stem, leaf, and branch tissues, as well as the growth rate of trees in TFE plot compared to control plot. However, decadalscale soil moisture depletion increased biomass loss of trees in the experimentally droughted plot. Moreover, highly significant decreases in xylem vulnerability with diameter at breast height (DBH) across TFE and control plots were found, suggesting a greater risk of hydraulic dysfunction in large trees than the smaller ones. Based on the results from this study, tree mortality is, thus, most likely triggered by hydraulic deterioration, which subsequently results in the limitations of carbon uptake, or also known as carbon starvation.

Powell et al. (2017) investigated how variation in plant hydraulic traits, including leaf water potential (Ψ) and xylem vulnerability, associate with drought tolerance and tropical trees growing in two large-scale ecosystem drought experiment (throughfall exclusion)–the Caxiuana (CAX) and Tapajos (TNF) National Forests–in the Brazilian Amazon. The tropical trees selected for this study were placed into one of the four categories: drought-intolerant and drought-tolerant species (based on mortality rates observed in previous drought experiments), and into early- and late-successional stage (based on wood density). Dawn and midday Ψ were measured using pressure chamber method in control and drought-treated plots. Air injection technique was used to measure xylem vulnerability. The results showed that, from most of the studied tree species, dawn Ψ were near zero in both control and drought-treated plots, whereas midday Ψ was observed to be significantly reduced in the drought plots. Moreover, the drought-intolerant species were more prone to xylem cavitation compared to that in drought-tolerant species. However, no significant difference in xylem vulnerability between the two successions was found. This demonstrates that the association of hydraulic traits and mortality is not related to wood density. In summary, the differences in plant hydraulic trait found among tropical tree species in this study could be crucial in defining the risk of the Amazon rainforest to changes in rainfall pattern under future climate.

Barros et al. (2019) assessed how different precipitation patterns in Amazon forests would result in community-scale differences in hydraulic traits and in species responses to severe drought. To pursue this objective, hydraulic traits of dominant tree species in two forests with different precipitation regimes, low seasonality forest (LSF) and high seasonality forest (HSF), were studied during a typical dry season and during one induced by the El Niño-Southern Oscillation (ENSO). Xylem vulnerability at 50% and 88% loss of conductivity (P_{50} and P_{88}) measured by bench dehydration method and minimum leaf water potential (Ψ_{min}) measured by pressure chamber technique were included as part of the studied hydraulic traits. Canopy conductance (G_s) using eddy covariance technique was also measured to elucidate the ecosystem-level behavior of the two forests. The results showed that, Ψ_{min} was significantly lower during the ENSO period at both sites with marginal impacts. In addition, LSF had less resistance to cavitation than HSF due to higher P_{88} and P_{50}, although both forests sustained the same canopy conductance. These results indicated that higher drought-tolerant ability in HSF compensated for the drier soil and allowed it to maintain similar G_s to a drier atmosphere compared to LSF, even though their water transport systems operated at different water potential ranges. Overall, the difference in precipitation patterns could lead to different constructions of hydraulic traits and vegetation composition at community level, which potentially plays an important role in forecasting forest responses to future climate variability.

Bittencourt et al. (2020) determined whether hydraulic traits of Amazon rainforest trees could acclimate to long-term (>15 years) drought experiment. Plant hydraulic traits and hydraulic status were measured to assess the plasticity (adjusting in hydraulic traits) and acclimation (maintaining of hydraulic status) of tropical trees affected by a drought experiment (throughfall exclusion–TFE). The study site was located in the Caxiuana National Forest, Brazil, where a TFE experiment was begun since 2002. The measurements of hydraulic traits and status included xylem water potential at which 50% and 88% hydraulic conductivity are lost (P_{50} and P_{88}) by using bench dehydration method, and midday leaf water potentials (Ψ_{md}) by using pressure chamber method. The results showed that, significantly lower Ψ_{md} was observed in the TFE plot as opposed to the control plot. Moreover, no plasticity was observed as key hydraulic traits (P_{50} and P_{88}) did not change in response to the drought experiment. These results revealed that tropical trees could not adjust their hydraulic systems to prolonged drought for the purpose of maintaining the hydraulic status compared to non-droughted tress, and therefore avoid hydraulic failure in their water transport systems. This study, thus, suggests that Amazon rainforest trees have limited capacity to acclimate to long-term drought, and also provides new understandings on how Amazonian trees may respond to future climate variability.

Nolf et al. (2015) studied the association of stem and leaf hydraulic properties in tropical tree species found in the Daintree Rainforest Observatory, Queensland, Australia. Measurements of hydraulic properties including vulnerability to cavitation in stems (using bench dehydration technique) and leaves (using leaf rehydration and bench dehydration techniques) were performed, together with predawn and midday water potentials (using pressure chamber technique) in leaves (Ψ_{leaf}) and stems (Ψ_{stem}). The results showed that, predawn Ψ_{leaf} and Ψ_{stem} in all studied trees were similar, ranging from -0.3 to -0.5 MPa. The difference between leaf and stem water potentials were more distinct during midday, in which Ψ_{leaf} dropped to its minimum of -1.2 to -1.6 MPa while Ψ_{stem} sustained between -0.7 to -1.0 MPa. The percentage loss of hydraulic conductivity at 50% (P_{50}) was at -1.7 to -2.2 MPa in leaves and at -2.1 to -3.1 MPa in stems. These results implied that trees in this region maintained water potential at the levels that avoid cavitation in the stems, while operated with close to those causing loss of water transport efficiency in leaves. The strategy of sacrificing leaves in favor of stems, therefore, revealed the association of stem and leaf hydraulic traits in this tropical rain forest.

Trueba et al. (2017) examined the relationships between 50% loss of xylem conductivity (P_{50}) along with conduit types (vessel vs tracheid), stem and leaf functional traits, and habitat variables from common tree species found in New Caledonia. Xylem vulnerability was assessed using a centrifugation-based technique called ‘Caviton’. In this study, functional traits comprised of wood density, leaf mass per area (LMA), and leaf vein density (VD). Percentage of species occurrences, elevation, mean annual temperature (MAT), and mean annual precipitation (MAP) were used as habitat parameters. The results showed that, P_{50} from selected tree species ranged between -2.00 to -4.03 MPa, with most species had P_{50} around -2.7 MPa. Weak association between P_{50} and the measured functional traits was found in this study, as well as insignificant differences in cavitation resistance between conduit types. Nevertheless, elevation, MAT, and percentage of species occurrences was significantly associated with P_{50}, becoming an index that closely relates to the ecological differentiation. On the whole, these findings highlight the significant of xylem resistance as a major driver of rain forest species distribution.

Chen et al. (2017) determined how tropical lianas combat hot and windy conditions on the top of forest canopy. The study site was located in Xishuangbanna tropical botanical garden, China. Stem hydraulic properties, leaf and stem water potentials (Ψ_{leaf} and Ψ_{stem}), stem specific conductivity (K_{smax}), sap flux density and other key physiological parameters were investigated in tropical lianas, as well as those in co-occurring trees for the comparison. Water potential at 50% loss of conductivity (P_{50}) and native percentage loss of conductivity at midday (midday PLC) were measured using bench dehydration and air-injection techniques. Ψ_{leaf} and Ψ_{stem} were measured using pressure chamber method. K_{smax} and sap flux density were examined using the conductivity measurement following Sperry et al. (1988) and thermal dissipation sensors following Granier (1987), respectively. The results showed that, lianas maintained higher midday Ψ_{stem} than trees, but midday Ψ_{leaf} in lianas and trees were comparable. Lianas also had higher K_{smax} and sap flux density than the coexisting trees. Moreover, P_{50} and midday PLC in lianas were found to be higher than trees in this studied site. Altogether, these results indicate that lianas seem to be less resistant to drought-induced cavitation, as shown by higher P_{50} and midday PLC values. Nevertheless, greater water transport efficiency (higher K_{smax} and sap flow) might facilitate lianas to sustain Ψ_{stem} within a safe level to prevent xylem cavitation and thrive in the tropical forest canopy.

Zhu et al. (2017) studied how different in soil water availability would affect the species composition and forest structure through plant hydraulic traits in tropical karst forest (KF) and non-karst rainforest (NKF). These two forest types were located adjacent to the Xishuangbanna tropical botanical garden, China. In this study, hydraulic conductivity (K_s) following Sperry et al. (1988), vulnerability to cavitation (P_{50}) using air injection method, and wood anatomy including sapwood density (WD) and vessel diameter (D_H) were determined in 23 abundant woody tree and liana species from KF and NKF. The results shown that, higher WD, smaller D_H, lower K_s, and lower P_{50} values were observed from woody plant species in KF, where water availability was more limited. Moreover, P_{50} was found to be positively linked with K_s and D_H, but negatively related with WD from all the woody species in KF and NKF, indicating an important trade-off between hydraulic efficiency and safety. To sum up, these results revealed a better hydraulic adaptation of woody plant species in KF to water-limited environment, as well as the hydraulic trade-off which might be a crucial mechanism determining species distribution across the two forests.

Zhu et al. (2018) investigated the association among tree survival with hydraulic efficiency and drought tolerance of 16 woody species from a plantation with mixed native tree species in a damaged hilly area. The study site was conducted in the Heshan Hilly Land Interdisciplinary Experimental Station, South China. Hydraulic traits measured in this study included sapwood density (WD), hydraulic conductivity (K_s), cavitation resistance (P_{50}), minimum stem water potential (Ψ_{min}), hydraulic safety margin (HSM; $\Psi_{min} – P_{50}$), and leaf turgor loss point (π_{tlp}). Air injection method was performed to examine P_{50} from the selected tree species. The results shown that, a broad range of tree survival was observed among the 16 native tree species, ranging from 1% to 96%. Across species, tree survival was significantly related with drought tolerance traits, including π_{tlp}, P_{50}, Ψ_{min}, and HSM. The species with high survival rate appeared to possess low π_{tlp} and P_{50}, and high Ψ_{min} and HSM. However, the relationships between tree survival and the other hydraulic traits, WD and K_s, were not observed, indicating unsuitable predictors for tree survival in this study. Given these points, drought tolerance traits are recommended as useful index for selecting tree species suitable for the restoration projects.

Tan et al. (2020) conducted a study of hydraulic strategies of plant species during normal and extreme drought periods through hydraulic safety margins (HSM). This study was conducted in three plant groups; evergreen trees, brevi-deciduous trees, and lianas, found in a tropical karst forest in Xishuangbanna tropical botanical garden, China. Minimum leaf water potential was measured by pressure chamber technique. Leaf and branch hydraulic conductivities were determined using rehydration kinetics

(Brodribb and Holbrook, 2003) and bench dehydration, respectively. HSM were represented as differences in (1) minimum leaf water potential and that at 50% loss of leaf hydraulic conductivity (HSM_{leaf}), (2) the water potentials at stomatal closure and that at 50% loss of branch hydraulic conductivity (stomatal safety margin; $HSM_{stomatal}$), and (3) water potentials at 50% loss of leaf hydraulic conductivity and that at 50% loss of branch hydraulic conductivity ($HSM_{segmentation}$). The results shown that, similar and positive HSM_{leaf} was observed from the three plant assemblies in the typical dry season. In the extreme dry season, however, HSM_{leaf} of evergreen trees decreased to a more negative value compared to the other groups. This suggests that evergreen trees are less resistent to hydraulic dysfunction during drought event, while brevi-deciduous trees and lianas are able to sustain HSM_{leaf} within a safe range in both typical and extreme dry seasons. Moreover, significant correlations among $HSM_{segmentation}$ with $HSM_{stomatal}$ and $HSM_{leaf\_extreme}$ (HSM_{leaf} in extreme dry season) were observed across species, showing that species with smaller $HSM_{segmentation}$ tend to have lower $HSM_{stomatal}$ but higher $HSM_{leaf\_ extreme}$. To summarize, this study reveals a possibility of karst evergreen species to undergo leaf hydraulic dysfunction when severe drought occurs, and potential associations between branch and leaf hydraulic safety adjustments.

Table 2.2 Summary of hydraulic traits from woody species in tropical forests reviewed in this proposal. Mean values (± SD if available) are presented. The abbreviations are MVL (cm), maximum vessel length; K_s (kg m^{-1} s^{-1} MPa^{-1}), sapwood specific hydraulic conductivity; P_{50} (MPa), xylem tension at 50% loss of hydraulic conductivity; and Ψ (MPa), leaf water potential. NA indicates not available data.

Region	Reference	Location	Condition	Species	MVL	K_s	P_{50}	Ψ	
Neotropics	Rowland et al. (2015)	Caxiuana National Forest, State of Pará, Brazil. (1° 43′ S, 51° 27′ W)	Control	*Eschweilera grandiflora*	NA	NA	-0.8 ± 0.28	NA	
				Eschweilera coracea			-1		
				Eschweilera pedicellata			-2.5		
				Licania membranacea			-4.5 ± 3.2		
				Licania octandra			-3.3		
				Pouteria anomala			-1.67 ± 0.46		
				Protium tenuifolium			-2.37 ± 0.55		
				Swartzia racemose			-1.53 ± 0.21		
				Inga alba			-1.65 ± 0.35		
			Through-fall exclusion (drought-treated experiment)	*Eschweilera grandiflora*	NA	NA	-2.2 ± 0.71	NA	
				Eschweilera coracea			-1.53 ± 1.30		
				Licania membranacea			-4.2 ± 0.46		
				Pouteria anomala			-0.87 ± 0.57		
				Protium tenuifolium			-1.85 ± 0.92		
				Protium paniculatum			-2		
				Swartzia racemose			-1.77 ± 0.42		
				Inga alba			-1.45 ± 0.35		
	Powell et al. (2017)	Caxiuana National Forests, State of Pará, Brazil. (1.737°S, 51.458°W)	P_{50} was estimated during throughfall exclusion experiment (TFE). Midday Ψ was measured in control (left in Ψ column) and TFE (right in Ψ column) experiments.	*Inga alba*	NA	NA	-1.4	-0.38	-0.44
				Eschweilera coriacea			-1.2	-0.74	-1.95
				Protium tenuifolium			-2.3	-1.42	-1.91
				Licania octandra			-2.2	-0.14	-0.35
		Tapajos National Forests, State of Pará, Brazil. (2.897°S, 54.952°W)	P_{50} was estimated during throughfall exclusion experiment (TFE).	*Inga alba*	NA	NA	-1.1	NA	
				Eschweilera coriacea			-2.0		
				Protium tenuifolium			-1.8		
				Licania octandra			-1.6		
	Barros et al. (2019)	Low seasonality forest (LSF): Cuieras Biological Reserve,	P_{50} was done once throughout the study.	*Caryocar glabrum*	NA	NA	-1.78	-0.71	-1.1
				Dypterix odorata			-4.47	-0.95	-2.61
				Eschweilera coriaceae			-1.57	-1.41	-1.54

Region	Reference	Location	Condition	Species	MVL	K_s	P_{50}	Ψ	
		Manaus, Amazonas, Brazil (60°210 W, 2°610 S)	Minimum Ψ was measured during the peak of the dry season of non-ENSO (left in Ψ column) and ENSO (right in Ψ column) years.	*Eschweilera cyathiformis*			-3.05	-0.8	-2.89
				Eschweilera sp.			-2.47	-1.71	-2.54
				Eschweilera wachenheimii			-2.19	-1.51	-1.59
				Goupia glabra			-2.2	-0.57	-1.14
				Gustavia elliptica			-2.75	-1.43	-1.63
				Lecyths prancei			-1.8	-2.09	-1.93
				Maquira sclerophylla			-2.21	-1.07	-1.72
				Minquartia guianensis			-2.16	-1.28	-1.8
				Ocotea sp.			-1.84	-0.91	-2.16
				Pouteria anomala			-1.01	-0.9	-1.35
				Pouteria erythrochrysa			-3.92	-0.88	-1.43
				Protium hebetatum			-1.49	-0.71	-1.16
				Scleronema micranthum			-1.77	-1.16	-1.13
				Zygia racemosa			-3.02	-0.49	-1.16
		Higher seasonality forest (HSF): Tapajos National Forest, Santarem, Para, Brazil (54°580 W, 2°510 S)		*Amphyrrhox longifolia*	NA	NA	-2.28	-2.12	-1.93
				Chamaecrista xinguensis			-3.14	-2.68	-2.58
				Coussarea albescens			-4.86	-2.25	-3.21
				Endopleura uchi			-1.52	-1.1	-1.62
				Erisma unsinatum			-2.12	-1.22	-1.06
				Manilkara huberi			-1.75	NA	NA
				Mezilaurus itauba			-2.98	-1.64	-1.98
				Miconia lepidota			-5.02	-1.06	-3.01
				Minquartia guianensis			-2.37	NA	NA
				Protium apiculatum			-1.94	-1.38	-1.29
				Rinourea passourea			-2.99	-2.58	-4.43
				Tachigali chrysophylla			-3.79	NA	NA
	Bittencourt et al. (2020)	Caxiuana National Forest, State of Pará, Brazil. (1° 43′ S, 51° 27′ W)	Control	*Aspidosperma* sp.	NA	3.3 ± 3.3	−1.9 ± 0.38	−2.2 ± 0.74	
				Eschweilera sp.		4.1 ± 2.4	−2.3 ± 1.1	−1.7 ± 0.39	
				Inga sp.		6.7 ± 1.9	−2.6 ± 0.98	−1.9 ± 0.37	
				Licania sp.		0.86 ± 0.51	−2 ± 0.73	−1.3 ± 0.27	
				Micropholis sp.		3.6 ± 0.41	−1.2 ± 0.63	−2.4 ± 0.88	
				Minquartia sp.		2.5 ± 0.88	−2 ± 0.89	−1.5 ± 0.21	
				Pouteria sp.		2.9 ± 1.2	−2.2 ± 1.2	−2.2 ± 0.48	
				Protium sp.		3.4 ± 1.7	−2.3 ± 0.72	−1.5 ± 0.44	
				Swartzia sp.		5.2 ± 3.1	−3.1 ± 1.6	−2.1 ± 0.52	
				Syzygiopsis sp.		2.8 ± 0.87	−1.4 ± 0.75	−1.8 ± 0.19	
				Virola sp.		NA	−1.9 ± 1.4	−2.4 ± 0.21	

Region	Reference	Location	Condition	Species	MVL	K_s	P_{50}		Ψ	
				Vouacapoua sp.		2.4 ± 2.2	−3 ± 0.59		−2.1 ± 0.73	
			Through-fall exclusion (drought-treated experiment)	*Aspidosperma* sp.	NA	0.97 ± 0.97	−3.1 ± NA		−1.9 ± 0.67	
				Eschweilera sp.		5.1 ± 1.9	−2.6 ± 1.1		−2.1 ± 0.45	
				Inga sp.		6.8 ± 3.3	−2.3 ± 1.2		−2 ± 0.2	
				Licania sp.		0.81 ± 0.85	−3.2 ± 0.51		−1.1 ± 0.29	
				Micropholis sp.		4.4 ± 1.3	−1.1 ± NA		−2.2 ± 0.46	
				Minquartia sp.		2.5 ± 1.4	−1.3 ± 0.87		−1.4 ± 0.27	
				Pouteria sp.		2.3 ±0.74	−1.4 ± 0.49		−2.7 ± 0.82	
				Protium sp.		4.3 ± 1.7	−2.7 ± 0.78		−1.7 ± 0.67	
				Swartzia sp.		3.1 ± 1.6	−3.1 ± 1.1		−2.2 ± 0.41	
				Syzygiopsis sp.		2.8 ± 0.69	−1.5 ± 0.74		−2.7 ± 0.72	
				Virola sp.		NA	−1.6 ± 0.85		−2.5 ± 0.53	
				Vouacapoua sp.		3.5 ± 2.5	−2.6 ± 1.6		−2.8 ± 0.79	
Australasian	Nolf et al. (2015)	Daintree Rainforest Observatory Research Facility, Cape Tribulation, Queensland, Australia (S 16.104°, E 145.449°)	P_{50} was estimated in stems (left in P_{50} column) and leaves (right in P_{50} column). Midday Ψ was measured in stems (left in Ψ column) and leaves (right in Ψ column).	*Dysoxylum papuanum*	NA	NA	-2.63	-2.24	-1.01	-1.56
				Elaeocarpus grandis			-3.06	-1.66	-0.83	-1.62
				Syzygium sayeri			-2.10	-1.72	-0.75	-1.23
	Trueba et al. (2017)	New Caledonia, the north of the Tropic of Capricorn in the southwest Pacific Ocean	-	*Amborella trichopoda*	NA	NA	-2.7 ± 0.19		NA	
				Ascarina rubricaulis			-2.2 ± 0.26			
				Cryptocarya aristata			-2.0 ± 0.22			
				Hedycarya cupulata			-3.2 ± 0.23			
				Hedycarya parvifolia			-3.1 ± 0.09			
				Kibaropsis caledonica			-2.4 ± 0.21			
				Nemuaron viellardii			-2.3 ± 0.16			
				Paracryphia alticola			-2.1 ± 0.35			
				Quintinia major			-2.5 ± 0.34			
				Zygogynum acsmithii			-2.7 ± 0.10			
				Zygogynum crassifolium			-4.0 ± 0.26			
				Zygogynum stipitatum			-2.4 ± 0.26			
				Zygogynum thieghemii			-2.2 ± 0.28			
Indomalayan	Chen et al. (2017)	Xishuangbanna Tropical Botanical	Lianas	*Celastrus paniculatus*	301	8.62	-1.42		NA	
				Marsdenia sinensis	235	10.57	-1.04			
				Ventilago calyculata	110	4.8	-1.57			

Region	Reference	Location	Condition	Species	MVL	K_s	P_{50}	Ψ
		Garden, Yunnan Province, China. (21°540N, 101°460E)		*Mucuna interrupta*	NA	NA	NA	
			Trees	*Celtis tetrandra*	120	6.21	-1.53	-
				Ficus concinna	61	3.95	-1.43	
				Harpullia cupanioides	192	2.2	-2.51	
				Michelia hypolampra	74	1.69	-2.25	
				Streblus asper	72	1.86	-2.93	
	Zhu et al. (2017)	Xishuangbanna Tropical Botanical Garden, Yunnan Province, China. (21°540N, 101°460E	Data collected in tropical karst forest	*Bauhinia purpurea*	NA	11.79	-1.3	NA
				Bauhinia variegate		10.58	-1.2	
				Bischofia javanica		7.89	-1.2	
				Castanopsis indica		4.45	-1.3	
				Lagerstroemia tomentosa		7.74	-1.4	
				Millettia cubitti		7.73	-1.1	
				Millettia leptobotrya		4.61	-1.6	
				Syzygium cumini		6.15	-1.2	
				Syzygium latilimbum		4.57	-2.0	
				Syzygium szemaoense		8.06	-1.3	
				Millettia pachycarpa		11.51	-1.1	
				Uncaria macrophylla		12.38	-1.0	
				Byttneria integrifolia		10.57	-0.9	
			Data collected in non-karst rain forest	*Alphonsea monogyna*	NA	3.47	-1.9	NA
				Celtis philippensis		3.45	-2.1	
				Cipadessa baccifera		3.89	-2.3	
				Cleistanthus sumatranus		1.57	-3.4	
				Croton crassifolius		4.07	-1.6	
				Lasiococca comberi		2.12	-2.0	
				Pistacia weinmannifolia		2.01	-4.1	
				Turpinia pomifera		2.73	-2.2	
				Combretum latifolium		4.52	-1.5	
				Ventilago calyculata		5.14	-1.3	
	Zhu et al. (2018)	Heshan Hilly Land Interdisciplinary Experimental Station, Guangdong Province, China. (22 °34’N, 112 °50’E)	-	*Bischofia javanica*	NA	1.54	-1.19	-1.38
				Cinnamomum burmannii		1.96	-3.85	-1.10
				Cinnamomum camphora		4.78	-3.77	-0.96
				Castanopsis hystrix		7.45	-1.46	-1.12
				Elaeocarpus apiculatus		2.17	-2.02	-1.34
				Garcinia oblongifolia		1.52	-1.42	-1.57
				Litsea cubeba		4.19	-1.40	-1.56

Region	Reference	Location	Condition	Species	MVL	K_s	P_{50}		Ψ	
				Liquidambar formosana		3.32	-2.66		-1.35	
				Machilus chinensis		1.16	-3.14		-1.29	
				Manglietia glauca		6.09	-2.53		-1.31	
				Michelia macclurei		1.32	-3.54		-1.16	
				Michelia maudiae		1.45	-3.50		-1.23	
				Syzygium hainanense		5.15	-1.30		-1.08	
				Schima superba		3.11	-4.19		-0.80	
				Trema cannabina		4.13	-1.24		-1.44	
				Tsoongiodendron odorum		1.50	-3.04		-1.27	
	Tan et al. (2020)	Tropical karst forest in Xishuangbanna Tropical Botanical Garden, Yunnan Province, China. (21°540N, 101°460E)	P_{50} was estimated in branches (left in P_{50} column) and leaves (right in P_{50} column). Minimum Ψ was measured in normal dry season (left in Ψ column) and extreme dry season (right in Ψ column).	Evergreen						
				Alphonsea monogyna	NA	NA	-2.76	-2.68	-0.98	-2.43
				Celtis philippensis			-2.69	-2.30	-1.58	-4.36
				Cleidion bracteosum			-2.55	-2.49	-1.45	-2.13
				Cleistanthus sumatranus			-3.23	-2.43	-1.73	-6.55
				Pistacia weinmannifolia			-4.12	-3.65	-2.41	-4.98
				Lasiococca comberi			-2.23	-3.14	-1.75	-5.55
				Turpinia pomifera			-1.96	-2.78	-1.02	-2.29
				Brevi-deciduous						
				Cipadessa baccifera			-2.23	-2.67	-1.43	-1.46
				Croton crassifolius			-1.44	-1.87	-1.69	-2.68
				Ficus pisocarpa			-0.80	-2.20	-1.34	-1.10
				Lagerstroemia tomentosa			-1.24	-1.96	-1.35	-2.66
				Mayodendron igneum			-2.40	-2.30	-1.80	-1.99
				Liana						
				Bauhinia touranensis			-2.06	-2.26	-0.90	-2.22
				Combretum latifolium			-1.17	-1.96	-1.33	-2.22
				Gnetum montanum			-1.30	-2.14	-0.60	-0.65
				Ventilago calyculata			-1.27	-2.47	-1.60	-2.95

CHAPTER 3
METHODOLOGY

3.1 Study site description

The study site was done in different forest successional stages located in Khao Yai National Park, Thailand (14º26′31″ N, 101º22′55″ E, Figure. 3.1). The average elevation ranges 700–800 meters above sea level. 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 the data during 1994 to 2014, the overall mean annual temperature was 22.4 °C, with monthly temperature ranging from 19.4 °C in December to 24.3 °C in April. The mean annual rainfall is 2,073 mm. Khao Yai National Park comprises the mosaic fragments in different forest successional stages, ranging from old-growth forests to different ages of secondary forests that naturally regenerated from either natural disturbance (i.e., fires or fallen trees) or anthropogenic impacts (i.e., deforestation or land conversion). In this study, three forest stands representing different forest successional stages including an old-growth forest (OF), an intermediate forest (IF) and a young forest (YF) were selected for the study sites. The study plot for OF is in the 30-ha Mo Singto forest dynamics plot (Figure 3.2A), one of the ForestGEO plots of the Centre for Tropical Forest Science (CTFS) network, with the age over 200 years (Brockelman et al., 2017). The IF plot is located in the northern side of OF (Figure 3.2B). This plot has an area of 1 hectare and is about 45 years old (Chanthorn et al., 2017). The last study plot, representing young forest stage (YF, Figure 3.2C), is located approximately 3 km away in the southeastern of OF with the area of 2 ha and the age of ~5 years (Chanthorn et al., 2017). More information of each plot is presented in Table 3.1.

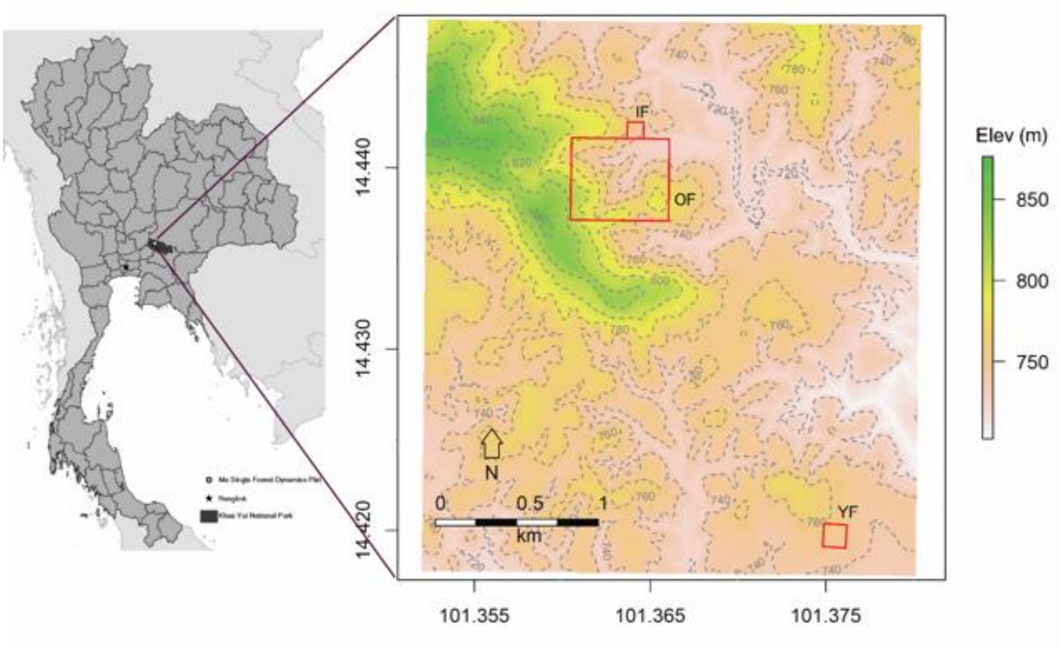

Figure 3.1 Locations of old-growth forest (OF), intermediate forest (IF), and young forest (YF) in Khao Yai National Park[16]

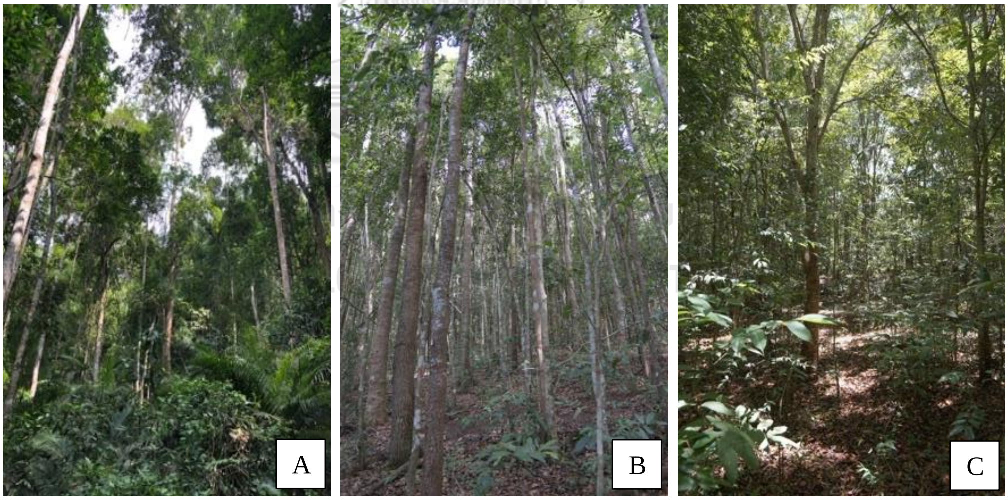

Figure 3.2 The study sites in Khao Yai National Park
A. Old-growth forest (OF), **B.** Intermediate forest (IF), and **C.** Young forest (YF)

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[16] Taken from Tor-ngern, P., Chart-asa, C., Chanthorn, W., Rodtassana, C., Yampum, S., Unawong, W., Nathalang, A., Brockelman, W., Srinoppawan, K., Chen, Y. J., & Hasselquist, N. J. (2021). Variation of leaf-level gas exchange rates and leaf functional traits of dominant trees across three successional stages in a Southeast Asian tropical forest. *Forest Ecology and Management*, *489*.

Table 3.1 Information of the study sites in Khao Yai National Park

Variables	**Old-growth forest (OF)**	**Intermediate forest (IF)**	**Young forest (YF)**
Geographical location	14°26'31.33"N 101°21'52.10"E	14°26'31.33"N 101°21'52.10"E	14°25'11.27"N 101°22'30"E
Age	>200	40–50	5
Altitude (m)	725	753	748
MAT (°C)	22.4	22.4	22.4
MAP (mm)	2,073	2,073	2,073
Soil type	Gray-Brown soil	Gray-Brown soil	Gray-Brown soil
Dominant species	*Dipterocarpus gracilis,* *Sloanea sigun,* *Ilex chevalieri,* *Symplocos cochinchinensis,* *Schima wallichii*	*Schima wallichii,* *Machilus gamblei,* *Eurya acuminate,* *Symplocos cochinchinensis,* *Syzygium nervosum*	*Cratoxylum cochinchinense,* *Syzygium antisepticum,* *Adinandra integerrima,* *Syzygium nervosum,* *Symplocos cochinchinensis*
Average canopy height (m)	45	25	15
Leaf area index	5	6	Not available

3.2 Species selection

The dominant tree species in each forest stage 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. In forestry, basal area is a measure of cross-sectional area at breast height of trees and widely used to describe the coverage of a particular species in a forest (Bettinger et al., 2017). Linking with forest fluxes, relative basal area was used to classify the dominant tree species in this study instead of other criteria, e.g., relative frequency or relative density, because it can represent the contribution of a species to ecosystem functions related to the water and carbon cycle (Balderas Torres & Lovett, 2012; Gardon et al., 2020; Paulick et al., 2017). The higher relative basal area of a species represents the higher coverage of that species in a forest, and thus the more contribution to the forest fluxes. Once obtaining species ranking information, five dominant tree species and five individuals per species from each plot were selected for all measurements. This selection results in a total of 75 tree samples and 11 woody species from the three successional forests, with some species existing in multiple sites including *Schima wallichii* (OF and IF), *Syzygium nervosum* (IF and YF), and *Symplocos cochinchinensis* (all sites). A list of selected dominant tree species is shown in Table 3.2 and detailed information about the flora and stand characteristics of selected species is described in Brockelman et al. (2017). The selected dominant tree species were also grouped into different successional species, including pioneer, generalist, and late-coming species (Tor-ngern et al., 2021). According to Chanthorn et al. (2017), species richness and diversity are greatly higher in OF compared to that in the other forest stages. The relative dominance of the species in OF is thus seemingly low, though they are the most abundant tree species within the plot (Table 3.2). Tree community in IF and YF, on the other hand, are more homogenous in terms of species composition and dominated by only a few species, which lead to drastic differences in the relative abundance for some species in IF and YF (Table 3.2). For the sample trees, stem size was limited to 10-20 cm in diameter at breast height (DBH) to control for the age group. This limitation helps to find the desired trees within the plots because tree size in this range is relatively abundant for all species. It also helps to control for any physiological changes that may result from different age classes for each species (Ewers et al., 2005; Groover, 2017).

Table 3.2 Characteristics of dominant tree species from the study sites of different forest succession in Khao Yai National Park.

Species	Family	Relative basal area	Successional species	Leaf habit[17]	Diameter at breast height	Canopy (sampling) height
Old-growth forest (OF)						
Dipterocarpus gracilis	Dipterocarpaceae	10.54 %	Late-coming	Deciduous	12-19 cm	15-18 m (6-10 m)
Sloanea sigun	Elaeocarpaceae	8.09 %	Late-coming	Evergreen	10-16 cm	10-16 m (6-8 m)
Ilex chevalieri	Aquifoliaceae	5.00 %	Late-coming	Evergreen	13-20 cm	13-22 m (5-7 m)
Symplocos cochinchinensis	Symplocaceae	3.40 %	Generalist	Evergreen	13-20 cm	13-19 m (7-10 m)
Schima wallichii	Theaceae	1.58 %	Generalist	Evergreen	11-16 cm	11-15 m (5-7 m)
Intermediate forest (IF)						
Schima wallichii	Theaceae	36.00 %	Generalist	Evergreen	11-16 cm	11-16 m (7-10 m)
Machilus gamblei	Lauraceae	36.00 %	Pioneer	Evergreen	11-20 cm	11-19 m (7-9 m)
Eurya acuminata	Pentaphylacaceae	4.00 %	Pioneer	Evergreen	10-12 cm	10-11 m (5-6 m)
Symplocos cochinchinensis	Symplocaceae	3.00 %	Generalist	Evergreen	11-16 cm	11-15 m (7-10 m)
Syzygium nervosum	Myrtaceae	2.00 %	Generalist	Evergreen	11-17 cm	10-16 m (8-9 m)
Young forest (YF)						
Cratoxylum cochinchinense	Clusiaceae	30.75 %	Pioneer	Deciduous	12-19 cm	11-18 m (5 m)
Syzygium antisepticum	Myrtaceae	26.52 %	Generalist	Evergreen	11-16 cm	10-15 m (5-6 m)
Adinandra integerrima	Pentaphylacaceae	12.08 %	Pioneer	Evergreen	12-18 cm	12-17 m (4 m)
Syzygium nervosum	Myrtaceae	11.95 %	Generalist	Evergreen	13-20 cm	12-19 m (4 m)
Symplocos cochinchinensis	Symplocaceae	3.24 %	Generalist	Evergreen	13-20 cm	13-18 m (4-7 m)

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[17] Taken Brockelman, W. Y., Nathalang, A., & Maxwell, J. F. (2017). *Mo Singto Forest Dynamics Plot: Flora and Ecology*. National Science and Technology Development Agency.

3.3 Measurement of midday leaf water potential (Ψ_{md})

Midday leaf water potential (Ψ_{md}) is a quantify of water tension (negative pressure) in the xylem during the driest period of the day, which is mostly close to noon when a maximum deficit of water occurs (Perez-Harguindeguy et al., 2013). Ψ_{md} is a useful index representing degree of plant water stress (Markesteijn et al., 2010). The lower (more negative) value of Ψ_{md} of a plant indicates a more dehydrated leaf (high water stress). Following Turner (1988), Ψ_{md} was determined with the pressure chamber technique by using a portable pressure chamber (Model 1505D-EXP, PMS instrument, Albany, OR, USA) during 10:00–14:00 in all study sites. The measurement was conducted two times during the dry season (November - April) and the wet season (May - October) to characterize seasonal variation in Ψ_{md} from all species. For each tree species, three-five individuals with equivalent stem diameter (10–20 cm DBH) were chosen for this measurement. For each individual tree, three healthy leaves with good exposure to sunlight were randomly selected from the lower and the edge of canopy branches, which was be around 4–10 meters above ground. Each selected leaf was cut with a razor blade and put inside the pressure chamber with its cut end of the leaf stalk protruding from the sealing port (Figure 3.3). The chamber was then gradually pressurized using nitrogen gas (N_2) until a drop of water appeared at the cut surface of the stalk. The accurate observe of this end point was alleviated by using a magnifying glass. The pressure inside the chamber, which is equivalent to Ψ_{md}, was then recorded, and the process was repeated with the other leaves. The applied pressure that causes water to emerge at the petiole, also called balance pressure, indicates how much tension the leaf is experiencing when the plant is still intact. To avoid the potential loss of water from the leaf, this measurement was conducted immediately after the leaf has been harvested from the tree.

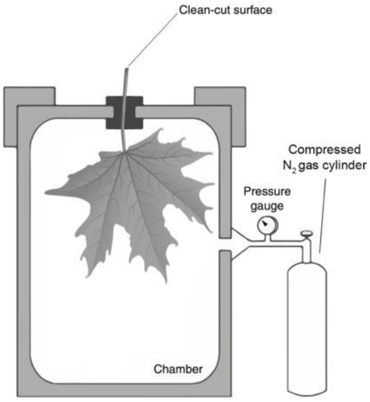

Figure 3.3 Diagram of Ψ_{md} measurement with a pressure chamber[18]

3.4 Measurement of xylem vulnerability to cavitation

The sensitivity of a tree species to cavitation was defined by a vulnerability curve, showing the percentage loss of hydraulic conductivity in the xylem to water stress-induced cavitation. In the present study, air-injection approach (Sperry & Saliendra, 1994) was applied to establish xylem cavitation vulnerability curves. The principle of this method is to use air pressurization to artificially induce cavitation to plant samples and determine their changes in xylem conductivity. The air that enters into a xylem vessel will expand and block water flow through this element. The increasing air pressure will cause more cavitated vessels in the sample, which therefore leads to greater loss of hydraulic conductivity. The capability of a tree species to tolerate high pressure without cavitation varies among species and plays a significant role in defining its drought tolerance level (Choat et al., 2012; Skelton et al., 2015; Venturas et al., 2017).

3.4.1 Sample preparation

Cavitation vulnerability curves were done in branch samples from the selected dominant tree species in each study site. Prior to sample collection, maximum xylem vessel length (MVL) for each species was estimated first to avoid the introduction of open xylem elements artifact (Martin-StPaul et al., 2014), which potentially leads to

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[18] Adapted from Perez-Harguindeguy, N., Diaz, S., Garnier, E., et al. (2016). New handbook for standardised measurement of plant functional traits worldwide *Australian Journal of Botany*, *64*(7-8), 715-716.

both overestimation and underestimation of xylem vulnerability. For each tree species, the estimation of MVL was made on three branches collected from the same tree individuals used for Ψ_{leaf} measurement. The estimation was done using air infiltration technique following Perez-Harguindeguy et al. (2016). Each branch sample ranging between 0.6–1.0 m in length and 5–10 mm in diameter was cut, and its bark was removed from the basal end (Figure 3.4A). A rubber tubing was then connected to the sample at the debarked end while the other end was immersed in water reservoir (Figure 3.4B). To apply the pressure, an air-filled syringe was attached to the rubber tubing, prior to pushing its plunger to generate compressed air to the sample. Given that compressed air cannot move freely through water-conducting element end walls (Ewers & Fisher, 1989), bubbles can emanate in the water after applying the pressure if at least one xylem is cut open at both ends. This procedure was proceeded with the sample's distal end (the one immerged in water) was successively shortened by 1 cm, until bubbles were emerged. Once bubbles were seen, a slightly longer than the remaining length was defined as MVL of this sample.

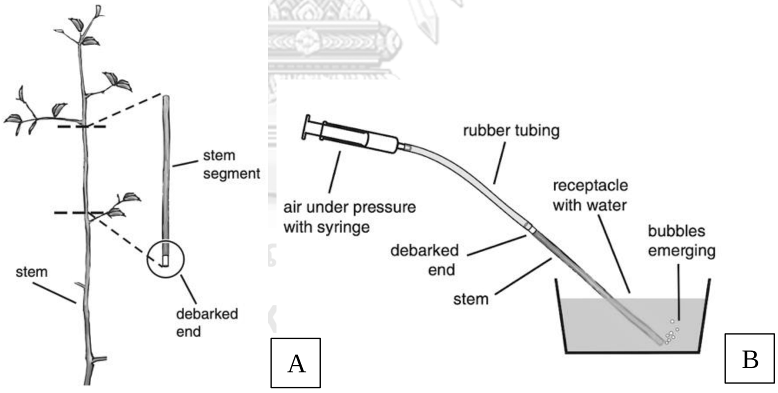

Figure 3.4 Measurement of maximum vessel length (MVL)[19]
A. An excised segment with bark detached from its basal end, and
B. A simple procedure to determine MVL using air infiltration technique

For each plot, three terminal branches which are as high as the tree canopy (5–10 meters above ground) was collected from the selected individuals for each species. The selected segments should be straight, similar in diameter (5–10 mm), and

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[19] Adapted from Perez-Harguindeguy, N., Diaz, S., Garnier, E., et al. (2016). New handbook for standardised measurement of plant functional traits worldwide *Australian Journal of Botany*, *64*(7-8), 715-716.

longer than MVL. The function of the selected segment is mainly responsible for water uptake and transport in plants (Pallardy, 2008). In addition, samples were collected in the morning to obtain samples with more water-saturated xylem vessels than the cavitated ones. Once the collections were made, samples were cut again at their ends under water and kept immersing in cold water (~4 ºC) to avoid microbial activity before being transported to the laboratory for further measurements.

3.4.2 Measurement of xylem conductivity

The xylem specific conductivity (K_s) is used to describe the efficiency of water transport through a xylem segment according to Darcy's Law (Edwards & Jaris, 1982) and defined as:

$$K_s = \frac{Ql}{\Delta PA_s}\frac{\eta}{\eta_0} \qquad \text{Eq 3.1}$$

where K_s is the xylem specific conductivity in kg m^{-1} s^{-1} MPa^{-1}, Q is the flow rate of fluid (kg s^{-1}), l is the length of the segment (m), ΔP is the pressure difference between two ends of the segment (MPa), As is the sapwood cross-sectional area (m^2), η is the viscosity of the fluid at the temperature when the experiment is performed (N s m^{-2}), and η_0 is the reference viscosity at 25 °C (N s m^{-2}).

In this study, K_s was measured by determining the fluid flow through a plant segment after applying a pressure head driven by a gravity (Melcher et al., 2012). At the start of this measurement, the ends of the segment was cleaned with a fresh razor blade and flushed to remove cavitated vessels using a syringe that is full of perfusing solution, de-ionized and ultra-filtered water (DI water) (PURELAB Chorus 1 Complete, ELGA LabWater, Woodridge, IL, USA) that was degassed by boiling and adjusted to an acidic pH (2-3) with HCl. This removal allowed the segment to restore its maximum conductivity (K_{smax}). The selected perfusing solution has been shown to be superior to other perfusing solutions, for being able to prevent microorganism growth and thus clogged xylem from organic precipitation (Sperry & Saliendra, 1994). After the removal of cavitation, the segment was connected to a tubing apparatus with the basal end attached to the perfusing solution reservoir (upstream) and the other end connected to a pipette (downstream) (Figure 3.5). The height difference between water levels in the upstream and in the downstream section created the hydraulic gradient due to gravitational force, causing pressure difference (ΔP) at which the solution was provided to the segment. Once the perfusing solution was passed through the segment, the resulting flow rate (Q) was measured by timing the intervals for the solution to reach marks on the pipette. The segment was then removed from the tubing apparatus and measured its length (l) and the cross-sectional area (A_s). The temperature of the perfusing solution was also be recorded before and after K_s measurements, and all the calculations following Eq 3.1 were modified to 25°C, which accounted for variations in fluid viscosity with temperature.

Figure 3.5 Diagram for measuring flow rates through a stem segment[20]

3.4.3 Constructing a vulnerability curve

The air injection technique was conducted in this study to construct xylem cavitation vulnerability curves (Sperry & Saliendra, 1994). After determining K_{smax}, a segment from the collected samples was placed inside a cavitation chamber (a double-ended pressure sleeve) with both ends emerging. The chamber was then connected with a pressure chamber (the same instrument used for Ψ_{md} measurement) and injected with compressed air, nitrogen gas (N_2), to induce cavitation. First, the chamber was applied with a small pressure, 0.5 MPa, and maintained for at least two minutes before reducing the pressure back to atmospheric level. After pressurization, the segment was rested for 10-30 minutes for the balanced system and K_s with induced cavitation was determined by the same process used for K_{smax}. This procedure was repeated by increasing the injection pressure from 0.5 or 1 MPa steps (depending on species), until more than 85% loss of K_s was reached. The percentage loss of hydraulic conductivity (PLC) can be calculated as:

$$PLC = 100 \times \left(1 - \frac{K_s}{K_{smax}}\right) \qquad \text{Eq 3.2}$$

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[20] Adapted from Perez-Harguindeguy, N., Diaz, S., Garnier, E., et al. (2016). New handbook for standardised measurement of plant functional traits worldwide *Australian Journal of Botany*, *64*(7-8), 715-716.

where K_s is the xylem specific conductivity following each step of increased pressure and $K_{s(max)}$ is the maximum conductivity measured after removal of cavitation.

Then, xylem vulnerability curves was created as the function of PLC and the applied pressure and fitted by the following sigmoidal equation described by Pammenter and Vander Willigen (1998):

$$PLC = \frac{100}{(1+\exp(a(P - b)))} \qquad \text{Eq 3.3}$$

where a is the indicator of the slope, P is the applied pressure, and b is the pressure causing 50% loss of xylem conductivity (P_{50}), which was used to compare cavitation resistance among species and forest succession. Additionally, the constructed vulnerability curves were also used to calculate the percentage loss of hydraulic conductivity corresponding to midday leaf water potential during the dry season (PLC_{dry}) to further assess the potential cavitation during water-limited conditions from each studied tree species.

3.5 Data analysis

Data analyses was done using various computational methods. To accomplish Objective 1, two sets of analysis were performed to detect and confirm significant differences across successional stages and seasons. The first set was to test for overall difference among successional stages using combined data from all dominant species within each succession, while the second set was to further evaluate the difference among forest stages by focusing only the data from species found in multiple sites. For the first set of the analysis, one-way analysis of variance (ANOVA) was performed to evaluate the significant difference of Ψ_{md} among forest successions in same season. Then, in each succession, an independent sample *t-test* was used to test the significant difference in Ψ_{md} between the wet and dry seasons. For the second set of the analysis, Ψ_{md} from the species occupying in all study sites, i.e., *Symplocos cochinchinensis,* was tested for the significant difference across the forest succession in each season by using one-way ANOVA, and tested the significant difference in seasonal variation by using independent sample *t-test*. For the species occupying in two sites, i.e., *Schima wallichii* in OF and IF and *Syzygium nervosum* in IF and YF, significant differences in Ψ_{md} between the forest succession and seasons were evaluated using independent sample *t-*

test. Tukey's post hoc test was used after the one-way ANOVA test to determine which pairwise comparisons are significantly different. To characterize xylem vulnerability of the study species (Objective 2), regression analysis using sigmoidal equation (Eq 3.3) was conducted to generate P_{50} and PLC_{dry} for all selected tree species. MVL, K_s, P_{50}, and PLC_{dry} were also tested using one-way ANOVA with Tukey's post-hoc test to evaluate the significant differences among forest successions by using pooled data from the dominant tree species, and across the dominant tree species within each forest succession if the sample size allows. All analyses in this study were performed using R (version 4.0.3) and all statistical tests were considered at 95% significance level. All graphs and regression analysis were made by SigmaPlot 12.0 (Systat Software, Inc., San Jose, California, USA).

CHAPTER 4

RESULTS AND DISCUSSION

4.1 Environmental conditions in the study area and characteristics of dominant tree species along the forest successional gradient

Meteorological data in the study area were taken from the weather station located at Khao Yai National Park headquarters, which was about 1-3 km away from the forest plots. Based on 21-year period of data collection (1994-2014), the periods from May to October in this area are considered to be wet season, while from November to April are considered to be dry season, as monthly rainfall is less than 100 mm (Figure 4.1) (Brockelman et al., 2017). The mean annual rainfall during 1994 to 2014 was 2,073 mm, the annual rainfall ranging from 1,264 mm in 1998 to 2,939 mm in 1996. The lowest rainfall fell in December, with a mean of 6.3 mm, while the highest rainfall occurred in September, with a mean of 348 mm. During the study period, annual rainfall in the study area was 1,160 mm in 2019 and 1,778 mm in 2020, which was lower than the 21-year mean annual rainfall around 45% in 2019 and 15% in 2020. A drastic drop of rainfall in the year 2019 was partially caused by El Niño–Southern Oscillation (ENSO) event, which was also the case in 1998, and marked the year of Thailand’s lowest annual rainfall since 1981 (Thaiwater, 2019). Due to seemingly unreliable data readings in some years during 1994-2014, annual and monthly means of temperature in this area were based on ten years of reliable data from the year 1994, 2002-2003, and 2007-2013 (Brockelman et al., 2017). This selection results in the overall annual mean temperature of 22.4 °C and monthly mean ranging from a minimum of 19.4 °C in December to a high of 24.3 °C in April.

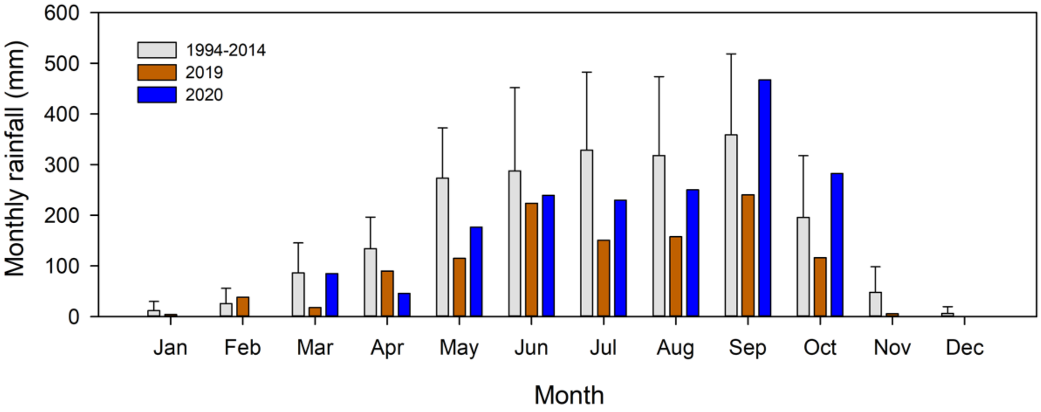

Figure 4.1 Monthly rainfall at Khao Yai National Park, Thailand. The average of 21-year monthly rainfall from 1994-2014 is shown in bars with one standard deviation. Total monthly rainfall in 2019 and 2020 are represented in brown and blue bars, respectively.

Meteorological data in the study area during the survey of study trees and measurement of midday leaf water potential (Ψ_{md}) (July 2019-July 2020) is shown in Figure 4.2. The meteorological data included rainfall and atmospheric demand for water, which is represented by daily rainfall and vapor pressure deficit (VPD), respectively. Estimated from atmospheric temperature and relative humidity, VPD represents the quantity of water vapor that the air can carry for a given temperature (Lawrence, 2005) and is a significant driver for plant functioning (Grossiord et al., 2020; Rawson et al., 1977; Yuan et al., 2019). During this period, significant amount of rainfall (> 100 mm) occurred mostly in the months of July through October (DOY 182-304) in 2019 and May to July (DOY 122-213) in 2020, representing the wet season (Figure 4.2, bars). The average monthly rainfall during November in 2019 until April in 2020 (DOY 305 in 2019 to DOY 121 in 2020) was lower than 100 mm, representing the dry season. The average daily VPD inversely corresponded with rainfall, being low when rainfall occurred, and was significantly higher in the dry season than in the wet season (0.580 ± 0.184 kPa and 0.403 ± 0.233 kPa; independent sample *t-test*, $p < 0.0001$) (Figure 4.2, line).

During July – September in 2019 (DOY 182-273 in 2019), the survey of study trees was conducted in three different forest successional stages representing an old-growth forest (OF), an intermediate forest (IF), and a young forest (YF). Then, the measurements of Ψ_{md} were performed twice in the dry season, November (DOY 320-321 and 326-328) and December (DOY 359-362 and 364-365) in 2019, and twice in the wet season, May (DOY 135-140) and July (196-200) in 2020 (Figure 4.2, inset figures). In the wet and dry seasons, there was no rainfall during the measurement periods. The rainfall observed in the wet season (e.g., DOY 196 and 198, Figure 4.2) occurred mostly at night. The average daily VPD from the sampling days during the dry and wet seasons were similar (independent sample *t-test*, p = 0.338), averaging 0.499 ± 0.069 kPa and 0.465 ± 0.095 kPa, respectively.

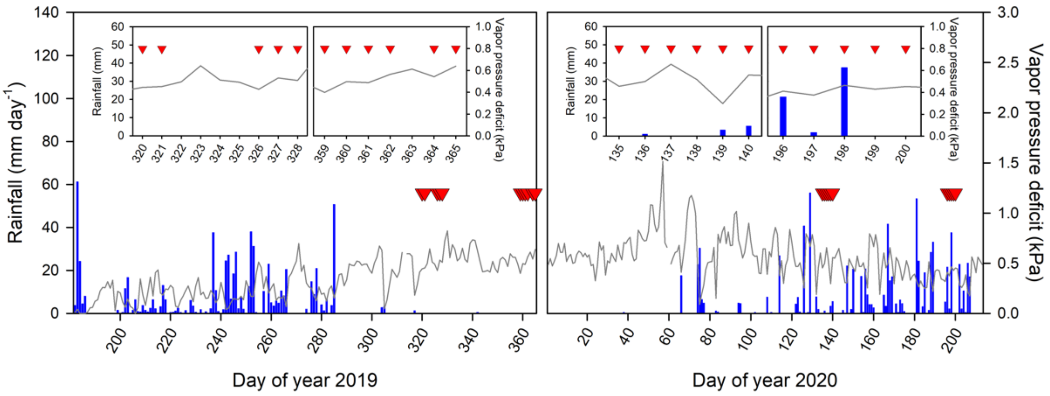

Figure 4.2 Distribution of rainfall (blue bars) and vapor pressure deficit (VPD, grey line) from 1st July 2019 (DOY 182 in 2019) to 30th July 2020 (DOY 213 in 2020) at Khao Yai National Park, Thailand. Red triangles indicate the sampling days for midday leaf water potential (Ψ_{md}) measurements. Inset figures show more details of daily rainfall and VPD patterns during the sampling periods of Ψ_{md} measurements.

Differences in forest structure among the forest successional stages, as indicated by different stem density, canopy coverage, and canopy height, may imply the differences in their micro-environments, including temperature, relative humidity, soil water availability, etc. (Hasselquist et al., 2010; Lebrija-Trejos et al., 2011; Pineda-Garcia et al., 2013). Unfortunately, no measurements of environmental conditions were made concurrently with the data collection. Nevertheless, soil moisture was preliminarily measured around the sampling trees in each study site during the onset of the dry season (February 2020) and compared across the three sites. The differences in soil moisture among forest stages were significant (one-way ANOVA, $p < 0.0001$), in which OF had the highest mean soil moisture (45.4 ± 8.72%), followed by IF (37.8 ± 6.97%), and YF (23.9 ± 5.34%), respectively. A combination of forest structure, environmental conditions, and human-induced disturbances could affect the strategies that trees use for survival (Lebrija-Trejos et al., 2008; Lebrija-Trejos et al., 2010), which may determine the assembly of different vegetation types along the successional gradient in Khao Yai National Park. Characteristics of dominant tree species across the forest successions are shown in Table 3.2. In this study, a total of 11 woody species were selected based on relative basal area abundance in each successional stage, with some species existing in multiple sites including *Schima wallichii* (OF and IF), *Syzygium nervosum* (IF and YF), and *Symplocos cochinchinensis* (all sites). According to Brockelman et al. (2017), *Dipterocarpus gracilis* and *Cratoxylum cochinchinense* are deciduous. They shed their leaves and stipules during February-March but were never completely leafless (field observations during the measurements). The other species are evergreen. A large canopy gap resulted from fallen trees was also observed around the sampled trees of *S. wallichii*, and some of the sampled trees of *S. cochinchinensis*. The sampled trees for dominant tree species in IF existed in a hilly forest land, where its canopy coverage was more homogeneous and denser compared to that of OF and YF (Chanthorn et al., 2016). All the sampled trees in YF experienced drier conditions and stronger radiation from more open canopy in contrast to OF and IF (Chanthorn et al., 2016; Tor-ngern et al., 2021).

4.2 Seasonal changes in midday leaf water potential of dominant tree species across forest successions

Overall, Ψ_{md} varied significantly among the successional stages in both wet and dry seasons (Table 4.1, Figure 4.3A.). Focusing on each season, difference in Ψ_{md} among the successions was more pronounced during the dry season, in which YF had the lowest Ψ_{md} (-1.54 ± 0.72 MPa), followed by Ψ_{md} in IF (-1.06 ± 0.50 MPa) and OF (-0.82 ± 0.46 MPa), respectively. During the wet season, YF also had the lowest Ψ_{md} (-1.17 ± 0.43 MPa), while Ψ_{md} in OF and IF were comparable (-0.89 ± 0.31 MPa in OF and -0.82 ± 0.25 MPa in IF). Within each forest stage, IF and YF showed significant seasonal variation in Ψ_{md}, with a slightly larger difference in YF than in IF (32% in YF vs. 29% in IF). However, no significant difference in Ψ_{md} between the two seasons was found in OF. This may imply that lower Ψ_{md} during water-limited conditions, e.g., dry season, and higher variation in Ψ_{md} induced by seasonal changes could occur frequently in the younger and drier sites.

For the species found in multiple sites, they exhibited different variations in Ψ_{md} between the seasons, and among the forest successions. For *S. cochinchinensis*, the lowest Ψ_{md} was found in YF, while Ψ_{md} was similar in OF and IF in both seasons (Figure 4.3B). Seasonal changes in Ψ_{md} were found significant in OF and IF, with a lower average in the wet season for OF and IF by 69% and 28%, respectively, compared to the dry season. There was no seasonal variation in Ψ_{md} for *S. cochinchinensis* growing in YF. For *S. wallichii*, the lower Ψ_{md} was found in OF than in IF (Figure 4.3C). Seasonal difference in Ψ_{md} was detected only in IF, with a 19% lower Ψ_{md} during the dry season than in the wet season. In *S. nervosum*, lower Ψ_{md} was significantly found in YF compared to IF only in the wet season (Figure 4.3D). Only *S. nervosum* in YF was affected by seasonal changes, with a 47% lower in Ψ_{md} during the wet season.

Table 4.1 Midday leaf water potential (Ψ_{md}, MPa) of selected dominant tree species from different forest successions during the wet and dry seasons in Khao Yai National Park, Thailand. Values are mean ± one standard deviation for site averages (n=150) and species averages (n=30). Different upper- and lower-case letters represent significant differences among the forest successions and within each forest succession, respectively (one-way ANOVA with Tukey's post-hoc test, significance level of 0.05). Significant tests on seasonal difference in Ψ_{md} are based on independent sample *t-test*.

Species	Ψ_{md} in the dry season	Ψ_{md} in the wet season	Seasonal difference
Old-growth forest (OF)	**-0.82 ± 0.46 A**	**-0.89 ± 0.31 A**	**$p = 0.102$**
Dipterocarpus gracilis	-0.43 ± 0.25 d	-0.86 ± 0.28 b	$p < 0.0001$
Sloanea sigun	-0.77 ± 0.32 bc	-0.92 ± 0.20 ab	$p = 0.033$
Ilex chevalieri	-1.04 ± 0.29 ab	-0.60 ± 0.20 c	$p < 0.0001$
Symplocos cochinchinensis	-0.64 ± 0.34 cd	-1.08 ± 0.31 a	$p < 0.0001$
Schima wallichii	-1.21 ± 0.59 a	-1.01 ± 0.29 ab	$p = 0.104$
Intermediate forest (IF)	**-1.06 ± 0.50 B**	**-0.82 ± 0.25 A**	**$p < 0.0001$**
Schima wallichii	-0.88 ± 0.22 c	-0.74 ± 0.29 b	$p = 0.028$
Machilus gamblei	-1.29 ± 0.45 b	-0.85 ± 0.26 ab	$p < 0.0001$
Eurya acuminata	-1.68 ± 0.34 a	-0.78 ± 0.22 b	$p < 0.0001$
Symplocos cochinchinensis	-0.79 ± 0.37 cd	-1.01 ± 0.22 a	$p = 0.006$
Syzygium nervosum	-0.64 ± 0.21 d	-0.72 ± 0.16 b	$p = 0.134$
Young forest (YF)	**-1.54 ± 0.72 C**	**-1.17 ± 0.43 B**	**$p < 0.0001$**
Cratoxylum cochinchinense	-2.54 ± 0.37 a	-1.41 ± 0.38 a	$p < 0.0001$
Syzygium antisepticum	-1.49 ± 0.50 b	-0.80 ± 0.32 b	$p < 0.0001$
Adinandra integerrima	-1.60 ± 0.24 b	-1.33 ± 0.29 a	$p < 0.001$
Syzygium nervosum	-0.57 ± 0.24 c	-0.84 ± 0.19 b	$p < 0.0001$
Symplocos cochinchinensis	-1.49 ± 0.36 b	-1.46 ± 0.39 a	$p = 0.732$

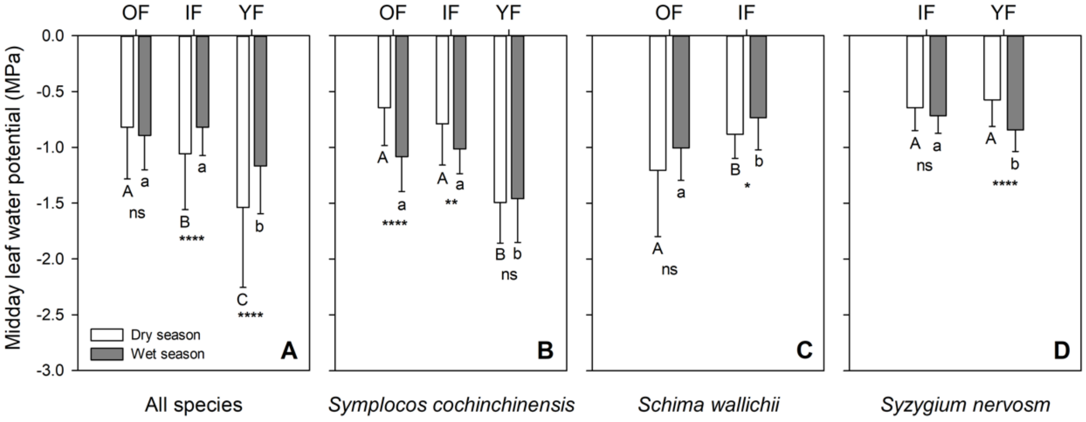

Figure 4.3 Average and one standard deviation of midday leaf water potential (Ψ_{md}) from different forest successions during the dry (white bars) and wet (dark grey) seasons in A. Forest level, B. *Symplocos cochinchinensis,* C. *Schima wallichii*, and D. *Syzygium nervosum.* Each bar represents the site averages for sample size of 150 (A.), and species averages for 30 samples (B., C., and D.). OF, IF, and YF stand for old-growth, intermediate, and young forests, respectively. For each panel, different upper- and lower-case letters represent significant differences in the wet and dry seasons, respectively (A. and B. One-way ANOVA with Tukey's post-hoc test, significance level of 0.05; C. and D. Independent sample *t-test*, significance level of 0.05). * indicates significant seasonal differences within the same successional stage based on independent sample *t-test*.; ns = not significant, * p<0.05, ** p<0.01, *** p <0.001, and **** p<0.0001.

Water availability is a significant environmental constraint for species occurrence in and among different successional stages in tropical forests (Comita & Engelbrecht, 2009; Pineda-Garcia et al., 2013; Zhu et al., 2017). The ability to withstand water stress during water deficit conditions could lead to the success of different tree species occupying in different habitats. Determining the mechanisms contributing to trees' responses to seasonal change is therefore crucial in understanding how trees survive during water stress. In this study, the dominant tree species along the forest successional gradient showed different patterns of seasonal variation in Ψ_{md}. At forest level, YF exhibited lower Ψ_{md} in both the wet and dry seasons, and had greater change in Ψ_{md} due to seasonal variation compared to OF and IF (Figure 4.3A). A drier environment, as a result of more open canopy coverage in YF, could play a crucial role for this instance. Lebrija-Trejos et al. (2011) studied the environmental changes during secondary succession in a tropical forest in southern Mexico, and found that the sparse-vegetation covered sites had low soil water content due to strong evaporation from direct solar heating that increased soil drying process. This finding supports our observation of contrasting soil water availability across the three forest successional stages. Moreover, compared to late successional forests, higher loads of direct irradiance owing to more open canopy in early succession also leads to drier conditions in the atmosphere (higher VPD) and higher temperature, which consequently results in lower Ψ_{md} in drier YF site as compared to moister OF and IF sites. The environmental conditions along successional stages could also be intensified during the onset of dry season, by showing lower Ψ_{md} in the drier sites, implying that species in early successional stages would experience more water stress than in late succession (Bretfeld et al., 2018). Interestingly, studies have shown that species found in drier sites have higher tolerance to desiccation, meaning the ability to remain alive at lower water potentials, which strongly correlated with species distribution and drought survival in tropical trees (Baltzer et al., 2008; Engelbrecht, Comita, et al., 2007; Engelbrecht, Tyree, et al., 2007; Kursar et al., 2009). The risk of tree mortality during water stress can be determined by a function of plant regulation of water use in response to critical thresholds associated with carbon starvation or hydraulic failure (Allen et al., 2010; Choat et al., 2018; McDowell et al., 2008). The process of carbon starvation and hydraulic failure are strongly interdependent (McDowell et al., 2011), by balancing the act of regulating stomatal control for photosynthetic carbon gain in relation to plant water status to avoid xylem cavitation. The lower Ψ_{md} in YF compared to OF and IF in both seasons, thus, could be an adaptive regulation that benefits higher stomatal conductivity and photosynthetic rate to assure the carbon acquisition and optimal growth under unfavorable conditions. This finding is accompanied by Tor-ngern et al. (2021) that found comparable stomatal conductance and photosynthesis across the successional stages in the wet season. However, allowing low Ψ_{md} in YF can also be detrimental for dehydration and hydraulic failure, especially during the dry season, if the value decreases beyond the critical threshold of xylem cavitation (Blackman et al., 2019).

To further investigate seasonal and forest successional variations in Ψ_{md} by excluding potential confounding effect from species, species existing in multiple sites were examined. As would be expected according to occupying in drier environment, *S. cochinchinensis* in YF exhibited the lowest Ψ_{md} in both seasons compared to OF and IF, with no significant seasonal difference in Ψ_{md} (Figure 4.3B). *S. cochinchinensis* in OF and IF showed comparable Ψ_{md} in both seasons; however, their Ψ_{md} during the wet season was lower than in the dry season, even with presumably better access to water. This unexpected pattern also occurred in *S. nervosum* in YF, when lower Ψ_{md} was found in the wet season compared to the dry season (Figure 4.3D). Between the two sites, *S. nervosum* in YF showed significantly lower Ψ_{md} in comparison to IF during the wet season, but not in the dry season. Such unexpected pattern may be explained by that, during the wet season, *S. cochinchinensis* in OF and IF and *S. nervosum* in YF deployed a less conservative water use regulation to allow higher photosynthetic rates when water is more abundant. This unexpected pattern can also be found in a few studies (Bucci et al., 2005; Prado et al., 2004), with no clear explanation provided. In *S. wallichii*, lower Ψ_{md} was found in OF contrasted to IF in both seasons (Figure 4.3C), with no seasonal impact in OF and a slight change in IF in the dry season. Even though they occupied in a relatively wetter environment, the sampled trees of *S. wallichii* in OF grew under a large gap created by tree falls. The higher intensity of light under the gap strongly influence the microclimate, leading to higher air temperature and lower air humidity compared to the adjacent area (Fetcher et al., 1985; McCarthy, 2001). Therefore, the leaf-level water deficits resulted from canopy gap may contribute to a lower value of Ψ_{md} in OF than in IF. Different changes and patterns in Ψ_{md} induced by seasonal changes found in this study seem to be species-specific, in which some species had a greater or lower impact than the others. These different strategies and regulatory mechanisms dealing with water-limited condition have a critical impact practically to xylem cavitation (Sperry et al., 2002; Zhu & Cao, 2009), and hence the potential risk of tree mortality resulted from water stress-induced hydraulic failure.

4.3 Xylem vulnerability of dominant tree species from different successional forests

Due to considerably high within-site variation among dominant tree species in each forest succession, most of the hydraulic properties were not statistically different across forest successions (K_s, P_{50}, PLC_{dry}; Table 4.2). Taken as a group, the average maximum vessel length (MVL) did not show a clear pattern along the forest successions. OF tended to have similar MVL to YF (34.90 ± 12.90 cm in OF and 38.40 ± 2.95 cm in YF); however, MVL of YF also appeared to be similar to that of IF (43.30 ± 4.54 cm in IF). There was no significant difference in average maximum xylem specific conductivity (K_{smax}) among the forest successions (one-way ANOVA, $p = 0.111$). The three forest successions did not differ statistically ($p = 0.54$) in xylem vulnerability, measured as xylem pressure at which 50% of hydraulic conductivity is lost (P_{50}). Xylem vulnerability ranged from potentially more vulnerable in OF (-2.87 ± 1.25 MPa) to less vulnerable in IF (-3.04 ± 0.70 MPa) and in YF (-3.71 ± 1.59 MPa). Species occupying in all study sites, i.e., *S. cochinchinensis*, exhibited comparable P_{50} across forest stages (-3.27 MPa in OF, -3.40 MPa in IF, and -3.23 MPa in YF). This trend was similar to other species existing in multiple sites. *S. wallichii* in OF and IF had P_{50} of -3.46 MPa and -3.01 MPa, respectively., while *S. nervosum* in IF and YF had P_{50} of -2.31 MPa and -2.23 MPa, respectively. The percentage loss of hydraulic conductivity corresponding to midday leaf water potential during in the dry season (PLC_{dry}) ranged from 4.5% in OF to 13% and 18% in IF and YF, respectively. When combining all data from all dominant tree species, P50 was found to be correlated with K_{smax} ($r = 0.52$, $p = 0.049$; Figure 4.5A), but not in MVL ($r = 0.33$, $p = 0.23$; Figure 4.5B).

Within each forest successional stage, hydraulic properties varied greatly among the dominant tree species (Table 4.2, Figure 4.4). In OF, MVL varied threefold across the dominant tree species, with significant interspecific variation ($p < 0.0001$). The shortest MVL of 15.33 ± 1.53 cm was found in *I. chevalieri*, while the longest MVL of 50.33 ± 4.16 cm was found in *D. gracilis*. The lowest P_{50} was also found in *I. chevalieri* (-4.16 MPa) with moderate K_{smax} (1.21 ± 0.38 kg m^{-1} s^{-1} MPa^{-1}), whereas the highest P_{50} and K_{smax} were found in *D. gracilis* (-0.88 MPa and 2.33 ± 0.10 kg m^{-1} s^{-1} MPa^{-1}). PLC_{dry} differed substantially across species in OF, in which *I. chevalieri* experienced relatively lower impact during the dry season (1.07 %), while a greater impact was exerted on *S. sigun* (7.91%) and *S. wallichii* (7.74%). In IF, similar MVL was found among the dominant tree species ($p = 0.248$). Compared to the other species within the same site, *E. acuminata* was more resistant to xylem cavitation (-4.02 MPa) and had the lowest K_{smax} (0.82 ± 0.29 kg m^{-1} s^{-1} MPa^{-1}). In contrast, *S. nervosum* had lower cavitation resistance (-2.31 MPa) and moderate K_{smax} (1.58 ± 0.50 kg m^{-1} s^{-1} MPa^{-1}) in comparison to the coexisting species. *S. cochinchinensis* tended to respond less to dry conditions in the dry season by losing relatively small hydraulic conductivity at midday during the dry season (2.60 %), while *M. gamblei* was potentially more affected (24.12 %) by the same instance. In YF, there was no significant difference in MVL among the dominant tree species ($p = 0.656$). Within this stage, the lowest P_{50} values was found in *A. integerrima*, at -5.97 MPa, with moderate K_{smax} (1.27 ± 0.16 kg m^{-1} s^{-1} MPa^{-1}) and low response to dry conditions as observed from midday PLC (1.41 %). *C. cochinchinense*, in contrast, had the highest P_{50} and K_{smax} (-2.41 MPa and 3.09 ± 0.17 kg m^{-1} s^{-1} MPa^{-1}), and the greatest response from losing hydraulic conductivity in the dry season (52.46 %) compared to the other species.

Table 4.2 Hydraulic properties of selected dominant tree species from different successions in Khao Yai National Park, Thailand. Values are means ± one standard deviation with sample size of 3. MVL, maximum vessel length; K_{smax}, maximum xylem specific conductivity; P_{50}, xylem pressure at 50% loss of hydraulic conductivity; PLC_{dry}, percentage loss of hydraulic conductivity corresponding to midday leaf water potential during the dry season. Different upper- and lower-case letters represent significant differences among the forest successions and within each forest succession, respectively (One-way ANOVA with Tukey's post-hoc test, significance level of 0.05).

Species	MVL (cm)	K_{smax} ($kg\ m^{-1}\ s^{-1}\ MPa^{-1}$)	P_{50} (MPa)	PLC_{dry} (%)
Old-growth forest (OF)	**34.90 ± 12.90 A**	**1.40 ± 0.57 A**	**-2.87 ± 1.25 A**	**4.46 ± 3.16 A**
Dipterocarpus gracilis	50.33 ± 4.16 d	2.33 ± 0.10 c	-0.88	2.55
Sloanea sigun	27.33 ± 2.08 b	1.32 ± 0.27 b	-2.56	7.91
Ilex chevalieri	15.33 ± 1.53 a	1.21 ± 0.38 ab	-4.16	1.07
Symplocos cochinchinensis	42.00 ± 3.00 c	0.71 ± 0.07 a	-3.27	3.04
Schima wallichii	39.70 ± 1.53 c	1.44 ± 0.14 b	-3.46	7.74
Intermediate forest (IF)	**43.30 ± 4.54 B**	**1.36 ± 0.59 A**	**-3.04 ± 0.70 A**	**12.6 ± 7.89 A**
Schima wallichii	46.33 ± 2.08 a	2.22 ± 0.26 b	-3.01	11.87
Machilus gamblei	45.67 ± 6.43 a	1.21 ± 0.26 a	-2.44	24.12
Eurya acuminata	41.33 ± 3.79 a	0.82 ± 0.29 a	-4.02	9.44
Symplocos cochinchinensis	44.00 ± 3.00 a	0.96 ± 0.21 a	-3.40	2.60
Syzygium nervosum	39.00 ± 4.36 a	1.58 ± 0.50 ab	-2.31	14.99
Young forest (YF)	**38.40 ± 2.95 AB**	**1.82 ± 0.77 A**	**-3.71 ± 1.59 A**	**18.3 ± 20.10 A**
Cratoxylum cochinchinense	40.00 ± 3.61 a	3.09 ± 0.17 d	-2.41	52.46
Syzygium antisepticum	39.00 ± 3.00 a	1.03 ± 0.13 a	-4.71	6.49
Adinandra integerrima	37.67 ± 3.79 a	1.27 ± 0.16 ab	-5.97	1.41
Syzygium nervosum	36.33 ± 3.06 a	1.76 ± 0.31 bc	-2.23	12.71
Symplocos cochinchinensis	39.00 ± 1.73 a	1.94 ± 0.31 c	-3.24	18.45

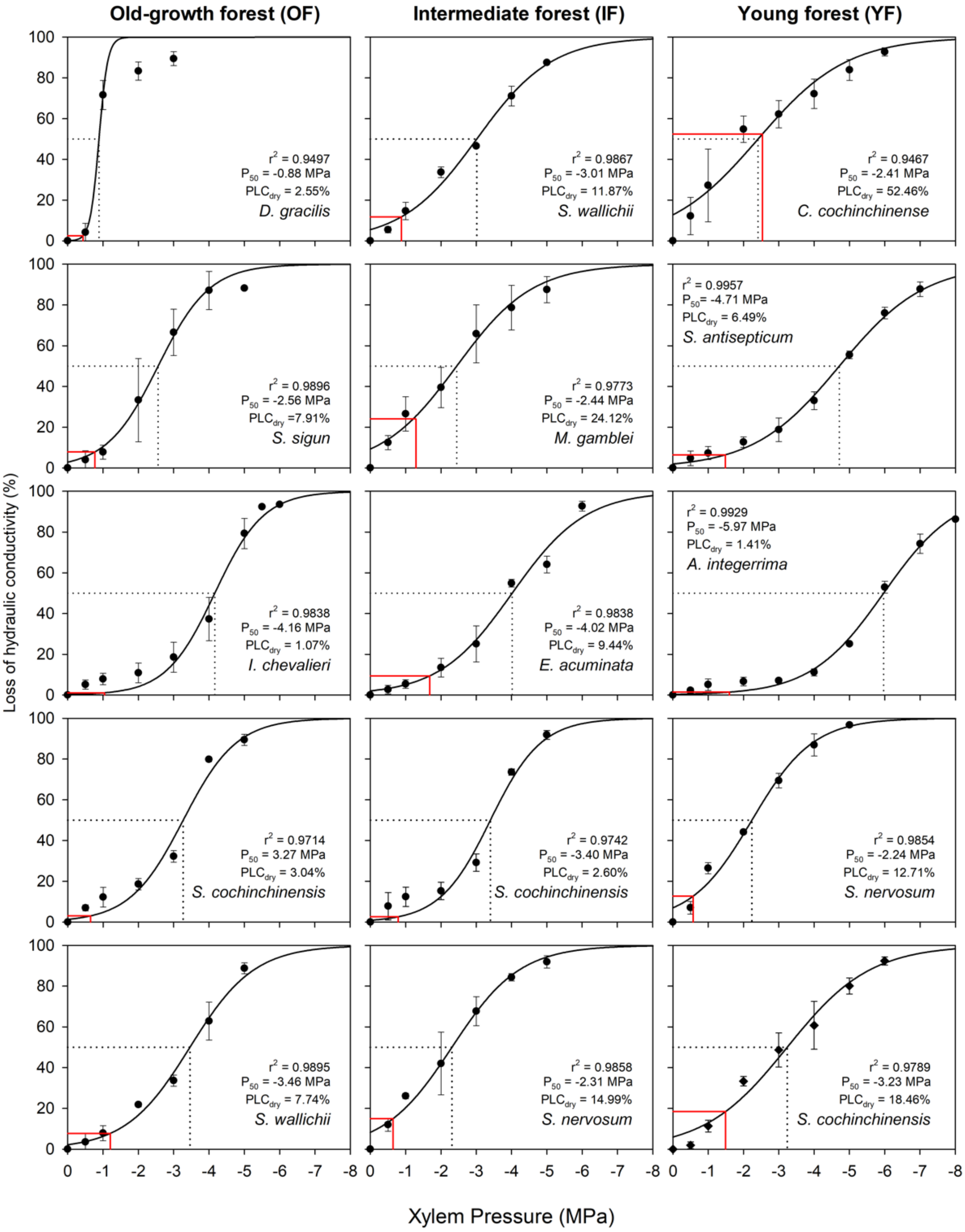

Figure 4.4 Vulnerability of xylem to cavitation of branches from dominant tree species from different successions in Khao Yai National Park, Thailand. Values are means ± one standard deviation with 3 branches per species. The dotted lines and red solid lines indicate the xylem pressure at 50% loss of hydraulic conductivity (P_{50}) and percentage loss of hydraulic conductivity corresponding to midday leaf water potential during the dry season (PLC_{dry}), respectively.

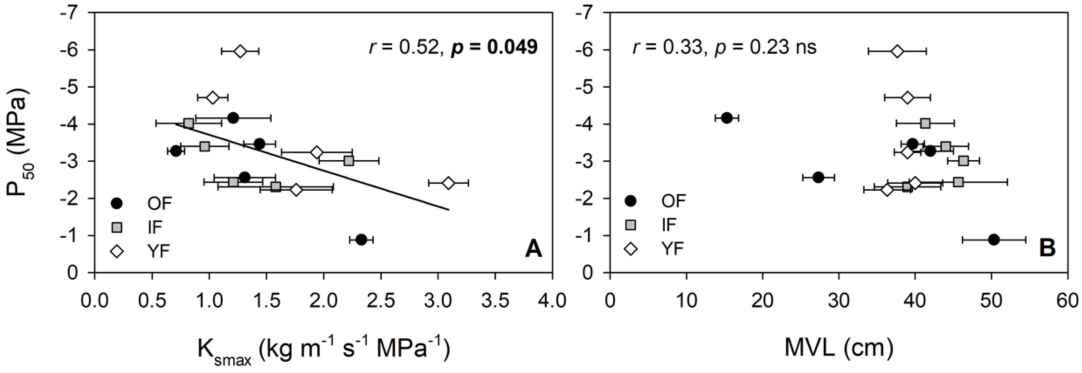

Figure 4.5 Correlations between xylem pressure at 50% loss of hydraulic conductivity (P_{50}) and A. maximum xylem specific conductivity (K_{smax}) and B. maximum vessel length (MVL). Black circles, grey rectangles, and white diamonds indicate species from old-growth forest (OF), intermediate forest (IF), and young forest (YF), respectively. Error bars represent one standard deviation. ns signifies non-significant correlation.

In this study, we examined species-level hydraulic properties that may contribute to differences in forest-level responses to water deficit conditions. Our study revealed a high level of interspecific variation in key hydraulic traits among the dominant tree species within the same site, which may obscure the average differences across the forest successions. Generally, we found no clear trends in MVL, K_s and P_{50} across the forest successional stages (Table 4.2). Many studies have documented that xylem vulnerability to cavitation vary substantially among trees from different habitats, in which species occupying in drier sites are generally less vulnerable to cavitation than those occupying in wetter sites (Barros et al., 2019; Choat et al., 2007; Vander Willigen et al., 2000; Vinya et al., 2013; Zhu et al., 2017). Supporting this statement, Larter et al. (2015) showed one of the most drought-resistant trees ever measured, *Callitris tuberculate*, with P_{50} of -18.8 ± 0.6 MPa. *C. tuberculate* can be found commonly in dry areas of southwestern Australia, where the average annual rainfall can be lower than 180 mm during the particularly dry years. In contrast, Maherali et al. (2004) reported that the most vulnerable tree to cavitation are from wet tropical forests, with some species reach up to 50% loss of hydraulic conductivity only at -0.18 MPa. In our study, there was a tendency for species at more xeric sites to have higher ability to resist xylem cavitation, despite non-statistical difference at forest level (Table 4.2, Figure 4.4). The most vulnerable species to xylem cavitation was found in OF, a deciduous tree species *D. gracilis* with the highest P_{50} of -0.88 MPa. On the other hand, *A. integerrima*, an evergreen tree species in YF, had the lowest P_{50}, at -5.97 MPa, standing out from the rest of the studied tree species from all forest successions. Comparing to the species in OF and YF, the dominant tree species in IF showed intermediate P_{50} values, ranging from -2.31 MPa in *S. nervosum* to -4.02 MPa in *E. acuminata*. The presence of species with lower P_{50} in more xeric sites could imply the adaptive importance of cavitation resistance in response to the environments where water stress is more pronounced (Maherali et al., 2004). Nevertheless, species occupying in multiple study sites, e.g., *S. cochinchinensis*, exhibited comparable P_{50}, suggesting the similar cavitation resistance across the forest successions. A lack of clear pattern along the successions of P_{50} was also observed by Pineda-Garcia et al. (2013). Based on plant water potential for 20%, 50% and 80% loss of hydraulic conductivity, the authors found no difference in resistance to drought stress between early- and late-successional species in a tropical dry forest. This may imply that evaluating species' performance under drought stress should be interpreted with care, since other mechanisms, e.g., stomatal regulation, sapwood water storage, or leaf-shedding strategy, could also contribute to xylem resistance to cavitation (Barnard et al., 2011; Domec et al., 2006; Markesteijn et al., 2011; Rosner et al., 2019).

There is ample evidence suggesting the hydraulic trade-off between the efficiency for xylem water transport (K_s) and the ability to resist xylem cavitation (P_{50}) (Hacke et al., 2006; Martinez-Vilalta et al., 2002; Tyree et al., 1994; Vinya et al., 2013). This trade-off is thought to reflect the hydraulic adaptation influencing the distribution of plant species in response to water availability. For example, species occupying in wetter sites usually have wider and longer vessels for a greater water transport efficiency but more susceptible to xylem cavitation than those from drier sites (Ewers, 1985; Loepfe et al., 2007; Pockman & Sperry, 2000). In this study, an association between P_{50} and K_s was found across the dominant tree species from all study sites, supporting the hydraulic efficiency-safety trade-off (Figure 4.5A). However, the trade-off seems to be unconventional, considering the potential difference in water availability across the forest successions. Li et al. (2018) and Zhu et al. (2017) found relationship between P_{50} and K_s across tree species from the habitats with contrasting water availability, in which species at drier site had lower K_s and more resistant to xylem cavitation than those from the wetter site. However, our results did not show distinct variation among sites under contrasting soil water availability, partly because of the insignificant variation in K_s and P_{50} across forest stages (Table 4.2). Moreover, we found no clear pattern in MVL across the forest successions (Table 4.2), and no significant relationship between MVL and P_{50} across the studies sites (Figure 4.5B). This could imply a weak influence of vessel length to cavitation resistance in this study, consistent with Markesteijn et al. (2011) that also found an unclear association between vessel length and xylem vulnerability in an Amazonian tropical forest.

In each forest succession, the coexisting dominant tree species differed in their hydraulic properties, especially cavitation resistance (Table 4.2, Figure 4.4). Larger variations in P_{50} were found in OF and YF than in IF, based on their coefficients of variation. Calculated from the percentage of the standard deviation to the mean, the coefficients of variation of P_{50} in OF and YF were 43.55% and 42.86%, respectively, while that in IF was 23.16%. Cartwright et al. (2020) suggests that substantial variability in drought response within an ecosystem can be driven by endogenous factors (i.e., morphological and phenological characters) and by exogenous factors (i.e., climate, topographic, and hydrologic characteristics). In this study, differences in leaf phenology among the dominant tree species can be found in OF and YF. Compared to the other evergreen species within the same site, deciduous tree species, *D. gracilis* in OF and *C. cochinchinense* in YF, showed a relatively less conservative hydraulic strategy, with more hydraulically efficient (higher K_s) but less resistance to xylem cavitation (lower P_{50}). Such risky hydraulic strategy deployed by deciduous tree species but not in evergreen was also found in other studies from tropical forests (Chen et al., 2017; Choat et al., 2005; Markesteijn et al., 2011) and subtropical forests (Krober et al., 2014). In addition, some exogenous factors may contribute to the large variation in P_{50}, particularly in OF. This could be explained by high microhabitat heterogeneity in OF (Brockelman et al., 2017), that might lead to spatial distribution of vegetation with varying sensitivity to water availability within the site. For example, species with presumably better access to water sources, e.g., *S. sigun* which dominated in flat lowland near streamside, showed higher vulnerability to cavitation among the others. On the contrary, species with limiting soil water, e.g., *I. chevalieri* which occupied in a hilly slope, showed relatively less vulnerable to cavitation compared to the rest of the species. Consistent with our finding, Zhang et al. (2021) and Zhu et al. (2017) found a wide range of P_{50} in tropical karst forests, in which species existing in the middle to top of hilly areas were more resistant to cavitation than species dominated in lowlands or valleys, resulting from soil water gradient. Nevertheless, further investigations on hydraulic architecture, sapwood water storage capacity, and rooting depth should be performed to confirm such speculations.

In terrestrial plants, the ability to sustain xylem water transport under water deficit conditions is crucial for plant growth and survival. Trees may operate close to their critical cavitation thresholds (e.g., P_{50}) to maximize stomatal conductivity and thus carbon assimilation (Brodribb & Feild, 2000; Jones & Sutherland, 1991; Mitchell et al., 2013; Santiago et al., 2004). However, operating close to or beyond the limits poses a significant risk of water stress-induced cavitation that reduces water transport efficiency (K_s) in xylem and consequently leads to plant dehydration and mortality (Blackman et al., 2019; Urli et al., 2013). Our results showed that all dominant tree species from each successional stage experienced the midday leaf water potentials during the dry season that could result in loss of hydraulic conductivity (PLC_{dry}) in different levels (Table 4.2, Figure 4.4). Based on xylem vulnerability curves and midday leaf water potential, most of the studied tree species operated well below P_{50} and their Ψ_{md} corresponded to about 4.5%, 13%, and 18% loss of hydraulic conductivity in OF, IF, and YF, respectively. As would be expected, species with higher resistance to xylem cavitation tended to lose little hydraulic conductivity during the dry season across the successions. For example, species with high cavitation resistance, e.g., *I. chevalieri* in OF, *S. cochinchinensis* in IF, and *A. integerrima* in YF, showed lower than 2% in PLC_{dry}. The reverse can be seen in species that are more vulnerable to cavitation, e.g., *S. sigun* in OF, *M. gamblei* in IF, *C. cochinchinense* in YF, which exhibited 7% to 53% loss of hydraulic conductance during water deficit condition. The probability of losing higher xylem water transport efficiency related to the tension experienced during the dry season appear to be associated with species' performance to deal with cavitation. Similar findings were obtained from a karstic woodland (Nardini et al., 2013), an Amazonian tropical forest (Markesteijn et al., 2011), and across forest biomes (Choat et al., 2012). This result, thus, imply the significance of cavitation resistance in determining species risk of hydraulic dysfunction during low water availability.

Differences in adaptive strategies and hydraulic properties among species can be seen as the resistance and resilience of a species to disturbances, such as climate change-induced water stress, and have broad implications on forest management and planning. In accordance with warming atmosphere and more variable droughts, it is important for forest restoration and conservation to consider the threshold at which tree mortality would occur (Hérault & Gourlet-Fleury, 2016), in order to maintain and promote the species that could well adapt in a particular place, both current and in the future conditions. With regards to forest restoration, there are several approaches proposed to facilitate natural forest recovery and restore desired ecosystem services in disturbed forests. One approach is to start with planting native fast-growing species, i.e., pioneer species, to create the canopy coverage, before recruiting other species (Lamb et al., 2005). Over time, these pioneer species would initiate the canopy architecture that draws seed dispersers, shades out light-demanding pasture grasses, increases soil nutrients, and reduces stressful microclimate conditions (Holl, 2012), which cooperatively creating a more suitable condition for seedling establishment and facilitating the recovery of the disturbed forests. Once the site condition is more favorable, planting the other species, i.e., generalist or late-coming species, can be done to increase the diversity, resiliency, and ecosystem services of the area. In the context of climate variability, selecting the pioneer species with low P_{50} and PLC_{dry}, e.g., *A. integerrima* or *E. acuminata*, instead of any fast-growing species would be more beneficial due to their abilities to rapidly recolonize and ameliorate the site conditions, as well as lower risk of cavitation-induced tree mortality from future warmer climate conditions. Likewise, for forest conservation, encouraging species with higher cavitation resistance (lower P_{50}) and ability to sustain higher xylem water transport during the dry season (lower PLC_{dry}) would be a better choice for maintaining forest health and vitality in response to a hotter and drier future. Several studies have demonstrated the ecosystem functions and services provided by tropical forests, such as the contribution in global water and carbon cycles, the conservation of biodiversity, or the protection of soil and water resources (Avissar & Werth, 2005; FAO & UNEP, 2020; Poker & MacDicken, 2016). Apart from human disturbances, tropical forests have been constantly affected by extreme climate events, especially drought that has the greatest impact on forested areas (McDowell et al., 2018; Reichstein et al., 2013).

The ongoing effect of droughts accelerates the rate of tree mortality and forest decline, particularly to the species that are more vulnerable to water deficit, leading to loss of biodiversity and adverse impacts on natural resources and ecosystem functions. Thus, encouraging species with higher resistant to drought-induce cavitation in tropical forests may help buffer against potential degradations of soil and hydrological conditions from future droughts, and thereby counteract the mortality of vulnerable species and maintain the overall resilience and integrity of the forests. All in all, under the scenarios of climate change, selecting the right tree species for the right site and appropriate condition is important to increase the likelihood of success and effectiveness in forest restoration and conservation for accelerating the natural recovery in degraded ecosystems close to the former condition (Elliott et al., 2003; Hérault & Piponiot, 2018; Vieira & Scariot, 2006).

To improve the understanding of plant hydraulic in Khao Yai National Park, there are some areas in need of further investigation. Environmental data from different forest successional stages should be measured to confirm the distinct differences in their microclimatic conditions. Additional studies on soil moisture dynamics, rooting depth, and species demographic rate (e.g., growth or mortality rates), as well as more frequent data collection of water potential can be done to gain insights into the behavior of plant water status from different forest successional stages at a more robust time series. Further studies on xylem anatomy, stem water storage, and pit functional properties are also recommended for a more persuasive conclusion of xylem water transport (K_s) and its association with xylem cavitation resistance (P_{50}) of different tree species. We also require a better understanding of plant hydraulic in different part of the tree, especially belowground, because tree mortality is likely to be resulted from a stack of impacts from different organs. By looking at the whole plant hydraulic basis, it will provide more useful data and definitive information for stating the limits of drought tolerance of different tree species and determining trends in future drought-induced mortality of forests in different successional stages.

CHAPTER 5
CONCLUSIONS

Given that the near-future droughts will become more frequent and more severe in Southeast Asia, the urge for an improved mechanistic understanding of forest responses to water stress is crucial. In this study, we evaluated seasonal variation in midday leaf water status (Ψ_{md}) and hydraulic properties of dominant tree species across forest successional stages in Khao Yai National Park, Thailand. Our results showed that, in general, seasonal variation in Ψ_{md} varied significantly, both at the forest and species levels. At the forest level, lower Ψ_{md} during water-limited conditions, e.g., dry season, and greater variation in Ψ_{md} resulted from seasonal changes were observed in younger and drier sites. This could be an adaptive strategy to optimize photosynthesis and growth with the cost of higher risk of dehydration and hydraulic failure. At the species level, species occupying in multiple sites (i.e., *S. cochinchinensis*, *S. wallichii*, and *S. nervosum*) were examined. For these species, there were different changes and patterns in Ψ_{md} induced by seasonal changes across the study sites, suggesting the species-specific response to environmental changes.

Our study also showed a high level of interspecific variation in key hydraulic properties among the dominant tree species in each plot, resulting in unclear variations in maximum vessel length (MVL), maximum xylem specific hydraulic conductivity (K_{smax}), and xylem vulnerability (P_{50}) across the forest successions. This substantial variability could be resulted from differences in plant phenological properties or large spatial differentiation within the site. Among the study sites, there was a tendency for some species at drier sites to possess xylem with higher cavitation resistance was found (e.g., *D. gracilis* in OF vs. *A. integerrima* in YF), although the same pattern was not observed in species in multiple sites. This may imply that using only the operational limits of plant water transport to evaluate species' performance to drought stress could be misleading. Combining the data from all species and successional stages, a negative association between P_{50} and K_{smax} was found, supporting the hydraulic efficiency-safety trade-off. However, P_{50} did not significantly related to MVL, suggesting a weak influence of vessel length to xylem cavitation in this study. We also found that all dominant tree species from each succession experienced changes in midday leaf water potentials during the dry season that could result in loss of hydraulic conductivity (PLC_{dry}) in different levels. Species with higher cavitation resistance tended to have lower PLC_{dry} across the successions, while species with higher xylem vulnerability appeared to lose more hydraulic conductivity during the dry season. This result may indicate the functional dependence of species' performance on cavitation resistance and their responses during water deficit.

Understanding how plants respond to water stress from different tree species and different forest successions is not only informative for the forest conservation and restoration efforts, but also the predictions of tree mortality across the successions. By selecting and promoting species that could be well adapted in a particular place, as represented by P_{50} and PLC_{dry}, the likelihood of success of forest restoration and conservation in a drier and hotter future could be enhanced. Nevertheless, studies involving xylem hydraulic architecture, stem water storage, and plant hydraulic belowground would be valuable for a more comprehensive understanding of the effect of low water availability on this significant ecosystem.

REFERENCES

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann, H., Cobb, R. C., Collins, A. D., Dickman, L. T., Duan, H., Ewers, B. E., Galiano, L., Galvez, D. A., Garcia-Forner, N., Gaylord, M. L., Germino, M. J., Gessler, A., Hacke, U. G., Hakamada, R., Hector, A., Jenkins, M. W., Kane, J. M., Kolb, T. E., Law, D. J., Lewis, J. D., Limousin, J.-M., Love, D. M., Macalady, A. K., Martínez-Vilalta, J., Mencuccini, M., Mitchell, P. J., Muss, J. D., O'Brien, M. J., O'Grady, A. P., Pangle, R. E., Pinkard, E. A., Piper, F. I., Plaut, J. A., Pockman, W. T., Quirk, J., Reinhardt, K., Ripullone, F., Ryan, M. G., Sala, A., Sevanto, S., Sperry, J. S., Vargas, R., Vennetier, M., Way, D. A., Xu, C., Yepez, E. A., & McDowell, N. G. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, *1*(9), 1285-1291. https://doi.org/10.1038/s41559-017-0248-x

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J. H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660-684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderegg, W. R. L., Kane, J. M., & Anderegg, L. D. L. (2013). Consequences of widespread tree Mortality triggered by drought and temperature stress. *Nature Climate Change*, *3*(1), 30-36. https://doi.org/DOI 10.1038/nclimate1635

Avissar, R., & Werth, D. (2005). Global hydroclimatological teleconnections resulting from tropical deforestation. *Journal of Hydrometeorology*, *6*(2), 134-145. https://doi.org/Doi 10.1175/Jhm406.1

Balderas Torres, A., & Lovett, J. C. (2012). Using basal area to estimate aboveground carbon stocks in forests: La Primavera Biosphere's Reserve, Mexico. *Forestry: An International Journal of Forest Research*, *86*(2), 267-281. https://doi.org/10.1093/forestry/cps084

Baltzer, J. L., Davies, S. J., Bunyavejchewin, S., & Noor, N. S. M. (2008). The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. *Functional Ecology*, *22*(2), 221-231. https://doi.org/10.1111/j.1365-2435.2007.01374.x

Barbeta, A., Mejia-Chang, M., Ogaya, R., Voltas, J., Dawson, T. E., & Penuelas, J. (2015). The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. *Global Change Biology*, *21*(3), 1213-1225. https://doi.org/10.1111/gcb.12785

Barnard, D. M., Meinzer, F. C., Lachenbruch, B., McCulloh, K. A., Johnson, D. M., & Woodruff, D. R. (2011). Climate-related trends in sapwood biophysical properties in two conifers: avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance. *Plant Cell and Environment*, *34*(4), 643-654. https://doi.org/10.1111/j.1365-3040.2010.02269.x

Barros, F. D., Bittencourt, P. R. L., Brum, M., Restrepo-Coupe, N., Pereira, L., Teodoro, G. S., Saleska, S. R., Borma, L. S., Christoffersen, B. O., Penha, D., Alves, L. F., Lima, A. J. N., Carneiro, V. M. C., Gentine, P., Lee, J. E., Aragao, L. E. O. C., Ivanov, V., Leal, L. S. M., Araujo, A. C., & Oliveira, R. S. (2019). Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Nino-induced drought. *New Phytologist*, *223*(3), 1253-1266. https://doi.org/10.1111/nph.15909

Bettinger, P., Boston, K., Siry, J., & Grebner, D. (2017). Valuing and Characterizing Forest Conditions. In (pp. 21-63). https://doi.org/10.1016/B978-0-12-809476-1.00002-3

Bittencourt, P. R. L., Oliveira, R. S., da Costa, A. C. L., Giles, A. L., Coughlin, I., Costa, P. B., Bartholomew, D. C., Ferreira, L. V., Vasconcelos, S. S., Barros, F. V., Junior, J. A. S., Oliveira, A. A. R., Mencuccini, M., Meir, P., & Rowland, L. (2020). Amazonia trees have limited capacity to acclimate plant hydraulic properties in response to long-term drought. *Global Change Biology*, *26*(6), 3569-3584. https://doi.org/https://doi.org/10.1111/gcb.15040

Blackman, C. J., Creek, D., Maier, C., Aspinwall, M. J., Drake, J. E., Pfautsch, S., O'Grady, A., Delzon, S., Medlyn, B. E., Tissue, D. T., & Choat, B. (2019). Drought response strategies and hydraulic traits contribute to mechanistic understanding of plant dry-down to hydraulic failure. *Tree Physiology*, *39*(6), 910-924. https://doi.org/10.1093/treephys/tpz016

Borchert, R., & Pockman, W. T. (2005). Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiology*, *25*(4), 457-466. https://doi.org/DOI 10.1093/treephys/25.4.457

Boyer, J. S., & Knipling, E. B. (1965). Isopiestic Technique for Measuring Leaf Water Potentials with a Thermocouple Psychrometer. *Proceedings of the National Academy of Sciences of the United States of America*, *54*(4), 1044-1051. https://pubmed.ncbi.nlm.nih.gov/5219815

Boyer, J. S., & Kramer, P. J. (1995). *Measuring the water status of plants and soils*. Academic Press.

Bretfeld, M., Ewers, B. E., & Hall, J. S. (2018). Plant water use responses along secondary forest succession during the 2015-2016 El Nino drought in Panama. *New Phytologist*, *219*(3), 885-899. https://doi.org/10.1111/nph.15071

Briggs, L. J. (1950). Limiting negative pressure of water [2]. In (Vol. 21, pp. 721-722).

Brockelman, W. Y., Nathalang, A., & Maxwell, J. F. (2017). *Mo Singto Forest Dynamics Plot: Flora and Ecology*. National Science and Technology Development Agency.

Brodribb, T. J., & Cochard, H. (2009). Hydraulic Failure Defines the Recovery and Point of Death in Water-Stressed Conifers. *Plant Physiology*, *149*(1), 575-584. https://doi.org/10.1104/pp.108.129783

Brodribb, T. J., & Feild, T. S. (2000). Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell and Environment*, *23*(12), 1381-1388. https://doi.org/DOI 10.1046/j.1365-3040.2000.00647.x

Brodribb, T. J., Skelton, R. P., McAdam, S. A. M., Bienaime, D., Lucani, C. J., & Marmottant, P. (2016). Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New Phytologist*, *209*(4), 1403-1409. https://doi.org/10.1111/nph.13846

Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., Campanello, P., & Scholz, F. G. (2005). Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in neotropical savanna trees. *Trees-Structure and Function*, *19*(3), 296-304. https://doi.org/10.1007/s00468-004-0391-2

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(4), 1474-1478. https://doi.org/10.1073/pnas.1010070108

Cartwright, J. M., Littlefield, C. E., Michalak, J. L., Lawler, J. J., & Dobrowski, S. Z. (2020). Topographic, soil, and climate drivers of drought sensitivity in forests and shrublands of the Pacific Northwest, USA. *Scientific Reports*, *10*(1). https://doi.org/ARTN 1848610.1038/s41598-020-75273-5

Chanthorn, W., Hartig, F., & Brockelman, W. Y. (2017). Structure and community composition in a tropical forest suggest a change of ecological processes during stand development. *Forest Ecology and Management*, *404*, 100-107. https://doi.org/10.1016/j.foreco.2017.08.001

Chanthorn, W., Ratanapongsai, Y., Brockelman, W., Allen, M., Favier, C., & Dubois, M.-A. (2016). Viewing tropical forest succession as a three-dimensional dynamical system. *Theoretical Ecology*, *9*. https://doi.org/10.1007/s12080-015-0278-4

Chazdon, R. (2013). Tropical Forest Regeneration. In (pp. 277-286). https://doi.org/10.1016/B978-0-12-384719-5.00377-4

Chen, Y. J., Schnitzer, S. A., Zhang, Y. J., Fan, Z. X., Goldstein, G., Tomlinson, K. W., Lin, H., Zhang, J. L., & Cao, K. F. (2017). Physiological regulation and efficient xylem water transport regulate diurnal water and carbon balances of tropical lianas. *Functional Ecology*, *31*(2), 306-317. https://doi.org/10.1111/1365-2435.12724

Choat, B., Ball, M. C., Luly, J. G., & Holtum, J. A. M. (2005). Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees-Structure and Function*, *19*(3), 305-311. https://doi.org/10.1007/s00468-004-0392-1

Choat, B., Brodersen, C. R., & McElrone, A. J. (2015). Synchrotron X-ray microtomography of xylem embolism in Sequoia sempervirens saplings during cycles of drought and recovery. *New Phytologist*, *205*(3), 1095-1105. https://doi.org/10.1111/nph.13110

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., Lopez, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531-539. https://doi.org/10.1038/s41586-018-0240-x

Choat, B., Cobb, A. R., & Jansen, S. (2008). Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. *New Phytologist*, *177*(3), 608-625. https://doi.org/10.1111/j.1469-8137.2007.02317.x

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., & Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*(7426), 752-+. https://doi.org/10.1038/nature11688

Choat, B., Sack, L., & Holbrook, N. M. (2007). Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. *New Phytologist*, *175*(4), 686-698. https://doi.org/10.1111/j.1469-8137.2007.02137.x

Cochard, H., Badel, E., Herbette, S., Delzon, S., Choat, B., & Jansen, S. (2013). Methods for measuring plant vulnerability to cavitation: a critical review. *Journal of Experimental Botany*, *64*(15), 4779-4791. https://doi.org/10.1093/jxb/ert193

Cochard, H., Herbette, S., Barigah, T., Badel, E., Ennajeh, M., & Vilagrosa, A. (2010). Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. *Plant Cell and Environment*, *33*(9), 1543-1552. https://doi.org/10.1111/j.1365-3040.2010.02163.x

Comita, L. S., & Engelbrecht, B. M. J. (2009). Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology*, *90*(10), 2755-2765. https://doi.org/Doi 10.1890/08-1482.1

Crist, E., Mora, C., & Engelman, R. (2017). The interaction of human population, food production, and biodiversity protection. *Science*, *356*(6335), 260. https://doi.org/10.1126/science.aal2011

Delzon, S., Douthe, C., Sala, A., & Cochard, H. (2010). Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant Cell and Environment*, *33*(12), 2101-2111. https://doi.org/10.1111/j.1365-3040.2010.02208.x

Dixon, H. H., & Joly, J. (1895). On the Ascent of Sap. *Philosophical Transactions of the Royal Society of London. B*, *186*, 563-576. http://www.jstor.org/stable/91804

Domec, J. C., King, J. S., Ward, E., Oishi, A. C., Palmroth, S., Radecki, A., Bell, D. M., Miao, G. F., Gavazzi, M., Johnson, D. M., McNulty, S. G., Sun, G., & Noormets, A. (2015). Conversion of natural forests to managed forest plantations decreases tree resistance to prolonged droughts. *Forest Ecology and Management*, *355*, 58-71. https://doi.org/10.1016/j.foreco.2015.04.012

Domec, J. C., Scholz, F. G., Bucci, S. J., Meinzer, F. C., Goldstein, G., & Villalobos-Vega, R. (2006). Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status. *Plant Cell and Environment*, *29*(1), 26-35. https://doi.org/DOI 10.1111/j.1365-3040.2005.01397.x

Edwards, W. R. N., & Jaris, P. G. (1982). Relations between water content, potential and permeability in stems of conifers. *Plant, Cell & Environment*, *5*(4), 271-277. https://doi.org/https://doi.org/10.1111/1365-3040.ep11572656

Elliott, S., Navakitbumrung, P., Kuarak, C., Zangkum, S., Anusarnsunthorn, V., & Blakesley, D. (2003). Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. *Forest Ecology and Management*, *184*(1-3), 177-191. https://doi.org/10.1016/S0378-1127(03)00211-1

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, *447*(7140), 80-U82. https://doi.org/10.1038/nature05747

Engelbrecht, B. M. J., Tyree, M. T., & Kursar, T. A. (2007). Visual assessment of wilting as a measure of leaf water potential and seedling drought survival. *Journal of Tropical Ecology*, *23*, 497-500. https://doi.org/10.1017/S026646740700421x

Estoque, R. C., Ooba, M., Avitabile, V., Hijioka, Y., DasGupta, R., Togawa, T., & Murayama, Y. (2019). The future of Southeast Asia's forests. *Nature Communications*, *10*. https://doi.org/ARTN 182910.1038/s41467-019-09646-4

Ewers, B. E., Gower, S. T., Bond-Lamberty, B., & Wang, C. K. (2005). Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell and Environment*, *28*(5), 660-678. https://doi.org/DOI 10.1111/j.1365-3040.2005.01312.x

Ewers, F. (1985). Xylem' Structure and Water Conduction in Conifer Trees, Dicot Trees, and Llanas. *Iawa Journal*, *6*, 309-317.

Ewers, F. W., & Fisher, J. B. (1989). TECHNIQUES FOR MEASURING VESSEL LENGTHS AND DIAMETERS IN STEMS OF WOODY PLANTS. *American Journal of Botany*, *76*(5), 645-656. https://doi.org/https://doi.org/10.1002/j.1537-2197.1989.tb11360.x

FAO. (2020). Global forest resources assessment 2020: Main report. https://doi.org/https://doi.org/10.4060/ca9825en

FAO, & UNEP. (2020). The State of the World’s Forests 2020. Forests, biodiversity and people. . https://doi.org/https://doi.org/10.4060/ca8642en.

Farooq, M., Hussain, M., Wahid, A., & Siddique, K. H. M. (2012). Drought Stress in Plants: An Overview. In R. Aroca (Ed.), *Plant Responses to Drought Stress: From Morphological to Molecular Features* (pp. 1-33). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-32653-0_1

Fetcher, N., Oberbauer, S. F., & Strain, B. R. (1985). Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology*, *29*(2), 145-155. https://doi.org/10.1007/BF02189035

Gardon, F. R., Toledo, R. M. d., Brentan, B. M., & Santos, R. F. d. (2020). Rainfall interception and plant community in young forest restorations. *Ecological Indicators*, *109*, 105779. https://doi.org/https://doi.org/10.1016/j.ecolind.2019.105779

Geldner, N. (2013). The Endodermis. *Annual Review of Plant Biology*, *64*(1), 531-558. https://doi.org/10.1146/annurev-arplant-050312-120050

González, L., & Reigosa Roger, M. J. (2001). Plant Water Status. In M. J. Reigosa Roger (Ed.), *Handbook of Plant Ecophysiology Techniques* (pp. 185-191). Springer Netherlands. https://doi.org/10.1007/0-306-48057-3_12

Granier, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, *3*(4), 309-320. https://doi.org/10.1093/treephys/3.4.309

Grebe, M. (2011). PLANT BIOLOGY Unveiling the Casparian strip. *Nature*, *473*(7347), 294-295. https://doi.org/DOI 10.1038/473294a

Groover, A. (2017). Age-Related Changes in Tree Growth and Physiology. In (pp. 1-7). https://doi.org/10.1002/9780470015902.a0023924

Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., Sperry, J. S., & McDowell, N. G. (2020). Plant responses to rising vapor pressure deficit. *New Phytologist*, *226*(6), 1550-1566. https://doi.org/https://doi.org/10.1111/nph.16485

Hacke, U. G., Sperry, J. S., Wheeler, J. K., & Castro, L. (2006). Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology*, *26*(6), 689-701. https://doi.org/DOI 10.1093/treephys/26.6.689

Hasselquist, N. J., Allen, M. F., & Santiago, L. S. (2010). Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia*, *164*(4), 881-890. https://doi.org/10.1007/s00442-010-1725-y

Heithecker, T. D., & Halpern, C. B. (2007). Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *Forest Ecology and Management*, *248*(3), 163-173. https://doi.org/10.1016/j.foreco.2007.05.003

Hérault, B., & Gourlet-Fleury, S. (2016). Will Tropical Rainforests Survive Climate Change? In E. Torquebiau (Ed.), *Climate Change and Agriculture Worldwide* (pp. 183-196). Springer Netherlands. https://doi.org/10.1007/978-94-017-7462-8_14

Hérault, B., & Piponiot, C. (2018). Key drivers of ecosystem recovery after disturbance in a neotropical forest. *Forest Ecosystems*, *5*(1), 2. https://doi.org/10.1186/s40663-017-0126-7

Holl, K. (2012). Tropical forest restoration. In A. Jelte van & A. James (Eds.), *Restoration Ecology: The New Frontier* (Second Edition ed., pp. 103-114). Blackwell Publishing.

Imai, N., Furukawa, T., Tsujino, R., Kitamura, S., & Yumoto, T. (2018). Factors affecting forest area change in Southeast Asia during 1980-2010 (vol 13, e0197391, 2018). *Plos One*, *13*(6). https://doi.org/ARTN e019990810.1371/journal.pone.0199908

IPCC. (2019). Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems.

Islam, M. A., Chan, A., Ashfold, M. J., Ooi, C. G., & Azari, M. (2018). Effects of El-Niño, Indian Ocean Dipole, and Madden-Julian Oscillation on Surface Air Temperature and Rainfall Anomalies over Southeast Asia in 2015. *Atmosphere*, *9*(9), 352. https://www.mdpi.com/2073-4433/9/9/352

Jones, H. G., & Sutherland, R. A. (1991). Stomatal control of xylem embolism. *Plant, Cell & Environment*, *14*(6), 607-612. https://doi.org/https://doi.org/10.1111/j.1365-3040.1991.tb01532.x

Jung, J.-H., Kim, S.-G., Seo, P. J., & Park, C.-M. (2008). Molecular Mechanisms Underlying Vascular Development. In J.-C. Kader & M. Delseny (Eds.), *Advances in Botanical Research* (Vol. 48, pp. 1-68). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-2296(08)00401-1

Kaewthongrach, R., Vitasse, Y., Lamjiak, T., & Chidthaisong, A. (2019). Impact of Severe Drought during the Strong 2015/2016 El Nino on the Phenology and Survival of Secondary Dry Dipterocarp Species in Western Thailand. *Forests*, *10*(11). https://doi.org/ARTN 96710.3390/f10110967

Kerstiens, G. (1996). Cuticular water permeability and its physiological significance. *Journal of Experimental Botany*, *47*(305), 1813-1832. https://doi.org/DOI 10.1093/jxb/47.12.1813

Krober, W., Zhang, S. R., Ehmig, M., & Bruelheide, H. (2014). Linking Xylem Hydraulic Conductivity and Vulnerability to the Leaf Economics Spectrum-A Cross-Species Study of 39 Evergreen and Deciduous Broadleaved Subtropical Tree Species. *Plos One*, *9*(11). https://doi.org/ARTN e10921110.1371/journal.pone.0109211

Kursar, T. A., Engelbrecht, B. M. J., Burke, A., Tyree, M. T., El Omari, B., & Giraldo, J. P. (2009). Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology*, *23*(1), 93-102. https://doi.org/10.1111/j.1365-2435.2008.01483.x

Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, *310*(5754), 1628-1632. https://doi.org/10.1126/science.1111773

Lambers, H., Chapin, F. S., & Pons, T. L. (1998). Photosynthesis, Respiration, and Long-Distance Transport. In *Plant Physiological Ecology* (pp. 10-153). Springer New York. https://doi.org/10.1007/978-1-4757-2855-2_2

Larter, M., Brodribb, T. J., Pfautsch, S., Burlett, R., Cochard, H., & Delzon, S. (2015). Extreme Aridity Pushes Trees to Their Physical Limits. *Plant Physiology*, *168*(3), 804-+. https://doi.org/10.1104/pp.15.00223

Lawrence, D., & Vandecar, K. (2015). Effects of tropical deforestation on climate and agriculture (vol 5, pg 27, 2015). *Nature Climate Change*, *5*(2), 174-174. https://doi.org/DOI 10.1038/nclimate2502

Lawrence, M. G. (2005). The relationship between relative humidity and the dewpoint temperature in moist air - A simple conversion and applications. *Bulletin of the American Meteorological Society*, *86*(2), 225-+. https://doi.org/10.1175/Bams-86-2-225

Lebrija-Trejos, E., Bongers, F., Garcia, E. A. P., & Meave, J. A. (2008). Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*, *40*(4), 422-431. https://doi.org/10.1111/j.1744-7429.2008.00398.x

Lebrija-Trejos, E., Perez-Garcia, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, *91*(2), 386-398. https://doi.org/Doi 10.1890/08-1449.1

Lebrija-Trejos, E., Perez-Garcia, E. A., Meave, J. A., Poorter, L., & Bongers, F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, *27*, 477-489. https://doi.org/10.1017/S0266467411000253

Lee, Y. K., Lee, D. K., Woo, S. Y., Abraham, E. R. G., Carandang, W. M., Yeo, U. S., & Park, C. (2006). Differences of tree species composition and microclimate between a mahogany (swietenia macrophylla king) plantation and a secondary forest in Mt. Makiling, Philippines. *Forest Science and Technology*, *2*(1), 1-12. https://doi.org/10.1080/21580103.2006.9656293

Li, X. M., Blackman, C. J., Choat, B., Duursma, R. A., Rymer, P. D., Medlyn, B. E., & Tissue, D. T. (2018). Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant Cell and Environment*, *41*(3), 646-660. https://doi.org/10.1111/pce.13129

Li, Y. Y., Sperry, J. S., Taneda, H., Bush, S. E., & Hacke, U. G. (2008). Evaluation of centrifugal methods for measuring xylem cavitation in conifers, diffuse- and ring-porous angiosperms. *New Phytologist*, *177*(2), 558-568. https://doi.org/10.1111/j.1469-8137.2007.02272.x

Loepfe, L., Martinez-Vilalta, J., Pinol, J., & Mencuccini, M. (2007). The relevance of xylem network structure for plant hydraulic efficiency and safety. *Journal of Theoretical Biology*, *247*(4), 788-803. https://doi.org/10.1016/j.jtbi.2007.03.036

Maherali, H., Pockman, W. T., & Jackson, R. B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, *85*(8), 2184-2199. https://doi.org/Doi 10.1890/02-0538

Markesteijn, L., Iraipi, J., Bongers, F., & Poorter, L. (2010). Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. *Journal of Tropical Ecology*, *26*, 497-508. https://doi.org/10.1017/S0266467410000271

Markesteijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant Cell and Environment*, *34*(1), 137-148. https://doi.org/10.1111/j.1365-3040.2010.02231.x

Marthews, T. R., Burslem, D. F. R. P., Paton, S. R., Yanyuez, F., & Mullins, C. E. (2008). Soil drying in a tropical forest: Three distinct environments controlled by gap size. *Ecological Modelling*, *216*(3-4), 369-384. https://doi.org/10.1016/j.ecolmodel.2008.05.011

Martin-StPaul, N., Delzon, S., & Cochard, H. (2017). Plant resistance to drought depends on timely stomatal closure. *Ecology Letters*, *20*(11), 1437-1447. https://doi.org/10.1111/ele.12851

Martin-StPaul, N. K., Longepierre, D., Huc, R., Delzon, S., Burlett, R., Joffre, R., Rambal, S., & Cochard, H. (2014). How reliable are methods to assess xylem vulnerability to cavitation? The issue of 'open vessel' artifact in oaks. *Tree Physiology*, *34*(8), 894-905. https://doi.org/10.1093/treephys/tpu059

Martinez-Vilalta, J., Anderegg, W. R. L., Sapes, G., & Sala, A. (2019). Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. *New Phytologist*, *223*(1), 22-32. https://doi.org/10.1111/nph.15644

Martinez-Vilalta, J., & Lloret, F. (2016). Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global and Planetary Change*, *144*, 94-108. https://doi.org/10.1016/j.gloplacha.2016.07.009

Martinez-Vilalta, J., Prat, E., Oliveras, I., & Pinol, J. (2002). Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia*, *133*(1), 19-29. https://doi.org/10.1007/s00442-002-1009-2

Matheny, A. M., Fiorella, R. P., Bohrer, G., Poulsen, C. J., Morin, T. H., Wunderlich, A., Vogel, C. S., & Curtis, P. S. (2017). Contrasting strategies of hydraulic control in two codominant temperate tree species. *Ecohydrology*, *10*(3). https://doi.org/ARTN e181510.1002/eco.1815

McCarthy, J. (2001). Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Reviews 9*, 1-59. https://doi.org/10.1139/er-9-1-1

McCully, M. E. (1999). Roots in soil: Unearthing the complexities of roots and their rhizospheres. *Annual Review of Plant Physiology and Plant Molecular Biology*, *50*, 695-+. https://doi.org/DOI 10.1146/annurev.arplant.50.1.695

McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C. G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D. J., Kassim, A. R., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malhi, Y., McMahon, S. M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H. C., Phillips, O. L., Powell, T., Sierra, C. A., Sperry, J., Warren, J., Xu, C., & Xu, X. (2018). Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol*, *219*(3), 851-869. https://doi.org/10.1111/nph.15027

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719-739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution*, *26*(10), 523-532. https://doi.org/10.1016/j.tree.2011.06.003

McDowell, N. G., Brodribb, T. J., & Nardini, A. (2019). Hydraulics in the 21st century. *New Phytologist*, *224*(2), 537-542. https://doi.org/https://doi.org/10.1111/nph.16151

Mencuccini, M. (2003). WATER RELATIONS OF PLANTS | Xylem. In (pp. 1440-1449). https://doi.org/10.1016/B0-12-227050-9/00107-1

Mitchell, P. J., O'Grady, A. P., Tissue, D. T., White, D. A., Ottenschlaeger, M. L., & Pinkard, E. A. (2013). Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist*, *197*(3), 862-872. https://doi.org/10.1111/nph.12064

Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., Garcia-Valdes, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports, 8*. https://doi.org/ARTN 562710.1038/s41598-018-23763-y

Mueller, R. C., Scudder, C. M., Porter, M. E., Trotter, R. T., Gehring, C. A., & Whitham, T. G. (2005). Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology, 93*(6), 1085-1093. https://doi.org/10.1111/j.1365-2745.2005.01042.x

Nardini, A., Battistuzzo, M., & Savi, T. (2013). Shoot desiccation and hydraulic failure in temperate woody angiosperms during an extreme summer drought. *New Phytologist*, *200*(2), 322-329. https://doi.org/10.1111/nph.12288

Nolf, M., Creek, D., Duursma, R., Holtum, J., Mayr, S., & Choat, B. (2015). Stem and leaf hydraulic properties are finely coordinated in three tropical rain forest tree species. *Plant Cell and Environment, 38*(12), 2652-2661. https://doi.org/10.1111/pce.12581

Nonami, H., Boyer, J. S., & Steudle, E. (1987). Pressure probe and isopiestic psychrometer measure similar turgor. *Plant Physiology*, *83*(3), 592-595. https://doi.org/10.1104/pp.83.3.592

Oren, R., & Pataki, D. E. (2001). Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. *Oecologia*, *127*(4), 549-559. https://doi.org/DOI 10.1007/s004420000622

Pallardy, S. G. (2008). CHAPTER 11 - Absorption of Water and Ascent of Sap. In S. G. Pallardy (Ed.), *Physiology of Woody Plants (Third Edition)* (pp. 287-323). Academic Press. https://doi.org/https://doi.org/10.1016/B978-012088765-1.50012-9

Pammenter, N. W., & Vander Willigen, C. (1998). A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology*, *18*(8-9), 589-593. https://doi.org/DOI 10.1093/treephys/18.8-9.589

Pan, Y. D., Birdsey, R. A., Fang, J. Y., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S. L., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, *333*(6045), 988-993. https://doi.org/10.1126/science.1201609

Passioura, J. B. (2010). Plant–Water Relations. In *eLS*. https://doi.org/https://doi.org/10.1002/9780470015902.a0001288.pub2

Paulick, S., Dislich, C., Homeier, J., Fischer, R., & Huth, A. (2017). The carbon fluxes in different successional stages: modelling the dynamics of tropical montane forests in South Ecuador. *Forest Ecosystems*, *4*(1), 5. https://doi.org/10.1186/s40663-017-0092-0

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quetier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S., & Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167-234. https://doi.org/10.1071/Bt12225

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quetier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S., & Cornelissen, J. H. C. (2016). New handbook for standardised measurement of plant functional traits worldwide *Australian Journal of Botany*, *64*(7-8), 715-716. https://doi.org/10.1071/Bt12225_Co

Pineda-Garcia, F., Paz, H., & Meinzer, F. C. (2013). Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant Cell and Environment*, *36*(2), 405-418. https://doi.org/10.1111/j.1365-3040.2012.02582.x

Pineda-Garcia, F., Paz, H., Meinzer, F. C., & Angeles, G. (2016). Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology*, *36*(2), 208-217. https://doi.org/10.1093/treephys/tpv124

Pockman, W. T., & Sperry, J. S. (2000). Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany*, *87*(9), 1287-1299. https://doi.org/Doi 10.2307/2656722

Pockman, W. T., Sperry, J. S., & Oleary, J. W. (1995). Sustained and Significant Negative Water-Pressure in Xylem. *Nature*, *378*(6558), 715-716. https://doi.org/DOI 10.1038/378715a0

Poker, J., & MacDicken, K. (2016). Tropical Forest Resources: Facts and Tables. In L. Pancel & M. Köhl (Eds.), *Tropical Forestry Handbook* (pp. 3-45). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-54601-3_7

Popradit, A., Srisatit, T., Kiratiprayoon, S., Yoshimura, J., Ishida, A., Shiyomi, M., Murayama, T., Chantaranothai, P., Outtaranakorn, S., & Phromma, I. (2015). Anthropogenic effects on a tropical forest according to the distance from human settlements. *Scientific Reports*, *5*. https://doi.org/ARTN 1468910.1038/srep14689

Powell, T. L., Wheeler, J. K., de Oliveira, A. A. R., da Costa, A. C. L., Saleska, S. R., Meir, P., & Moorcroft, P. R. (2017). Differences in xylem and leaf hydraulic traits explain differences in drought tolerance among mature Amazon rainforest trees. *Global Change Biology*, *23*(10), 4280-4293. https://doi.org/10.1111/gcb.13731

Power, K., Barnett, J., Dickinson, T., & Axelsson, J. (2020). The Role of El Nino in Driving Drought Conditions over the Last 2000 Years in Thailand. *Quaternary*, *3*(2). https://doi.org/ARTN 1810.3390/quat3020018

Prado, C. H. B. d. A., Wenhui, Z., Cardoza Rojas, M. H., & Souza, G. M. (2004). Seasonal leaf gas exchange and water potential in a woody cerrado species community. *Brazilian Journal of Plant Physiology*, *16*(1), 7-16. https://doi.org/10.1590/S1677-04202004000100002

Rawson, H. M., Begg, J. E., & Woodward, R. G. (1977). The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. *Planta*, *134*(1), 5-10. https://doi.org/10.1007/BF00390086

Reed, J., van Vianen, J., Foli, S., Clendenning, J., Yang, K., MacDonald, M., Petrokofsky, G., Padoch, C., & Sunderland, T. (2017). Trees for life: The ecosystem service contribution of trees to food production and livelihoods in the tropics. *Forest Policy and Economics*, *84*, 62-71. https://doi.org/https://doi.org/10.1016/j.forpol.2017.01.012

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., & Wattenbach, M. (2013). Climate extremes and the carbon cycle. *Nature*, *500*(7462), 287-295. https://doi.org/10.1038/nature12350

Rood, S. B., Patino, S., Coombs, K., & Tyree, M. T. (2000). Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees-Structure and Function*, *14*(5), 248-257. https://doi.org/DOI 10.1007/s004680050010

Rosner, S., Heinze, B., Savi, T., & Dalla-Salda, G. (2019). Prediction of hydraulic conductivity loss from relative water loss: new insights into water storage of tree stems and branches. *Physiologia Plantarum*, *165*(4), 843-854. https://doi.org/10.1111/ppl.12790

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., Pullen, A. M., Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V., Malhi, Y., Grace, J., Mencuccini, M., & Meir, P. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, *528*(7580), 119-122. https://doi.org/10.1038/nature15539

Ruggiero, A., Punzo, P., Landi, S., Costa, A., Van Oosten, M. J., & Grillo, S. (2017). Improving Plant Water Use Efficiency through Molecular Genetics. *Horticulturae*, *3*(2). https://doi.org/ARTN 3110.3390/horticulturae3020031

Ruiz-Benito, P., Ratcliffe, S., Zavala, M. A., Martinez-Vilalta, J., Vila-Cabrera, A., Lloret, F., Madrigal-Gonzalez, J., Wirth, C., Greenwood, S., Kandler, G., Lehtonen, A., Kattge, J., Dahlgren, J., & Jump, A. S. (2017). Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. *Global Change Biology*, *23*(10), 4162-4176. https://doi.org/10.1111/gcb.13728

Ryan, M. G., Harmon, M. E., Birdsey, R. A., Giardina, C. P., Heath, L. S., Houghton, R. A., Jackson, R. B., McKinley, D. C., Morrison, J. F., Murray, B. C., Pataki, D. E., & Skog, K. E. (2010). A synthesis of the science on forests and carbon for U.S. forests. Issues in Ecology. *Ecological Society of America: Issues In Ecology*, *13*, 1-16.

Ryan, S. J., Palace, M. W., Hartter, J., Diem, J. E., Chapman, C. A., & Southworth, J. (2017). Population pressure and global markets drive a decade of forest cover change in Africa's Albertine Rift. *Applied Geography*, *81*, 52-59. https://doi.org/10.1016/j.apgeog.2017.02.009

Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., & Jones, T. (2004). Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, *140*(4), 543-550. https://doi.org/10.1007/s00442-004-1624-1

Schlesinger, W. H., & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, *189*, 115-117. https://doi.org/10.1016/j.agrformet.2014.01.011

Secchi, F., Pagliarani, C., & Zwieniecki, M. A. (2017). The functional role of xylem parenchyma cells and aquaporins during recovery from severe water stress. *Plant Cell and Environment*, *40*(6), 858-871. https://doi.org/10.1111/pce.12831

Sevanto, S., McDowell, N. G., Dickman, L. T., Pangle, R., & Pockman, W. T. (2014). How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell and Environment*, *37*(1), 153-161. https://doi.org/10.1111/pce.12141

Shaw, J. D., Steed, B. E., & DeBlander, L. T. (2005). Forest Inventory and Analysis (FIA) annual inventory answers the question: What is happening to pinyon-juniper woodlands? *Journal of Forestry*, *103*(6), 280-285. <Go to ISI>://WOS:000232416300004

Skelton, R. P., West, A. G., & Dawson, T. E. (2015). Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(18), 5744-5749. https://doi.org/10.1073/pnas.1503376112

Slik, J. W. F., Arroyo-Rodriguez, V., Aiba, S. I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M. L., Bellingham, P. J., van den Berg, E., Bernacci, L., Bispo, P. D., Blanc, L., Bohning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., Hockemba, M. B. N., Bunyavejchewin, S., Matos, D. C. L., Castillo-Santiago, M., Catharino, E. L. M., Chai, S. L., Chen, Y. K., Colwell, R. K., Chazdon, R. L., Clark, C., Clark, D. B., Clark, D. A., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., DeWalt, S. J., Doucet, J. L., Duque, A., Durigan, G., Eichhorn, K. A. O., Eisenlohr, P. V., Eler, E., Ewango, C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., de Oliveira, A. T., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J. F., Amarnath, G., Griffith, D. M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. A., Joly, C. A., de Jong, B. H. J., Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F., Lawes, M. J., do Amaral, I. L., Letcher, S. G., Lindsell, J., Lu, X. H., Mansor, A., Marjokorpi, A., Martin,

E. H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Metzger, J. P., Millet, J., Mohandass, D., Montero, J. C., Valeriano, M. D., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Onrizal, Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M. T. F., Pitman, N. C. A., Poorter, L., Poulsen, A. D., Poulsen, J., Powers, J., Prasad, R. C., Puyravaud, J. P., Razafimahaimodison, J. C., Reitsma, J., dos Santos, J. R., Spironello, W. R., Romero-Saltos, H., Rovero, F., Rozak, A. H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B. A., Santos, F., Sarker, S. K., Satdichanh, M., Schmitt, C. B., Schongart, J., Schulze, M., Suganuma, M. S., Sheil, D., Pinheiro, E. D., Sist, P., Stevart, T., Sukumar, R., Sun, I. F., Sunderland, T., Suresh, H. S., Suzuki, E., Tabarelli, M., Tang, J. W., Targhetta, N., Theilade, I., Thomas, D. W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J. L. C. H., Do, T. V., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S. A., Webb, C. O., Whitfeld, T., Wich, S. A., Williams, J., Wittmann, F., Woll, H., Yang, X. B., Yao, C. Y. A., Yap, S. L., Yoneda, T., Zahawi, R. A., Zakaria, R., Zang, R., de Assis, R. L., Luize, B. G., & Venticinque, E. M. (2015). An estimate of the number of tropical tree species (vol 112, pg 7472, 2015). *Proceedings of the National Academy of Sciences of the United States of America*, *112*(33), E4628-E4629. https://doi.org/10.1073/pnas.1512611112

Sperry, J., Donnelly, J., & Tyree, M. (1988). A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment*, *11*, 35-40. https://doi.org/10.1111/j.1365-3040.1988.tb01774.x

Sperry, J. S., Hacke, U. G., Oren, R., & Comstock, J. P. (2002). Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment*, *25*(2), 251-263. https://doi.org/DOI 10.1046/j.0016-8025.2001.00799.x

Sperry, J. S., & Saliendra, N. Z. (1994). Intra-Plant and Inter-Plant Variation in Xylem Cavitation in Betula-Occidentalis. *Plant Cell and Environment*, *17*(11), 1233-1241. https://doi.org/DOI 10.1111/j.1365-3040.1994.tb02021.x

Steppe, K. (2018). The potential of the tree water potential. *Tree Physiology, 38*(7), 937-940. https://doi.org/10.1093/treephys/tpy064

Stibig, H. J., Achard, F., Carboni, S., Rasi, R., & Miettinen, J. (2014). Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences*, *11*(2), 247-258. https://doi.org/10.5194/bg-11-247-2014

Taiz, L., & Zeiger, E. (2003). Plant physiology. 3rd edn. *Annals of Botany, 91*. https://doi.org/10.1093/aob/mcg079

Tan, F. S., Song, H. Q., Fu, P. L., Chen, Y. J., Siddiq, Z., Cao, K. F., & Zhu, S. D. (2020). Hydraulic safety margins of co-occurring woody plants in a tropical karst forest experiencing frequent extreme droughts. *Agricultural and Forest Meteorology*, *292*. https://doi.org/ARTN 10810710.1016/j.agrformet.2020.108107

Teskey, R. O., & Hinckley, T. M. (1986). Moisture: Effects of Water Stress on Trees. In T. C. Hennessey, P. M. Dougherty, S. V. Kossuth, & J. D. Johnson (Eds.), *Stress physiology and forest productivity: Proceedings of the Physiology Working Group Technical Session. Society of American Foresters National Convention, Fort Collins, Colorado, USA, July 28–31, 1985* (pp. 9-33). Springer Netherlands. https://doi.org/10.1007/978-94-009-4424-4_2

Thaiwater. (2019). Thailand Water Situation 2019. https://tiwrm.hii.or.th/current/YearlyReport2019/summary.html

Tor-ngern, P., Chart-asa, C., Chanthorn, W., Rodtassana, C., Yampum, S., Unawong, W., Nathalang, A., Brockelman, W., Srinoppawan, K., Chen, Y. J., & Hasselquist, N. J. (2021). Variation of leaf-level gas exchange rates and leaf functional traits of dominant trees across three successional stages in a Southeast Asian tropical forest. *Forest Ecology and Management*, *489*. https://doi.org/ARTN 11910110.1016/j.foreco.2021.119101

Trueba, S., Pouteau, R., Lens, F., Feild, T. S., Isnard, S., Olson, M. E., & Delzon, S. (2017). Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island. *Plant Cell and Environment*, *40*(2), 277-289. https://doi.org/10.1111/pce.12859

Turner, N. C. (1988). Measurement of plant water status by the pressure chamber technique. *Irrigation Science*, *9*(4), 289-308. https://doi.org/10.1007/BF00296704

Tyree, M., Davis, S., & Cochard, H. (1994). Biophysical Perspectives of Xylem Evolution: Is There a Tradeoff of Hydraulic Efficiency for Vulnerability to Dysfunction? *IAWA journal / International Association of Wood Anatomists*, *15*, 335-360. https://doi.org/10.1163/22941932-90001369

Tyree, M. T., & Zimmermann, M. H. (2002). Xylem Structure and the Ascent of Sap. *Springer*.

Urli, M., Porte, A. J., Cochard, H., Guengant, Y., Burlett, R., & Delzon, S. (2013). Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*, *33*(7), 672-683. https://doi.org/10.1093/treephys/tpt030

Vander Willigen, C., Sherwin, H. W., & Pammenter, N. W. (2000). Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. *New Phytologist*, *145*(1), 51-59. https://doi.org/DOI 10.1046/j.1469-8137.2000.00549.x

Venturas, M. D., Sperry, J. S., & Hacke, U. G. (2017). Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, *59*(6), 356-389. https://doi.org/10.1111/jipb.12534

Vieira, D. L. M., & Scariot, A. (2006). Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, *14*(1), 11-20. https://doi.org/DOI 10.1111/j.1526-100X.2006.00100.x

Vilagrosa, A., Chirino, E., Peguero-Pina, J. J., Barigah, T. S., Cochard, H., & Gil-Pelegrín, E. (2012). Xylem Cavitation and Embolism in Plants Living in Water-Limited Ecosystems. In R. Aroca (Ed.), *Plant Responses to Drought Stress: From Morphological to Molecular Features* (pp. 63-109). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-32653-0_3

Vinya, R., Malhi, Y., Fisher, J. B., Brown, N., Brodribb, T. J., & Aragao, L. E. (2013). Xylem cavitation vulnerability influences tree species' habitat preferences in miombo woodlands. *Oecologia*, *173*(3), 711-720. https://doi.org/10.1007/s00442-013-2671-2

Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B., & Koh, L. P. (2013). Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, *28*(9), 531-540. https://doi.org/10.1016/j.tree.2013.04.005

Yuan, W. P., Zheng, Y., Piao, S. L., Ciais, P., Lombardozzi, D., Wang, Y. P., Ryu, Y., Chen, G. X., Dong, W. J., Hu, Z. M., Jain, A. K., Jiang, C. Y., Kato, E., Li, S. H., Lienert, S., Liu, S. G., Nabel, J. E. M. S., Qin, Z. C., Quine, T., Sitch, S., Smith, W. K., Wang, F., Wu, C. Y., Xiao, Z. Q., & Yang, S. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances*, *5*(8). https://doi.org/ARTN eaax139610.1126/sciadv.aax1396

Zeng, Z. Z., Estes, L., Ziegler, A. D., Chen, A. P., Searchinger, T., Hua, F. Y., Guan, K. Y., Jintrawet, A., & Wood, E. F. (2018). Highland cropland expansion and forest loss in Southeast Asia in the twenty-first century. *Nature Geoscience*, *11*(8), 556-+. https://doi.org/10.1038/s41561-018-0166-9

Zeng, Z. Z., Piao, S. L., Li, L. Z. X., Zhou, L. M., Ciais, P., Wang, T., Li, Y., Lian, X., Wood, E. F., Friedlingstein, P., Mao, J. F., Estes, L. D., Myneni, R. B., Peng, S. S., Shi, X. Y., Seneviratne, S. I., & Wang, Y. P. (2017). Climate mitigation from vegetation biophysical feedbacks during the past three decades. *Nature Climate Change*, *7*(6), 432-+. https://doi.org/10.1038/Nclimate3299

Zhang, Q. W., Zhu, S. D., Jansen, S., & Cao, K. F. (2021). Topography strongly affects drought stress and xylem embolism resistance in woody plants from a karst forest in Southwest China. *Functional Ecology*, *35*(3), 566-577. https://doi.org/10.1111/1365-2435.13731

Zhu, S. D., & Cao, K. F. (2009). Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. *Plant Ecology*, *204*(2), 295-304. https://doi.org/10.1007/s11258-009-9592-5

Zhu, S. D., Chen, Y. J., Fu, P. L., & Cao, K. F. (2017). Different hydraulic traits of woody plants from tropical forests with contrasting soil water availability. *Tree Physiology*, *37*(11), 1469-1477. https://doi.org/10.1093/treephys/tpx094

Zhu, S. D., He, P. C., Li, R. H., Fu, S. L., Lin, Y. B., Zhou, L. X., Cao, K. F., & Ye, Q. (2018). Drought tolerance traits predict survival ratio of native tree species planted in a subtropical degraded hilly area in South China. *Forest Ecology and Management*, *418*, 41-46. https://doi.org/10.1016/j.foreco.2017.09.016

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