

**VESSEL TRAITS ACROSS A LAND USE GRADIENT
IN THE TROPICAL RAINFORESTS OF SABAH,
MALAYSIA**

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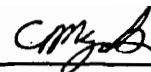


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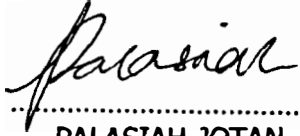


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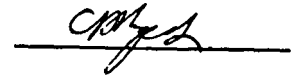
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ABSTRACT

Ecological plant strategies are reflected in anatomical constraints and trade-offs, influencing the distribution of species in different environmental conditions. In trees, wood anatomical traits serve multiple ecological functions such as structural stability, nutrient storage and water conductance. Vessel traits may determine the response of trees to disturbance such as selective logging which affected vast areas of forests in Borneo and which has been shown to change abiotic conditions. Trade-offs in vessel traits reflect different strategies used by trees to deal with water transport under various environmental conditions. Vessel traits can be essential for the fitness of trees especially when exposed to extreme (hot and dry) conditions in open gaps of selectively logged forest. This study investigates the differences in community level of vessel traits expression between old-growth (OG) and selectively logged forest (SL) in Sabah, Malaysian Borneo and explores the ecological trait variation of trees in these two different forest types. A total of 356 mature trees were sampled, capturing 192 species. From cross sections of branches, vessel area (A) and vessel diameter (VD) were measured and vessel lumen fraction (F), vessel density (N), hydraulically weighted diameter (D_h), vessel area to number ratio (S) also called as a vessel composition metric, and potential hydraulic conductivity (K_p) were calculated. Across all species S varied 61-fold and N showed 15-fold variation. There were significant differences in A ($\chi^2=3.60$; $p=0.044$), VD ($\chi^2=4.05$; $p=0.039$) and K_p ($\chi^2=4.37$; $p=0.035$) between OG and SL: vessel area and diameter were significantly larger in trees present in SL compared to OG forest. In SL, larger A and VD values also contributed to the hydraulic conductivity (K_p) being higher than that of OG forest. These differences in K_p can be explained by the presence of pioneer species in SL that represent fast growing trees which would need efficient water transport to support their fast growth rates. Therefore, logging in tropical forests drives differential expression of wood anatomical traits in response to the modified environments created by the disturbance. Vessel traits of common OG species adapted to ensure high hydraulic resistance when soil moisture is limiting while common species of SL developed an efficient water transport system but their vessels lacked hydraulic safety under stressful environmental conditions. The present study provided an important insight into vascular strategies of trees in Bornean rainforest and highlighted potential limitations on forest resilience during future climatic extremes.

ABSTRAK

SIFAT-SIFAT PEMBULUH KAYU DI SEPANJANG GRADIEN GUNA TANAH DI HUTAN HUJAN TROPIKA SABAH, MALAYSIA

Strategi ekologi tumbuhan dicerminkan dalam kekangan anatomi dan perubahan, mempengaruhi pengagihan spesies dalam keadaan persekitaran yang berbeza. Dalam pokok, ciri-ciri anatomi kayu mempunyai pelbagai fungsi ekologi seperti kestabilan struktur, penyimpanan nutrien dan kealiran air. Ciri-ciri pembuluh boleh menentukan tindak balas pokok kepada gangguan seperti pembalakan terpilih yang mempengaruhi kawasan hutan yang luas di Borneo dan yang telah ditunjukkan mengubah keadaan abiotik. Kelainan dalam ciri-ciri pembuluh menggambarkan strategi yang berbeza yang digunakan oleh pokok untuk menangani pengangkutan air di bawah pelbagai keadaan persekitaran. Ciri-ciri pembuluh boleh menjadi penting untuk daya tahan pokok terutamanya apabila terdedah kepada keadaan ekstrim (panas dan kering) dalam jurang terbuka hutan yang dibalak. Kajian ini menentukan perbezaan ciri-ciri pembuluh dalam komuniti antara hutan dara (HD) dan hutan yang dibalak secara terpilih (HDST) di Sabah, Malaysia dan menentukan variasi sifat ekologi pokok di kedua-dua jenis hutan yang berlainan. Sebanyak 356 pokok matang telah disampel, mewakili 192 spesies. Dari bahagian keratan rentas, saiz pembuluh (A) dan diameter pembuluh (VD) diukur dan pecahan lumen pembuluh (F), ketumpatan pembuluh (N), diameter hidraulik (D_h), kawasan pembuluh kepada nisbah nombor (S) sebagai metrik komposisi pembuluh, dan potensi kekonduksian hidraulik (K_p) dikira. Dalam semua spesies, S bervariasi 61 kali ganda dan N menunjukkan variasi 15 kali ganda. Terdapat perbezaan yang ketara dalam A ($\chi^2=3.60$; $p=0.044$), VD ($\chi^2=4.05$; $p=0.039$) dan K_p ($\chi^2=4.37$; $p=0.035$) antara HD dan HDST: saiz pembuluh dan diameter pembuluh jauh lebih besar pada pokok yang terdapat di HDST berbanding di HD. Dalam HDST, nilai A dan VD yang lebih besar juga menyumbang kepada potensi kekonduksian hidraulik (K_p) yang lebih tinggi daripada HD. Perbezaan dalam K_p ini dapat dijelaskan oleh kehadiran spesies perintis dalam HDST yang mewakili pokok yang berkembang pesat yang memerlukan pengangkutan air yang efisien untuk menyokong kadar pertumbuhan yang cepat. Oleh itu, pembalakan di hutan tropika memacu pembezaan berlainan sifat-sifat anatomi kayu sebagai tindak balas kepada persekitaran yang diubahsuai yang dicipta oleh gangguan tersebut. Ciri-ciri pembuluh spesies lazim HD beradaptasi untuk memastikan rintangan hidraulik yang tinggi apabila kelembapan tanah terhad sementara spesies lazim HDST memacu sistem pengangkutan air yang cekap tetapi pembuluh mereka kekurangan hidraulik di bawah keadaan persekitaran yang tertekan. Kajian ini memberikan satu gambaran penting mengenai strategi pokok vaskular di hutan hujan tropika dan menyerlahkan potensi batasan ketahanan hutan pada iklim ekstrim masa depan.

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LIST OF ABBREVIATIONS

A	- Vessel area
ANCOVA	- Analysis of covariance
ANOVA	- Analysis of variance
D_h	- Hydraulically weighted vessel diameter
DBH	- Diameter at breast height
F	- Vessel lumen fraction
FAA	- Formalin acetic acid alcohol
GEM	- Global Ecosystem Monitoring
GIMP	- GNU Image Manipulation program
IAWA	- International Association of Wood Anatomists
K_p	- Theoretical/potential hydraulic conductivity
N	- Vessel number per area (vessel density)
OG	- Old-growth
S	- Vessel area to number ratio (vessel composition)
SAFE	- Stability of Altered Forest Ecosystems (SAFE) Project
SEARRP	- South East Asia Rainforest Research Partnership (SEARRP)
SL	- Selectively logged forest
VD	- Vessel diameter

LIST OF SYMBOLS

%	- Percentage
°C	- Degree celcius
°	- Degree
α	- Alpha
Σ	- Sum
=	- Equal to
<	- Less than
x	- Times
'	- Minute
E	- East
g	- Gram
ha	- Hectare
μm	- Micrometer
ml	- Millilitre
mm	- Millimetre
m	- Metre
MPa	- Megapascal Pressure Unit
N	- North
s	- Second

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CHAPTER 1

INTRODUCTION

1.1 Background of the study

Plant functional traits are all measurable features (morphological, physiological and phenological) for individual plants that influence their survival, growth, reproduction and fitness (Pérez-Harguindeguy *et al.*, 2013; Violle *et al.*, 2007; Ackerly, 2003). Traits play a key role in linking taxonomic diversity to ecosystem function (Townsend *et al.*, 2008). Plant traits allow the investigation of the functions of different tissues and thus into functional trade-offs that influence species distributions in different environmental conditions (Kraft *et al.*, 2008). Ecologists have used functional traits to understand ecological plant strategies and adaptation to environmental stress, e.g., anatomical characteristics are known to affect the functional performance of wood xylem in various environmental conditions such as drought events (Carlquist & Schneider, 2001).

Knowledge of plant stem anatomy is essential to understanding water transport in trees (Campbell *et al.*, 2016). Specifically, xylem anatomical traits serve multiple ecological functions such as structural stability, nutrient storage but also water conductance (Fan *et al.*, 2012; Baas *et al.*, 2004). For example, xylem vessel size is an important plant hydraulic trait which ensures that water supply is sufficient from the roots to the leaves to maximize growth performance and survival (Schreiber *et al.*, 2015). Large vessels transport water more efficiently than the smaller ones (Zanne *et al.*, 2010) but are also prone to hydraulic failure which is major cause of water stress in plants due to cavitation, i.e. air-filled conduits (Meinzer *et al.*, 2001). In addition to vessel size, other vessel characteristics such as vessel density, fraction



and grouping have also direct bearing on water conductance efficiency through plant stems (Scholz *et al.*, 2013; Zanne *et al.*, 2010; Loepfe *et al.*, 2007; Tyree & Zimmerman, 2002). Hence, stem vessel size distribution, density and fractions all affect the hydraulic conductivity of xylem (Tyree & Ewers, 1991) and different combinations of vessel sizes and densities can reflect the strategies adopted by different plant species to deal with water deficit and to optimize water conductivity (Apgaua *et al.*, 2015; Zanne *et al.*, 2010) because variation in vessel traits will lead to a different hydraulic conductance (Hubbard *et al.*, 1999).

Different plant species are more successful in different landscapes or habitats because of the differences in their quantitative traits (Westoby & Wright, 2006). Better understanding of variation in vessel characteristics between tree species as well as in different environmental conditions is important for integrating and evaluating environmental influences on ecosystems (Zanne *et al.*, 2010) because xylem structure has important implications for whole plant function (Carlquist & Schneider, 2001; Tyree & Ewers, 1991; Carlquist & Hoekman, 1985). Better knowledge of both wood structure and function will improve our understanding of plant water use strategies especially in rainforest ecosystems (Apgaua *et al.*, 2015). Tropical forests are under increasing logging pressure (Asner *et al.*, 2009), and as a consequence, logged tropical forests are now more widespread than old-growth forests across most of the tropical regions (Edwards *et al.*, 2014). In anthropogenically modified forests, trees are exposed to altered conditions such as open areas with increased light but possibly also prolonged drought, under which different xylem traits may play a key role in plant growth and survival. Therefore, the study of wood anatomical traits and their variation among species is necessary to fully understand tree ecological strategies in both human disturbed and untouched tropical forest ecosystems.

Southeast Asian tropical rainforests are among the oldest, existing tropical ecosystems on Earth (Whitmore, 1984) and are globally known as biodiversity hotspots (Myers *et al.*, 2000) mostly dominated by tree species of the Dipterocarpaceae family (Brearley *et al.*, 2016; Rana *et al.*, 2009). However, in the

last decades, logging and conversion into agricultural land have been major drivers to forest degradation in Southeast Asia (Wilcove *et al.*, 2013; Sodhi *et al.*, 2004). Among SE Asia, Malaysian Borneo is a centre of both oil palm and selective logging industries (Bryan *et al.*, 2013), which results not only in loss of biodiversity and alteration of ecosystem functions, but also in effects on residual vegetation, soils and waterways (Bryan *et al.*, 2010; Asner *et al.*, 2005) and changing tree species composition (Cleary, 2017; Berry *et al.*, 2008). In selectively logged forests, changes in tree species composition may lead to changes in functional traits of tree community, however, although there is some information on the impact of selective logging on functional diversity (Osazuwa-peters *et al.*, 2015; Carreño-Rocabado *et al.*, 2012; Díaz *et al.*, 1999), studies on wood anatomical traits in logged forests are practically missing, even though vessel traits can be crucial for tree resilience in human-disturbed forests.

This study is part of the Biodiversity and Land-use Impacts on Tropical Ecosystem Function (BALI, <http://bali.hmtf.info>) project under the Human Modified Tropical Forest Programme (HMTF, <http://hmtf.info/>). The present study investigates wood anatomical traits; more specifically it focuses on vessel traits in old-growth and selectively logged forest, explores the variability of vessel traits and the relationships between different vessel characteristics, and aims to reveal differences in vessel traits expressed by species present in the two forest types. Differences in vessel traits between the two forest types (old-growth and selectively logged forest) are expected to arise due to the presence of pioneer species (fast growing species with low wood density) in selectively logged forest, therefore the hypothesis of this study is the vessel traits of species dominant in selectively logged forest would reflect their need to capture and transport resources to support their fast growth rates, while species of old-growth forest (such as dipterocarps) would display more conservative traits. To compare vessel traits between selectively logged and old-growth forest, cross sections of branches of tree species from both forest types were analysed for mean vessel size, vessel diameter, vessel number per unit area, hydraulically weighted diameter, vessel lumen fraction, and vessel area to number ratio. Moreover, potential hydraulic conductivity was calculated using vessel lumen fraction and vessel area to

number ratio, to reveal differences in the efficiency of water transport between the two forest types.

1.2 Significance of the study

Tree species with similar wood density may differ significantly in their xylem anatomy (Ziemińska *et al.*, 2013) and consequently also in their hydraulic conductivity. Studying wood density alone is not sufficient to fully understand water transport in trees, and alternative anatomical traits such as vessel characteristics should be explored. The present study provides important insights into vascular strategies of trees in the rainforests of Borneo. Because xylem vessels play a key role in ensuring enough water supply in trees, understanding how these traits vary across environments could potentially be important for selecting the most suitable trees to plant in restoration and reforestation. For example, planting tree species with a low hydraulic safety (i.e., with large vessels prone to embolism) should be avoided at sites where a water deficit may be expected, such as ridges exposed to potential desiccation. Moreover, knowledge of the vascular strategies of both old-growth and selectively logged forest species is crucial for preservation and management of these forests under future climate change. In Borneo the mean temperature and precipitation are predicted to rise and decline, respectively (Scriven *et al.*, 2015; IPCC, 2013), but the frequency and magnitude of El Niño Southern Oscillation (ENSO) droughts are also expected to increase (Herbert & Dixon, 2003; Walsh & Newbery, 1999). Recently sharp increases in tree mortality after drought were reported from both Bornean primary and secondary forests (Qie *et al.*, 2017). Hence an understanding of how trees cope with weather extremes is crucial for both preservation of old-growth forests and management and restoration of logged forests in Borneo.

1.3 Research objectives

- a. To investigate community level differences in wood anatomical trait expression between old-growth forest and selectively logged forests.
- b. To investigate ecological trait variation among trees in old-growth forest and selectively logged forest, and explore plant strategies with regards to wood anatomical properties.

1.4 Research questions

The thesis explores the following questions:

- a. What is the variation in vessel traits among species of Bornean lowland rainforest?
- b. What are the relationships between studied vessel characteristics, and do these relationships differ between old-growth and selectively logged forest?
- c. Are there significant differences in vessel traits between species of old growth forests and selectively logged forests at the community level and if so, can these differences be linked to differences in plant strategies?
- d. Do vessel traits in common species of selectively logged forest possess high hydraulic efficiency while vessel traits in common species of old-growth forest possess high hydraulic safety?

CHAPTER 2

LITERATURE REVIEW

2.1 Plant functional traits

Plant functional traits are all the morphological, physiological and phenological features measurable for an individual plant, from the cellular to the organismal level, which can affect its fitness (Pérez-Harguindeguy *et al.*, 2013; Violle *et al.*, 2007). Plant functional traits are widely used in ecological and evolutionary research for achieving a general predictive understanding of communities and ecosystems, and have become an active area of research on species distributional patterns at local, regional, and global scales (Cornwell & Ackerly, 2009; Ackerly & Cornwell, 2007; Violle *et al.*, 2007; Wright *et al.*, 2007). Ecologists use plant functional trait analyses as proxies for plant ecological strategies (Zanne *et al.*, 2010; Westoby, 1998). Trait based approaches are also increasing in the fields of agronomy and forestry (Garnier & Navas, 2012), nature conservation (Mace *et al.*, 2010) and archeobotany (Jones *et al.*, 2010).

Functional traits determine the response of organisms to stress or their effects on ecosystem processes (de Bello *et al.*, 2010). They may demonstrate adaptations to variation in the physical and biotic environments and display trade-offs among different functions within an organism. For example, drought-tolerant tree species often have narrow and small leaves with low specific leaf area (SLA) (Fonseca *et al.*, 2000) and high wood density (Poorter & Markesteijn, 2008). Variation in morphological and physiological traits within and among plant species underpins a continuum of plant strategies in response to important ecological processes at a range of scales (Pérez-Harguindeguy *et al.*, 2013; Reich *et al.*, 2003).



The relationship between plant characteristics and environmental conditions has long been recognized in the development of plant ecology (Cowles, 1899). Different types of plants are successful under different environmental conditions (Tardieu, 2013). The ecological and physiological processes that determine these relationships are still active areas of research even after more than a century, especially the examination of traits that contribute to ecosystem processes and species interactions (Sandel *et al.*, 2010; McGill *et al.*, 2006; Hooper *et al.*, 2005; Suding *et al.*, 2005). Hence, an approach that scales up traits from species level to community level gives further insights into how plant communities respond to environmental change and thus affect ecosystem processes (Mayfield *et al.*, 2010; Suding & Goldstein, 2008).

The functional traits of trees are essential for understanding the ecology of trees and forests (Swenson & Enquist, 2007; Westoby & Wright, 2006). Differences in quantitative traits that provide some adaptive advantage may contribute to variation in competitive ability of trees under specific circumstances (Westoby & Wright, 2006; Ackerly, 2003), for instance, higher leaf nitrogen concentrations may enhance carbon assimilation and tree growth in high irradiance (Poorter & Bongers, 2006) while higher wood density is usually associated with greater drought tolerance (Ackerly & Cornwell, 2007).

2.2 Functional traits in wood anatomy

A functioning water conducting system is essential to maximize tree growth rate and survival, therefore functional traits have been attributed to wood from the earliest day of botanical science and detailed studies on wood structure and function, mainly on tree hydraulics, are one of the most exciting fields in plant biology, evolution and forest ecology (Hacke & Sperry, 2015). According to Baas *et al.* (2016), understanding how functional traits of wood arise during wood formation in response to environmental changes is key to interpreting past wood reactions and predicting future growth responses. Each individual plant through its structure of cells, tissues and organs provides information regarding its past life and environment (Wimmer,

2002). Investigating traits that are specifically related to water conductivity in trees provides understanding on how drought events affect metabolic processes such as photosynthesis, transpiration and growth (Apgaua *et al.*, 2015).

Wood is involved directly in tree hydraulics, and the biophysical and functional anatomical traits of wood such as tissue density and xylem vessel size can be used to determine strategies used by different tree species to assure conductivity, safety of the pathway from embolism and capacitance (Beeckman, 2016; Apgaua *et al.*, 2015). Wood density has been traditionally regarded as a key plant trait affecting mechanical and physiological performance and has been linked with hydraulic strategies (Chave *et al.*, 2009), although it is now known that species with similar wood density might have different and diverse anatomies (Ziemińska *et al.*, 2013). Low wood density has been associated with fast growth (Chave *et al.*, 2006; Wright *et al.*, 2003) while in contrast high wood density is linked with high stress tolerance (Hacke & Sperry, 2015) and survival because of its association with higher hydraulic safety, stronger biomechanical support and resistance to pests and pathogens (Jacobsen *et al.*, 2007; Gelder *et al.*, 2006). Variation in wood density can be achieved anatomically by altering morphology (e.g., cell wall thickness and lumen area) or changing relative proportion of tissues (e.g., area in vessel fraction, fibre wall and lumen, and parenchyma) (Martínez-Cabrera *et al.*, 2009).

Hydraulic conductivity is an absolute measure of the ability of xylem to transport water and is highly variable across species (Melcher *et al.*, 2012). Vessel diameter, length and frequency are anatomical features that assist plants to deal with excessive water stress in a dry environment (Scholz *et al.*, 2013; Markesteijn *et al.*, 2011). Wide vessels are much more efficient water conductors than narrow ones, therefore, wood consisting of wider vessels has low density with high hydraulic conductivity, whereas wood composed of narrow vessels within a fibre matrix will be dense with low hydraulic conductivity (Preston *et al.*, 2006). Consequently, xylem vessel diameter represents an important plant hydraulic trait to ensure that water supply is sufficient from the roots to the leaves to maximize growth performance and survival (Schreiber *et al.*, 2015). Increased vessel diameter increases efficiency of

water conduction dramatically, however it decreases safety because larger vessels are more prone to cavitation by air seeding whereas smaller vessels are less vulnerable to embolism (Hacke *et al.*, 2006; Choat *et al.*, 2003). Xylem cavitation and embolism are known to be a major cause of water stress in plants (Tyree & Sperry, 1989). Cavitation represents a break in the water column and occurs due to a pressure difference between the external environment and inside the vessel (Tyree & Zimmerman, 2002). During cavitation water spontaneously transitions from liquid to a gas that gets trapped within the xylem conduits under excessive tension causing embolism (Baltzer *et al.*, 2009; Choat *et al.*, 2007). An embolism results from cavitated conduits becoming air-filled, which affects water conductivity efficiency to the canopy (Meinzer *et al.*, 2001) leading to branch sacrifice and even plant death (Anderegg *et al.*, 2012; Brodribb *et al.*, 2010).

2.3 Wood tissues

Angiosperm wood is a complex tissue composed of various cell types (Figure 2.1) (Evert, 2006). The key anatomical components of wood are defined by distinct tissues and cell types such as fibres, parenchyma and vessels (Figure 2.2), and these cell types can be directly related to specific ecological functions (Osazuwa-peters *et al.*, 2015). Fibres are usually the most abundant tissues in wood that function mainly in mechanical strength which is determined by the thickness of their cell walls and they also provide mechanical support for the photosynthetic leaf surfaces in a tree's canopy (Wiedenhoef, 2010). Parenchyma derived by secondary cambium, which are physiologically living cells, is the second most abundant wood tissue and mainly function as nutrient storage and transport, pathogen defence and water storage but die during heartwood formation (Taylor *et al.*, 2002). There are two types of parenchyma: axial parenchyma which consists of axially elongate cells and runs along the long stem axis, and ray parenchyma which runs perpendicular to the long stem axis. Vessels represent the third most abundant wood tissue type and are composed of a series of individual cells, the vessel elements that are stacked one on top of the other whose main function is conduction of water and other substances in xylem from the soil to photosynthetic surfaces (Liew *et al.*, 2015; Zheng & Martínez-Cabrera, 2013; Tyree & Zimmerman, 2002).

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