



UNIVERSITI PUTRA MALAYSIA

***AGE-RELATED CHANGES IN *Shorea dasyphylla*
FOXW. GROWTH AND PHYSIOLOGY***

IRA CARLBRENIE SIMOL

FSPM 2021 7



**AGE-RELATED CHANGES IN *Shorea dasyphylla* FOXW. GROWTH AND
PHYSIOLOGY**

By

IRA CARLBRENIE SIMOL

**Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in
Fulfilment of the Requirements for the Degree of Master of Science**

November 2021

All material contained within the thesis, including without limitation text, logos, icons, photographs and all other artwork, is copyright material of Universiti Putra Malaysia unless otherwise stated. Use may be made of any material contained within the thesis for non-commercial purposes from the copyright holder. Commercial use of material may only be made with the express, prior, written permission of Universiti Putra Malaysia.

Copyright © Universiti Putra Malaysia



Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirements for the degree of Master of Science

AGE-RELATED CHANGES IN *Shorea dasyphylla* Foxw. GROWTH AND PHYSIOLOGY

By

IRA CARLBRENIE SIMOL

November 2021

Chairman : Ong Kian Huat, PhD
Faculty : Agricultural and Forestry Sciences (Bintulu Campus)

Shorea dasyphylla Foxw. is an important indigenous timber species in Malaysian forestry. In recent years, initiation of restoration programmes using indigenous tree species such as *S. dasyphylla* is due to continued demand of tropical timbers, especially dipterocarps. However information regarding age-related change in tree growth and physiology is scarce. This study was specifically conducted to assess the growth performance of *Shorea dasyphylla* trees at different stand ages through its physiological and morphological measurements. The study plots were located at the Universiti Putra Malaysia–Mitsubishi Forest Restoration project area of Universiti Putra Malaysia Bintulu, Sarawak Campus. Plots of 300 m² were selected, representing stands of different ages namely 1- (P1), 9- (P9), 14- (P14), and 20- (P20) years old. Four *S. dasyphylla* trees or seedlings were selected from in each plot for the study. Tree morphology measurements were assessed every six months for a period of 18 months. On the other hand, the morphology and physiology properties of the leaves as well as the soil properties were also determined. Both total height and diameter breast height growth showed a sigmoid trend as the tree aged. P9 recorded the slowest total height increment pace than the other three stands. P1 focused on both shoot apical meristem growth, especially in the third measurement interval, whereas P20 focused primarily on radial growth. In the third measurement interval of the study (after one year), a significant height increase in P1 was seen, which was most likely due to the well-established root systems that let these seedlings absorb more soil moisture and nutrients. Apart from that, the leaf area, width, length, thickness and chlorophyll content showed significant increment as the tree aged. P1 stand was also observed to have narrow, short and thin leaves compared to both canopy layers of the older stands (P14 and P20). The transpiration rate in P1 leaf was the highest, which then linearly declined over time. No significant difference was observed for leaf stomatal density in all stand age. The photosynthetic rate and stomatal conductance increased gradually until they reached their peak ages (12 to 18 years and 14 years respectively) and the decline continuously over time with a clear polynomial trend. There was no significant relationship identified between leaf N concentration and stand age. P9 recorded the lowest leaf N while the highest was recorded by P14. A constant decrease in P content was found in the leaf over

time with polynomial trend. The leaf K, Mg and Ca content shared a similar trend where the value decreased until a certain age 14 years (K), 9 years (Mg) and 9 years (Ca) respectively before they started to increase afterward. Soil available P and exchangeable Mg showed reduction in values with increasing stand age as these nutrients were greatly consumed for tree growth. The value of soil exchangeable K declined until year 10 before it started to increase with a polynomial association. The soil exchangeable Ca increased exponentially with time and significantly higher value was recorded by the oldest stand. The overall results suggested that age does influence the growth, and leaf morphological and physiological development of *S. dasyphylla*.



Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Master Sains

PERUBAHAN PERKAITAN UMUR DALAM PERTUMBUHAN DAN FISILOGI *Shorea dasyphylla* Foxw.

Oleh

IRA CARLBRENIE SIMOL

November 2021

Pengerusi : Ong Kian Huat, PhD
Fakulti : Sains Pertanian dan Perhutanan (Kampus Bintulu)

Shorea dasyphylla Foxw. adalah spesies kayu asli yang penting dalam perhutanan Malaysia. Di dalam beberapa tahun kebelakangan ini, program pemulihan menggunakan spesies pokok tempatan seperti *S. dasyphylla* dimulakan disebabkan oleh permintaan kayu tropika yang berterusan, terutamanya dipterocarp. Walaubagaimanapun maklumat mengenai perubahan berkaitan umur dalam pertumbuhan dan fisiologi pokok adalah terhad. Kajian ini dilakukan secara khusus untuk menilai prestasi pertumbuhan pokok *Shorea dasyphylla* pada dirian usia yang berlainan melalui pengukuran fisiologi dan morfologi. Petak kajian terletak di dalam kawasan projek Hutan Permuliharaan Universiti Putra Malaysia–Mitsubishi, Universiti Putra Malaysia Kampus Bintulu Sarawak. Petak kajian seluas 300 m² telah dipilih, yang mewakili kumpulan umur yang berbeza iaitu anak pokok yang berumur 1 (P1), 9 (P9), 14 (P14) dan 20 (P20) tahun. Empat pokok *S. dasyphylla* telah dipilih sebagai pokok kajian dari setiap petak. Pengukuran morfologi pokok dinilai setiap enam bulan untuk jangka masa 18 bulan. Morfologi dan fisiologi daun serta sifat tanah juga ditentukan. Pertumbuhan ketinggian total dan DBH menunjukkan tren sigmoid selari dengan umur pokok. P9 merekodkan peningkatan ketinggian keseluruhan yang paling lambat berbanding pokok-pokok kumpulan umur yang lain. Dalam kajian semasa, P1 *S. dasyphylla* memfokuskan pada pertumbuhan meristem apikal, terutama pada separuh ketiga pengukuran, sedangkan P20 memberi tumpuan terutamanya pada pertumbuhan radial. Pada separuh ketiga kajian (setelah satu tahun), peningkatan ketinggian P1 yang ketara dilihat, yang kemungkinan besar disebabkan oleh sistem akar yang telah mantap di mana dapat membantu anak pokok lebih banyak kelembapan dan nutrien. Selain itu, luas daun, lebar, panjang, ketebalan dan kandungan klorofil menunjukkan kenaikan yang ketara seiring dengan penuaan pokok. Dirian pokok P1 juga didapati mempunyai daun yang tirus, pendek dan nipis jika dibandingkan dengan daun-daun dari pokok yang lebih tua (P14 dan P20). Kadar transpirasi pada daun P1 adalah tertinggi dan kemudian menurun secara linear mengikut masa. Tidak ada perbezaan yang bererti untuk ketumpatan stomatal daun pada semua usia pokok. Kadar fotosintesis dan konduktans stomata meningkat secara beransur-ansur sehingga mencapai usia puncaknya (masing-masing 12 hingga 18 tahun dan 14 tahun) dan selepas ini mencatat dengan menunjukkan pola polinomial

yang jelas. Tidak terdapat hubungan yang signifikan antara kepekatan daun N dan usia dirian. P9 mencatatkan jumlah N daun yang paling rendah manakala P14 mencatatkan jumlah N daun yang tertinggi. Jumlah kandungan K, Mg dan Ca pada daun menunjukkan corak yang sama di mana kandungan menurun sehingga umurnya 14 tahun, 9 tahun (K) dan 9 tahun (Mg dan Ca) sebelum mereka mulai meningkat kembali mengikut masa. Kandungan tanah P tersedia dan Mg tukarganti menunjukkan pengurangan dengan peningkatan usia pokok, kerana nutrien ini banyak diserap bagi menampung pertumbuhan pokok. Jumlah kandungan tanah K tukar ganti juga merosot sehingga tahun ke 10 sebelum nilainya meningkat dengan tren polinomial. Jumlah kandungan tanah Ca tukrganti meningkat secara eksponen dengan masa dan dirian yang tua merekodkan nilai yang tinggi serta bererti. Berdasarkan hasil kajian ini, usia pokok dikatakan mempengaruhi pertumbuhan, dan morfologi dan fisiologi daun *S. dasyphylla*.



ACKNOWLEDGEMENTS

All praise and thanks to the Almighty God for giving me the strength and inspiration to complete this thesis.

I would like to express my very great appreciation to my supervisor, Associate Professor Dr. Ong Kian Huat for his valuable and constructive suggestions during the planning and development of this research work. My sincerest thanks to my co-supervisor, Associate Professor Dr. John Keen Anak Chubo for his advices and assistance in keeping my progress on schedule and his willingness to give his time so generously has been very much appreciated.

I must express my very profound gratitude to my parents, Mr. Freddie Japat Simol and Mrs. Angelica Irene Francis Mojingol, and my parents-in-law Mr. Stephen Pasin and Mrs. Nancy Dawang, my lovely husband Herman Anak Stephen, my wonderful children's Aaron Hendrick Anak Herman, Aamethyst Hosanna Anak Herman and Aabner Hansanon Paseen Anak Herman, my siblings, Carlsten, Carlmila, Carlina, Peter Romey, Ezra Carlstine, Annie Avun, and Sapphira Carllima, my nephews and nieces, Corinthians Don Juan, Elysha Carmen, Ava Pearl Butiza Sangon, Ethan Hans, Emerald Hannessa, and Ethaniel Hanns. I also place on record, my sincere gratitude to Mr. Rayner Francis Mojingol, Mr. Johnnie Chai, Ms. Lili Swandani, Sekuh Bai Mangin and Paganakan Francis Mojingol for providing me with unfailing support and continuous encouragement throughout my years of study and through the process of researching and writing this thesis. This accomplishment would not have been possible without them.

Sincerest gratitude also to all staff at Faculty of Agricultural and Forestry Sciences, UPM Bintulu Sarawak Campus for all the support. Special thanks to staff in the Department of Forestry Science, Mr. George Bala Empin, and Mr. Muaish Sait for assisting and support during my research. I also would like to thank Mrs. Elizabeth Andrew Anyah from the Department of Crop Science as well as Mr. Khalid Nawi and Mr. Awang Marzuki Awg Musthafa from the University Agriculture Park Division. I also thank Dr. Latifah Omar and Ms. Chew Cindy for helping me with the SAS analysis. Gratitude is also due to all friends who help me during the study.

Finally, I wish to thank my department, RISDA (Rubber Industry Association Development Authority) for the support and encouragement throughout my study.

I certify that a Thesis Examination Committee has met on 26 November 2021 to conduct the final examination of Ira Carlbenie Simol on her thesis entitled "Age-Related Changes in *Shorea dasyphylla* Foxw. Growth and Physiology" in accordance with the Universities and University Colleges Act 1971 and the Constitution of the Universiti Putra Malaysia [P.U.(A) 106] 15 March 1998. The Committee recommends that the student be awarded the Master of Science.

Members of the Thesis Examination Committee were as follows:

Shahrulrazid Sarbini, PhD

Professor

Faculty of Agricultural and Forestry Sciences (Bintulu Sarawak Campus)

Universiti Putra Malaysia

(Chairman)

Roland Kueh Jui Heng, PhD

Associate Professor

Faculty of Agricultural and Forestry Sciences (Bintulu Sarawak Campus)

Universiti Putra Malaysia

(Internal Examiner)

Ismail Jusoh, PhD

Professor

Faculty of Resources Science and Technology

Universiti Malaysia Sarawak

Malaysia

(External Examiner)

SITI SALWA ABD GANI, PhD

Associate Professor ChM. and Deputy Dean

School of Graduate Studies

Universiti Putra Malaysia

Date: 1 August 2022

This thesis was submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfilment of the requirement for the degree of Master of Science. The members of the Supervisory Committee were as follows:

Ong Kian Huat, PhD

Associate Professor
Faculty of Agricultural and Forestry Sciences
Universiti Putra Malaysia Bintulu Sarawak Campus
(Chairman)

John Keen Anak Chubo, PhD

Associate Professor
Faculty of Agricultural and Forestry Sciences
Universiti Putra Malaysia Bintulu Sarawak Campus
(Member)

ZALILAH MOHD SHARIFF, PhD

Professor and Dean
School of Graduate Studies
Universiti Putra Malaysia

Date: 11 August 2022

Declaration by graduate student

I hereby confirm that:

- this thesis is my original work;
- quotations, illustrations and citations have been duly referenced;
- this thesis has not been submitted previously or concurrently for any other degree at any other institutions;
- intellectual property from the thesis and copyright of thesis are fully-owned by Universiti Putra Malaysia, as according to the Universiti Putra Malaysia (Research) Rules 2012;
- written permission must be obtained from supervisor and the office of Deputy Vice-Chancellor (Research and Innovation) before thesis is published (in the form of written, printed or in electronic form) including books, journals, modules, proceedings, popular writings, seminar papers, manuscripts, posters, reports, lecture notes, learning modules or any other materials as stated in the Universiti Putra Malaysia (Research) Rules 2012;
- there is no plagiarism or data falsification/fabrication in the thesis, and scholarly integrity is upheld as according to the Universiti Putra Malaysia (Graduate Studies) Rules 2003 (Revision 2012-2013) and the Universiti Putra Malaysia (Research) Rules 2012. The thesis has undergone plagiarism detection software.

Signature: _____ Date: _____

Name and Matric No.: Ira Carlbrenie Simol, GS45060

Declaration by Members of Supervisory Committee

This is to confirm that:

- the research conducted and the writing of this thesis was under our supervision;
- supervision responsibilities as stated in the Universiti Putra Malaysia (Graduate Studies) Rules 2003 (Revision 2012-2013) are adhered to.

Signature: _____

Name of Chairman of Supervisory
Committee: _____

Ong Kian Huat

Signature: _____

Name of Member of
Supervisory Committee: _____

John Keen Anak Chubo

TABLE OF CONTENTS

	Page
ABSTRACT	i
ABSTRAK	iii
ACKNOWLEDGEMENTS	v
APPROVAL	vi
DECLARATION	viii
LIST OF TABLES	xiii
LIST OF FIGURES	xiv
LIST OF ABBREVIATIONS	xvii

CHAPTER

1	INTRODUCTION	
	1.1 General Background	1
	1.2 Problem Statement	2
	1.3 Study Objectives	3
2	LITERATURE REVIEW	
	2.1 Dipterocarps	4
	2.1.1 Distribution	4
	2.1.2 Taxonomy and Botany of Dipterocarpaceae	7
	2.1.3 Ecology of Dipterocarps	7
	2.1.4 Biological Groups of Asian's Dipterocarp	8
	2.2 <i>Shorea</i>	8
	2.2.1 Taxonomy and Botany of <i>Shorea</i>	9
	2.2.2 Ecology	10
	2.2.3 Biological Groups	10
	2.2.4 Uses	11
	2.2.5 Conservation Status	11
	2.3 <i>Shorea dasyphylla</i> Foxw.	11
	2.3.1 Botanical Descriptions	12
	2.3.2 Ecology	12
	2.3.3 Uses and Conservation Status	12
	2.4 Tree Growth	13
	2.4.1 Growth Curve	15
	2.4.2 Whole-tree Development (Ontogeny)	16
3	MATERIALS AND METHODS	
	3.1 Study Site and Tree Species	19
	3.2 Tree Morphology Measurements	19
	3.2.1 Measurement of Height	20
	3.2.2 Measurement of Diameter at Breast Height	20
	3.3 Leaf Morphology Study	20
	3.3.1 Length and Width of Leaves Measurement	20
	3.3.2 Leaf Area Surface Measurement	21
	3.3.3 Leaf Thickness and Stomata Density	21

3.4	Leaf Physiological Study	21
3.4.1	Leaf Gas Exchange Studies	21
3.4.2	Determination of Chlorophyll Content	21
3.5	Determination of Leaf Nutrient Concentrations	22
3.6	Soil Nutrients Study	23
3.6.1	Soil Available Phosphorus (P)	23
3.6.2	Soil Exchangeable Cations (K, Ca, and Mg)	23
3.7	Growth Models	24
3.8	Data Analysis	24
4	RESULTS	
4.1	Tree Morphology	25
4.1.1	Tree Height	25
4.1.2	Diameter at Breast Height	26
4.2	Leaf Characteristics	27
4.2.1	Area	27
4.2.2	Width	28
4.2.3	Length	30
4.2.4	Thickness	31
4.2.5	Stomata Density	32
4.2.6	Photosynthetic Rate	33
4.2.7	Transpiration Rate	34
4.2.8	Stomatal Conductance	35
4.2.9	Chlorophyll Content	37
4.3	Leaf Nutrient Concentrations	38
4.3.1	Nitrogen	38
4.3.2	Phosphorus	39
4.3.3	Potassium	40
4.3.4	Magnesium	42
4.3.5	Calcium	43
4.4	Soil Nutrient Concentrations	44
4.4.1	Available Phosphorus	44
4.4.2	Exchangeable Potassium	45
4.4.3	Exchangeable Magnesium	46
4.4.4	Exchangeable Calcium	47
4.5	Relationship between Tree Morphology Properties with Selected Leaf and Soil Properties, and Physiological Characteristics	48
5	DISCUSSIONS	
5.1	Tree Morphology	50
5.2	Leaf Morphological and Physiological Characteristics	51
5.3	Soil Nutrients	57
6	CONCLUSION AND RECOMMENDATIONS FOR FUTURE RESEARCH	
6.1	Conclusion	58
6.2	Recommendations for Future Study	59

REFERENCES	61
BIODATA OF STUDENT	80
PUBLICATION	81



LIST OF TABLES

Table		Page
3.1	Location and establishment year of each study site	19
3.2	Equipment used to measure height and canopy depth	20
3.3	Growth curve model expressions	24
4.1	Leaf area of <i>Shorea dasyphylla</i>	28
4.2	Leaf width of <i>Shorea dasyphylla</i>	29
4.3	Leaf length of <i>Shorea dasyphylla</i>	30
4.4	Leaf thickness of <i>Shorea dasyphylla</i>	31
4.5	Stomata density of <i>Shorea dasyphylla</i>	32
4.6	Photosynthetic rate of <i>Shorea dasyphylla</i>	34
4.7	Transpiration rate of <i>Shorea dasyphylla</i>	35
4.8	Stomatal conductance of <i>Shorea dasyphylla</i>	36
4.9	Chlorophyll content of <i>Shorea dasyphylla</i>	38
4.10	Leaf nitrogen concentration of <i>Shorea dasyphylla</i>	39
4.11	Leaf phosphorus concentration of <i>Shorea dasyphylla</i>	40
4.12	Leaf potassium concentration of <i>Shorea dasyphylla</i>	41
4.13	Leaf magnesium concentration of <i>Shorea dasyphylla</i>	42
4.14	Leaf calcium concentration of <i>Shorea dasyphylla</i>	44
4.15	Soil available phosphorus in <i>Shorea dasyphylla</i> stands	45
4.16	Soil exchangeable potassium in <i>Shorea dasyphylla</i> stands	46
4.17	Soil exchangeable magnesium in <i>Shorea dasyphylla</i> stands	47
4.18	Soil exchangeable calcium in <i>Shorea dasyphylla</i> stands	48
4.19	Correlation between tree morphologies and leaf parameters	48
4.20	Correlation between tree morphologies and soil nutrients	49

LIST OF FIGURES

Figure		Page
2.1	Dipterocarpaceae distribution	6
2.2	Sigmoidal growth curve	15
4.1	Total height increment of <i>Shorea dasyphylla</i>	25
4.2	Relationship between total height growth and stand age of <i>Shorea dasyphylla</i>	26
4.3	Diameter at breast height increment of <i>Shorea dasyphylla</i>	26
4.4	Relationship between diameter at breast height and stand age of <i>Shorea dasyphylla</i>	27
4.5	Relationship between upper canopy leaf area and stand age of <i>Shorea dasyphylla</i>	28
4.6	Relationship between upper canopy leaf width and stand age of <i>Shorea dasyphylla</i>	29
4.7	Relationship between upper canopy leaf length and stand age of <i>Shorea dasyphylla</i>	30
4.8	Relationship between upper canopy leaf thickness and stand age of <i>Shorea dasyphylla</i>	31
4.9	Relationship between upper canopy stomata density and stand age of <i>Shorea dasyphylla</i>	32
4.10	Relationship between photosynthetic rate of upper canopy and stand age of <i>Shorea dasyphylla</i>	33
4.11	Relationship between transpiration rate of upper canopy and stand age of <i>Shorea dasyphylla</i>	34
4.12	Relationship between stomatal conductance of upper canopy and stand age of <i>Shorea dasyphylla</i>	36
4.13	Relationship between chlorophyll content of upper canopy and stand age of <i>Shorea dasyphylla</i>	37
4.14	Relationship between leaf nitrogen concentration of upper canopy and stand age of <i>Shorea dasyphylla</i>	39

4.15	Relationship between leaf phosphorus concentration of upper canopy and stand age of <i>Shorea dasyphylla</i>	40
4.16	Relationship between leaf potassium concentration of upper canopy and stand age of <i>Shorea dasyphylla</i>	41
4.17	Relationship between leaf magnesium concentration of upper canopy and stand age of <i>Shorea dasyphylla</i>	42
4.18	Relationship between leaf calcium concentration of upper canopy and stand age of <i>Shorea dasyphylla</i>	43
4.19	Relationship between soil available phosphorus and stand age of <i>Shorea dasyphylla</i>	44
4.20	Relationship between soil exchangeable potassium and stand age of <i>Shorea dasyphylla</i>	45
4.21	Relationship between soil exchangeable magnesium and stand age of <i>Shorea dasyphylla</i>	46
4.22	Relationship between soil exchangeable calcium and stand age of <i>Shorea dasyphylla</i>	47

LIST OF ABBREVIATIONS

%	Percentage
μmol	Micromole
$^{\circ}\text{C}$	Temperature (degree Celsius)
A/Q	Photosynthetic light response curves
A_{1500}	Light saturated net photosynthesis
A_{max}	Maximum photosynthetic rate
APAR	Absorbed photosynthetically active radiation
ATP	Adenosine triphosphate
C	Carbon
CO_2	Carbon dioxide
Ca	Calcium
CAI	Current annual increment
CIFOR	Center for International Forestry Research
cm	Centimetre
cm^2	Square centimeter
cm^3	Cubic centimeter
cmol	Centimole
CR	Critically Endangered
DBH	Diameter at breast height
DD	Data Deficient
EN	Endangered
IUCN	International Union for Conservation of Nature
ITTO	International Tropical Timber Organisation

NT	Near Threatened
PAI	Periodic annual increment
PPFD	Photosynthetic photon flux density
RAPA	Regional Office for Asia and Pacific (FAO)
VU	Vulnerable
WWF	World Wildlife Fund



CHAPTER 1

INTRODUCTION

1.1 General Background

Tropical rainforests has one of the most diverse plant communities, with several mono-dominant tree species reported to be endemic in specific regions (Makana *et al.*, 2004). Over the past few decades, tropical rainforests have been intensively degraded into several patches of forest across Southeast Asia (Okuda *et al.*, 2013). Forest degradation activities have greatly affected the dipterocarp forests (Corlett, 2014), owing to the fact that the tree species are ecologically dominant and economically significant. In 2020, tropical timber production accounted for 16.8% of total global production (ITTO, 2021). In Malaysia, dipterocarp is a source of hardwood for wooden furniture, plywood, and sawn timber accounted for almost 72% in the total export value of timber in 2020 (MTC, 2021).

In order to return the degraded forest to a stable and productive condition dominated by trees, forest rehabilitation has been introduced. The fast-growing indigenous tree species, in particular dipterocarp, have now been planted to continuously rehabilitate the forest to a high state of biodiversity (Kobayashi *et al.*, 2001; McNamara *et al.*, 2006; Kenzo *et al.*, 2007).

Shorea dasyphylla Foxw. or locally known as *Meranti batu* is one of the dipterocarp species used in the rehabilitation effort owing to availability of seeds supply in Sarawak. *Shorea dasyphylla* produces light red *Meranti* timber and belong to the medium hardwood. This species possesses reddish sapwood and reddish-brown heartwood (Schulte and Schone, 1996). *Shorea dasyphylla* is widely distributed and can be found in mixed dipterocarp forests of Peninsular Malaysia, Sumatra and Borneo (Chua *et al.*, 2010; Yong *et al.*, 2011). Naturally, this species is an emergent tree, and can grow up to 45 m tall with diameter up to 110 cm with stout buttresses (Soepadmo *et al.*, 2004). Globally *S. dasyphylla* is labelled as an endangered species (IUCN, 2021), however, regionally this species is categorized as vulnerable in Peninsular Malaysia (Chua *et al.*, 2010) and least concern in Sarawak respectively (Julai *et al.*, 2014).

Once established on site, trees are subjected to countless environmental conditions as they survive and grow across different ontogenetic stages. As they aged, trees experienced complex changes in morphology and biology that developed into versatile structures (Coste *et al.*, 2009). Plasticity of leaves morphology and physiology characteristics is momentarily affected by development of tree structure. Leaves are a crucial organ of a tree. They have an ability to produce food and act as the sensor to detect changes for a tree. Their adaptability in various environmental conditions is remarkable. Shape of leaves, their sizes and permanency may vary significantly as tree age (Kertiens, 1996b).

Leaf gas exchange performance is greatly influenced by changes in its traits (Kertiens, 1996a). Leaf upper surface effectively gathers energy from sunlight while the underside exchanges CO₂ and O₂. To facilitate the gas diffusion process, leaf thickness is optimally minimized. Exteriorly, epidermal cell layers that stash waxy and impermeable cuticles to protect the leaf from dehydration. Interiorly, the number of stomata and chlorophyll content directly influence gas exchange properties. Lawson and Blatt (2014) suggested that the abundant number of stomata may directly affect the rate of photosynthesis, stomatal conductance, and transpiration rate. However these leaf gas exchange characteristics may differ as the tree age due to ever changing environmental conditions in rainforest and dynamic tree structures (Day *et al.*, 2001; Hubbard *et al.*, 2001).

Tree species vary sustainably in acquiring resources (C, nutrient, and water), investing them into different tissue parts, and losing them through turnover although most of these species have similar basic physiological roles. Cornewell *et al.* (2014) reported that up to 10% of the world's plant species noticeable traits such as leaf, wood, or seed are now made available. As more data accumulated, more predictions on plant growth, lifespan, and performance patterns were conducted (Van Kleunen *et al.*, 2010; Wright *et al.*, 2010; Adler *et al.*, 2014). Recently Visser *et al.* (2016) and Gibert *et al.* (2016) have established that plant growth can be altered by plant size. Woody plants growth rates when expressed as height, or diameter incline to display hump-shaped relationships with size (Hérault *et al.*, 2011; King, 2011).

There is still a lack of available information on the growth performance of different age as well as relationship responses between the tree characteristics and physiological changes over time. This study was carried out to observe the growth performance of *S. dasyphylla* during the different stages of tree development. Measurement conducted also help to understand the physiological and morphological changes of the leaves.

1.2 Problem Statement

The problem to be addressed by this study is the lack of information on age-related changes in growth and leaf traits (form and physiology) over the long life spans of tropical wood species.

As a tree grows and ages, changes in terms of morphology and biology become more complex, while various environment conditions across ontogenetic phases, changes its growth, size and structure (Coste *et al.*, 2009). Large amount of research findings were reported on age and size-related changes as summarized by Hincklet *et al.* (2011). They also identified research gaps needed to improve the understanding of changes in structure and function changes that happen over the lifespan of a tree. Differences in pattern needed to be clarified among taxonomic groups (angiosperms and gymnosperms) and different stages of growth. Angiosperms and gymnosperms usually followed different developmental and physiological directions. Reported research is currently concentrated more on gymnosperms. In recent years, tree species in angiosperms are getting more attention. Although tropical rainforests accounted for a significant portion of global primary production (Kumagai *et al.*, 2004), information on age- or size-related changes

in growth and leaf traits is much lacking (see Literature Review). Therefore, there is a need for a detailed understanding of the changes in growth and leaf characteristics over their lifetime.

Most trees planted or grown naturally in multi-cohort stands will experience diverse environmental conditions over their life cycle. They are subjected to different light regimes, wind intensities, water stress, temperature variation and space competition (Sanches *et al.*, 2010). In an unpredictable environment, trees will change their growth traits in order to continue to survive by maximizing their fitness (Bazzaz, 1991). Over a lifetime, seedling stage is one of the most selective for tropical tree species as they usually experienced higher mortality rate due to availability of limited supply of resources due to their underdeveloped and shallow root systems and their low photosynthetic capacity (Ishida *et al.*, 2005). Many found that under similar light conditions, fully expended leaves differ in leaf traits among different stages of ontogenetic development, however the reasons for these differences still remain unclear (Ishida *et al.*, 2005). Therefore, to understand the establishment and growth processes of trees, concurrent measurement during different phases of ontogenetic development are critical. Available information will provide additional details to develop CO₂ fixation models for tropical rainforests (Kenzo *et al.*, 2006).

1.3 Study Objectives

This study was conducted specifically to:

- i. assess growth performance of *S. dasyphylla* trees at different age;
- ii. determine physiological and morphological of *S. dasyphylla* leaves at the different stages of tree development; and
- iii. establish the relationship between growth performance, leaf physiological and morphological, and soil characteristic properties.

REFERENCES

- Adam, J. H. (2001). Changes in forest community structures of tropical montane rain forest on the slope of Mt. Trus Madi in Sabah, Malaysia. *Journal of Tropical Forest Science*, 13: 76–92.
- Adams, H. D., and Thomas E. K. (2005). Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *Journal of Biogeography*, 32: 1629–1640.
- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., and Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, 111: 740–745.
- Aighewi, B. A., and Ekanayake, I. J. (2004). In-situ chlorophyll fluorescence and related growth of white Guinea yam at different ages. *Tropical Science*, 44(4): 201–206.
- Allaby, M. (2006). *Tropical Rain Forests*. New York: Chelsea House.
- Allaby, M., and Garratt, R. (2010). *Exploration: New Lands, New Worlds*. New York: Infobase Publishing.
- Ambrose, A. R., Sillett, S. C., and Dawson, T. E. (2009). Effects of tree height on branch hydraulics, leaf structure and gas exchange in California redwoods. *Plant, Cell and Environment*, 32: 743–757.
- Andriankaja, M., Dhondt, S., De Bodt, S., Vanhaeren, H., Coppens, F., and De Milde, L. (2012). Exit from proliferation during leaf development in *Arabidopsis thaliana*: a not-so-gradual process. *Developmental Cell*, 22(1): 64–78.
- Anten, N. P. R., and Selaya, N. G. (2011). Ecophysiology of secondary succession in tropical moist forest: scaling from individual traits to whole-plant performance. In: Meinzer, F.C., Lachenbruch, B., and Dawson, T.E. (eds.) *Size and age-related changes in tree structure and function*. Springer, Dordrecht, pp 429–454.
- Apple, M., Tiekotter, K., Snow, M., Young, J., Soeldner, A., Phillips, D., Tingey, D., and Bond, B. J. (2002). Needle anatomy changes with increasing tree age in Douglas-fir. *Tree Physiology*, 22: 129–136.
- Arnon, D. E. (1949). Copper enzymes in isolated chloroplasts polyphenol oxidase (*Beta vulgaris*). *Plant Physiology*, 24: 1–15.
- Ashton, P. S. (1968). *A manual of the dipterocarp trees of Brunei State and of Sarawak; Borneo Literature Bureau for Sarawak Forest Department, Kuching.*
- Ashton, P. S. (1969). Speciation among tropical forest trees: Some deductions in the light of recent evidence. *Biological Journal of the Linnean Society*, 1:155–96.

- Ashton, P.S. (1979). Some geographic trends in morphological variation in the Asian tropics and their possible significance. *Tropical Botany*. Kai Larsen and Lauritz B. Holm-Nielsen Academic Press London, New York.
- Ashton, P. S. (1981). The need for information regarding tree age and growth in tropical forests. In: Bormann, F.H., and Berlyn, G. (eds.) *Age and growth rate of tropical trees; new directions for research*. Yale University, School of Forestry and Environmental Studies. *Bulletin*, 94: 3–6.
- Ashton, P. S. (1982). Dipterocarpaceae. In: Van Steenis, C.G.G.J. (ed.) *Flora Malesiana* I, 9: 237–552.
- Ashton, P. S. (1988). Dipterocarp biology as a window to the understanding of tropical forest structure. *Annual Review of Ecology and Systematics*, 19: 340–370.
- Ashton, P. S. (1989). Dipterocarp reproductive biology. In: Lieth, H., and Werger, M.J.A. (eds.) *Tropical rain forest ecosystems*, Elsevier, Amsterdam, pp. 219–240.
- Ashton, P. S. (2004). Dipterocarpaceae. In *Tree Flora of Sabah and Sarawak*. E. Soepadmo, L. G. Saw, and R. C. K. Chung (Eds.) (Vol. 5). Forest Research Institute Malaysia, Kepong.
- Ashton, P., and Kettle, C. J. (2012). Dipterocarp Biology as a Window to the Understanding of Tropical Forest Structure: Where are we Looking Now? *Biotropica*, 44(5): 575–576.
- Ashton, M. S., Singhakumara, B. M. P., and Gamage, H. K. (2006). Interaction between light and drought affect performance of Asian tropical tree species that have differing topographic affinities. *Forest Ecology and Management*, 221: 42–51.
- Axtell, B. L., and Fairman, R. M. (1992). *Minor oil crops*. FAO Agricultural Services Bulletin, 94. FAO, Rome.
- Ball, J. T., and Berry, J. A. (1982). The Ci/Cs ratio: a basis for predicting stomatal control of photosynthesis. *Carnegie Institution of Washington*, 81: 88–92.
- Baltzer, J. L., Thomas, S. C., Nilus, R., and Burslem, D. (2005). Edaphic specialization in tropical trees: Physiological correlates and responses to reciprocal transplantation. *Ecology*, 86: 3063–3077.
- Banin, L., Feldpausch, T. R., Phillips, O. L., et al. (2012). What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, 21:1179–1190.
- Bassirirad, H. (2000). Kinetics of nutrient uptake by roots: responses to global change. *New Phytologist*, 147(1):155–169.
- Bazzaz, E. A. (1991) Regeneration of tropical forests. Physiological responses of secondary species. In: Gomez-Pompa, A., Whitmore, T.C. and Halley, M., Eds., *Rain Forest Regeneration and Management*, Parthenon Publishing Group and UNESCO, Paris, 91–118.

- Boardman, N. K. (1977). Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, 28: 355–377.
- Bond, B. J. (2000). Age-related changes in photosynthesis of woody plants. *Trends in Plant Science*, 5: 349–353.
- Bond, B. J., Czarnomski, C., Cooper, C., Day, M. E., and Greenwood, M. S. (2007). Developmental decline in height growth in Douglas-fir. *Tree Physiology*, 27:441–453.
- Boratyńska, K., Jasińska, A. K., and Ciepluch, E. (2008). Effect of tree age on needle morphology and anatomy of *Pinus uliginosa* and *Pinus silvestris*—species-specific character separation during ontogenesis. *Flora*, 203: 617–626.
- Browne, F. G. (1955). *Forest Trees of Sarawak and Brunei and their Products*, Sarawak Government Printing, Kuching.
- Brozek, S. (1990). Effect of soil changes caused by red alder (*Alnus rubra*) on biomass and nutrient status of Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Canadian Journal of Forest Research*, 20: 1320–1325.
- Cakmak, I., and Yazici, A. M. (2010). Magnesium: A forgotten element in crop production. *Better Crops*, 94(2), 23–25.
- Casson, S., and Gray, J. E. (2008). Influence of environmental factors on stomatal development. *New Phytologist*, 178(1): 9–23.
- Chan, H. T. (1977). Reproductive biology of some Malaysian dipterocarps. Unpublished Ph.D. thesis, University of Aberdeen, U.K. [Retrieved on March 20th, 2020].
- Chan, H. T. (1980). Reproductive biology of some Malaysian dipterocarps. 2. Fruiting biology and seedling studies. *Malaysian Forester*, 43: 438–451.
- Chan, H. T. (1981). Reproductive biology of some Malaysian dipterocarps. III. Breeding systems. *Malaysian Forester*, 38:160–170.
- Chang, Y. C., and Miller, W. B. (2004). The Relationship between leaf enclosure, transpiration, and upper leaf necrosis on *Liliumstar gazer*. *Journal of the American Society for Horticultural Science*, 129(1): 128–133.
- Chapin III, F. S., Matson, P. A., and Vitousek, P. (2011). *Principles of Terrestrial Ecosystem Ecology*. New York: Springer.
- Chazdon, R. L. and Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology*, 72: 553–564.
- Chien, C. T., Chen, S. Y., Tsai, C. C., Baskin, J. M., Baskin, C. C., and Huang, L. L. K. (2011). Deep simple epicotyl morphophysiological dormancy in seeds of two *Viburnum* species, with special reference to shoot growth and development inside the seed. *Annals of Botany*, 108: 13–22.

- Chua, L. S. L., Suhaida, M., Hamidah, M., and Saw, L. G. (2010). Malaysia Plant Red List: Peninsular Malaysian Dipterocarpaceae. Research Pamphlet No. 129. Forest Research Institute Malaysia (FRIM) and Ministry of Natural Resources and Environment Malaysia, Malaysia. 210 pages.
- Clark, D. A., and Clark, D. B. (1994). Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. *Journal of Ecology*, 82 (4): 865–872.
- Comerford, N. B. (2005). Soil factors affecting nutrient bioavailability. In *Nutrient Acquisition by Plants*. New York: Springer.
- Condit, R. (1995). Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution*, 10: 18–22.
- Corlett, R. (2014). *The ecology of tropical East Asia*. Oxford: Oxford University Press.
- Cornelissen, J. H. C., Cerabolini, B., Castro-Díez, P., Villar-Salvador, P., et al. (2003). Functional traits of woody plants: correspondence of species ranking between field adults and laboratory grown seedlings. *Journal of Vegetation Science*, 14: 311–322.
- Cornwell, W. K., Westoby, M., Falster, D. S., FitzJohn, R. G., and et al. (2014). Functional distinctiveness of major plant lineages. *Journal of Ecology*, 102: 345–356.
- Coste, S., Roggy, J. C., Garraud, L., Heuret, P., Nicolini, E., and et al. (2009). Does ontogeny modulate irradiance-elicited plasticity of leaf traits in saplings of rain-forest tree species? A test with *Dicorynia guianensis* and *Tachigali melinonii* (Fabaceae, Caesalpinioideae). *Annals of Forest Science*, 66: 1–12.
- Curran, L. M., and Leighton, M. (2000). Vertebrate Responses to Spatiotemporal Variation in Seed Production of Mast-Fruiting Dipterocarpaceae, 70(1): 101–128.
- Day, M. E., Greenwood, M. S., and White, A. S. (2001). Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, 21: 1195–1204.
- de Foresta, H., Michon, G., Kusworo, A., and Levang, P. (2004). Damar agroforests in Sumatra, Indonesia: domestication of a forest ecosystem through domestication of dipterocarps for resin production. Koen Kuster and Brian Belcher (eds.). *Forest products, livelihoods and conservation: Case studies of non-timber forest product systems*. Volume 1 - Asia. Pages 207–226. CIFOR, Bogor.
- Delagrangé, S., Messier, C., Lechowicz, M. J., and Dizengremel, P. (2004). Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiology*, 24(7): 775–784.

- Deng, Y., Deng, X., Dong, J., Zhang, W., Hu, T., Nakamura, A., Song, X., Fu, P., and Cao, M. (2020). Detecting growth phase shifts based on leaf trait variation of a canopy dipterocarp tree species (*Parashorea chinensis*). *Forests*, 11: 1145.
- Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. Department of Biology, Tulane University, New Orleans, Louisiana 70118. *Annual Review of Ecology and Systematics*, 18:431–451.
- Domec, J. C., Lachenbruch, B., Meinzer, F. C., Woodruff, D. R., Warren, J. M., and McCulloh, K. A. (2008). Maximum height in a conifer is associated with conflicting requirements for xylem design. *Proceedings of the National Academy of Sciences of the United States of America*, 105:12069–12074.
- Duvigneaud, P. (1961) Dipterocarpaceae. In: Exell, A.W., and Wild, H. (Eds.) *Flora Zambesiaca* 1, 2. Crown Agents for Overseas Governments and Administration, London, pp. 407–420.
- England, J. R., and Attiwill, P. M. (2006). Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. *Trees*, 20: 79–90.
- Eni, A., Dewantara, I., and Sisillia, L. (2018). Identification of tengkawang (*Shorea* spp) species as natural days of tenun ikat Kapuas Hulu Regency West Borneo. *Jurnal Hutan Lestari*, 6 (1): 7–15.
- Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia*, 78: 9–19.
- Evert, R. F. (2006). Phloem: secondary phloem and variations in its structure. Esau's *Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development*, 3: 407–425.
- Faisal, N. K., Martin, L., Gordon, T., and Douglas, L. G. (2008). Elevated atmospheric CO₂ changes phosphorus fractions in soils under a short rotation poplar plantation (EuroFACE). *Soil Biology and Biochemistry*, 40: 1716–1723.
- Falster, D., and Westoby, M. (2003). Leaf size and angle vary widely across species: What consequences for light interception? *New Phytologist*, 158(3): 509–525.
- FAO. (2007). *State of World's Forests*. Rome. Food and Agriculture Organization of the United Nations. [Retrieved on June 10th, 2020]
- Feldpausch, T. R., Rondon, M. A., Fernandez, E. C. M., Riha, S. J., and Wandelli, E. (2004). Carbon and nutrient accumulation in secondary forests generating on pastures in central Amazonia. *Ecological Applications*, 14: 164–176.
- Franks, N. R., and Britton, N. F. (2000). The possible role of reaction-diffusion in leaf shape. *Biological Sciences*, 267(1450): 1295–1300.
- Franks, P. J., and Beerling, D. J. (2009). Maximum leaf conductance driven by CO₂ effects on stomatal size and density over geologic time. *Proceedings of the*

National Academy of Sciences of the United States of America, 106(25): 10343–10347.

- Friend, A. D. (1993). The prediction and physiological significance of tree height. In *Vegetation dynamics and global change*. A. M. Solomon and H. H. Shugart. Eds. Chapman and Hall, New York. 101–115 p.
- Gibert, A., Gray, E. F., Westoby, M., Wright, I. J., and Falster, D. S. (2016). On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. *Journal of Ecology*, 104: 1488–1503.
- Givnish, T. J. (1988). Adaptation to sun and shade: a whole-plant perspective. *Functional Plant Biology*, 15(2): 63–92.
- Givnish, T. J., and Vermeij, G. J. (1976). Sizes and shapes of liane leaves. *American Naturalist*, 743–778.
- Gower, S. T., McMurtrie, R. E., and Murty, D. (1996). Aboveground net primary production decline with stand age: potential causes. *Trends in Ecology and Evolution*, 11: 378–382.
- Greenwood, M., Hooper, C. A., and Hutchison, K. W. (1989). Maturation in larch. I. Effect of age on shoot growth, foliar characteristics and DNA methylation. *Plant Physiology*, 90: 406–412.
- Greenwood, M. S., Ward, M. H., Day, M. E., Adams, S. L., and Bond, B. J. (2008). Age-related trends in red spruce foliar plasticity in relation to declining productivity. *Tree Physiology*, 28: 225–232.
- Greer, D. H., and Halligan, E. A. (2001). Photosynthetic and fluorescence light responses for kiwifruit (*Actinidia deliciosa*) leaves at different stages of development on vines grown at two different photon flux densities. *Functional Plant Biology*, 28(5): 373–382.
- Hammond, J. P., and White, P. J. (2008). Sucrose transport in the phloem: integrating root responses to phosphorus starvation. *Journal of Experimental Botany*, 59: 93–109.
- Hanba, Y. T., Miyazawa, S., and Terashima, I. (1999). The influence of leaf thickness on the CO₂ transfer conductance and leaf stable carbon isotope ratio for some evergreen tree species in Japanese warm-temperate forests. *Functional Ecology*, 13: 632–639.
- He, C. X., Li, J. Y., Zhou, P., Guo, M., and Zheng, Q. S. (2008). Changes of leaf morphological, anatomical structure and carbon isotope ratio with the height of the Wangtian tree (*Parashorea chinensis*) in Xishuangbanna, China. *Journal of Integrative Plant Biology*, 50: 168–173.
- Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C. E. T., Wagner, F., and Baraloto, C. (2011). Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, 99: 1431–1440.

- Hinckley, T. M., Lachenbruch, B., Meinzer, F. C., and Dawson, T. D. (2011). A Lifespan perspective on integrating structure and function in trees. In: Meinzer FC, Lachenbruch B, Dawson TE (eds.) Size and age-related changes in tree structure and function. Springer, Dordrecht, pp 3–30.
- Hochmal, A. K., Schulze, S., Trompelt, K., and Hippler, M. (2015). Calcium-dependent regulation of photosynthesis. *Biochimica et Biophysica Acta*, 1847: 993–1003.
- Holland, N., and Richardson, A. D. (2009). Stomatal length correlates with elevation of growth in four temperate species. *Journal of Sustainable Forestry*, 28: 63–73.
- Hubbard, R. M., Ryan, M. G., Stiller, V., and Sperry, J. S. (2001). Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell and Environment*, 24: 113–121.
- Husch, B., Beers, T. W., and Kershaw, J. A. (2003). Forest mensuration. 4th ed. Hoboken (NJ): Wiley. 443 p.
- Hutchinson, J., and Dalziel, J. M. (1954). Flora of West Tropical Africa. Vol. I, Part 1, 2nd Edition, Crown Agents for Overseas Governments Administrations, London.
- Ishida, A., Yazaki, K., and Ang, L. H. (2005). Ontogenetic transition of leaf physiology and anatomy from seedlings to mature trees of a rain forest pioneer tree, *Macaranga gigantean*. *Tree Physiology*, 25: 513–522.
- Ishii, H. (2011). How do changes in leaf/shoot morphology and crown architecture affect growth and physiological function of tall trees? In: Meinzer, F.C., Lachenbruch, B., and Dawson, T.E. (eds.) Size and age-related changes in tree structure and function. Springer, Dordrecht, pp 215–232.
- Ishii, H., Reynolds, J. H., Ford, E. D., and Shaw, D. C. (2000). Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State, USA. *Canadian Journal of Forest Research*, 30:17–24.
- Itoh, A., Rokujo, N., Kanzaki, M., Yamakura, T., Lafrankie, J. V., *et al.* (2004). An approach for assessing species specific density-dependence and habitat effects in recruitment of a tropical rainforest tree. In Losos, E. C., and Leigh Jr., E. G. (eds.). Tropical forest diversity and dynamism: Findings from a large-scale plot network, pp. 320–339. The University of Chicago Press, Chicago & London.
- Itoh, A., Nanami, S., Harata, T., Ohkubo, T., Tan, S., Chong, I., Davies, S., and Yamakura, T. (2012). The effect of habitat association and edaphic conditions on tree mortality during El nino-induced drought in a Bornean dipterocarp forest. *Biotropica*, 44: 606–617.
- ITTO. (2021). The International Tropical Timber Organization. Biennial review and assessment of the world timber situation 2019-2020. Yokohama. [Retrieved on March 30th, 2022]
- IUCN. (2021). International Union for Conservation of Nature's Red List of Threatened Species. <https://www.iucnredlist.org/> [Retrieved on March 30th, 2022]

- Jacobs, M. (1988). The dipterocarps. In: Earl of Cranbrook (ed.) Malaysia, 31-36. Key Environments Series. Pergamon Press, Oxford.
- Jaffe, M. J., and Forbes, S. (1993) Thigmomorphogenesis: the effect of mechanical perturbation on plants. *Plant Growth Regulation*, 12: 313–324.
- Johnson, C. M., Vieira, I. C. G., Zarin, D. J., Frizano, J., and Johnson, A. H. (2001). Carbon and nutrient storage in primary and secondary forests in eastern Amazonia. *Forest Ecology and Management*, 147:245–252.
- Johnson, S. E., and Abrams, M. D. (2009). Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. *Tree Physiology*, 29: 1317–1328.
- Johnson, K., and Lenhard, M. (2011). Genetic control of plant organ growth. *New Phytologist*, 191(2): 319–333.
- Jones, D. L., and Darrah, P. R. (1994). Role of root derived organic acids in the mobilization of nutrients from the rhizosphere. *Plant and Soil*, 166: 247–257.
- Juárez-López, F. J., Escudero, A., and Mediavilla, S. (2008). Ontogenetic changes in stomatal and biochemical limitations to photosynthesis of two co-occurring Mediterranean oaks differing in leaf life span. *Tree Physiology*, 28: 367–374.
- Julia, S., Chong, L., Vilma, B., Esther, S., and Pearce, K. G. (2014). Sarawak Plant Red List Dipterocarpaceae: Series I: *Dipterocarpus*, *Dryobalanops* and *Shorea*. Sarawak Forestry Corporation Sdn. Bhd., Kuching Malaysia. 193 pages.
- Keller, M. (2015). The Science of Grapevines: Anatomy and Physiology. Cambridge: Academic Press.
- Kenzo, T., Ichie, T., Ogawa, T., Kashimura, S., Hattori, D., Irino, K. O., and Ninomiya, I. (2007). Leaf physiological and morphological responses of seven dipterocarp seedlings to degraded forest environments in Sarawak, Malaysia: A case study of forest rehabilitation practice. *Tropics*, 17(1): 1–16.
- Kenzo, T., Ichie, T., Watanabe, Y., Yoneda, R., Ninomiya, I., and Koike, T. (2006). Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. *Tree Physiology*, 26: 865–873.
- Kenzo, T., Ichie, T., Yoneda, R., Kitahashi, Y., Watanabe, Y., Ninomiya, I., and Koike, T. (2004). Interspecific variation of photosynthesis and leaf characteristics in five canopy trees of Dipterocarpaceae in a tropical rain forest. *Tree Physiology*, 24: 1187–1192.
- Kenzo, T., Inoue, Y., Yoshimura, M., Yamashita, M., Tanaka-Oda, A., and Ichie, T. (2015). Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia*, 177: 191–202.

- Kenzo, T., Yoneda, R., Sano, M., Araki, M., Shimizu, A., Tanaka-Oda, A., and Chann, S. (2012). Variations in leaf photosynthetic and morphological traits with tree height in various tree species in a Cambodian tropical dry evergreen forest. *Japan Agricultural Research Quarterly*, 46: 167–180.
- Kerstiens, G. (1996a). Plant cuticles-An integrated functional approach. *Journal of Experimental Botany*, 47: 50–60.
- Kerstiens, G. (1996b). Signalling across the divide: A wider perspective of cuticular structure—function relationships. *Trends in Plant Science*, 1: 125–129.
- King, D. A. (2011). Size-related changes in tree proportions and their potential influence on the course of height growth. In: Meinzer FC, Lachenbruch B, Dawson TE (eds.) Size and age-related changes in tree structure and function. Springer, Dordrecht, pp 165–192.
- Kira, T., and T. Shidei. (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology*, 17: 70–87.
- Kira, T., and Yoda, K. (1989) Vertical stratification in microclimate. Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies (eds H. Lieth & M. J. A. Werger), pp. 55–71. Elsevier, Amsterdam.
- Kobayashi, S., Turnbull, J. W., and Cossalter, C. (2001). Rehabilitation of degraded tropical forest ecosystems, 1–16. *Workshop Proceedings*, Bogor. Cifor, pp.219.
- Koch, G. W., Sillett, S. C., Jennings, G. M., and Davis, S. D. (2004). The limits to tree height. *Nature*, 428: 851–854.
- Kochummen, K. M. (1961). Precocious flowering (paedogenesis) in Dipterocarpaceae. *Malayan Forester*, 24: 236–237.
- Korning, J., and Balslev, H. (1994). Growth-rates and mortality patterns of tropical lowland tree species and the relating to forest structure in Amazonian Ecuador. *Journal of Tropical Ecology*, 10: 151–166.
- Kozłowski, T. T., and Pallardy, S. G. (1996). Physiology of woody plants. Academic, San Diego.
- Kramer, P. (2012). Physiology of Woody Plants. Amsterdam: Elsevier.
- Krishnapillay, B. (2004). Dipterocarps. Encyclopedia of Forest Sciences, Pages 1682–1687. Jeffery Burley, Julian Evans, John Youngquist (editors). Academic Press, Oxford.
- Kull, O., and Koppel, A. (1987). Net photosynthetic response to light intensity of shoots from different crown positions and age in *Picea abies* (L.) Karst. *Scandinavian Journal of Forest Research*, 2: 157–166.

- Kumagai, T., Saitoh, T. M., Satoh, Y., Morooka, T., Manfroid, O. J., Kurajid, K., Suzuki, M. (2004). Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects. *Journal of Hydrology*, 287: 237–251.
- LaFrankie Jr., J. V., and Chan, H. T. (1991). Confirmation of sequential flowering in *Shorea* (Dipterocarpaceae), *Biotropica*, 23 (2): 200–203.
- Lambers, H., and Colmer, T. D. (2005). Plant and soil, Volume 274. Springer. Dordrecht/Boston/London.
- Lambers, H., Chapin, F. S. III., and Pons, T. L. (1998). Plant physiological ecology. Blackwell, Malden.
- Lang, G. E., and Knight, D. H. (1983). Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecology*, 64: 1075–1080.
- Lapok, E. Y., Ong, K. H., John, K. C., and Patricia, K. J. H. (2017). Growth of *Dryobalanops beccari* Dyer in restored forest and influences in soil properties in Sarawak, Malaysia. *Ecosystems and Development Journal*, 7(2): 3–13.
- Larcher, W. (1995). Physiological plant ecology, 3rd Ed. Springer, Berlin.
- Lau, O. S., and Bergmann, D. C. (2012). Stomatal development: a plant's perspective on cell polarity, cell fate transitions and intercellular communication. *Development*, 139: 3683–3692.
- Lavelle, P. (1987). Biological processes and productivity of soils in the humid tropics. In: Robert ED (ed) The geophysiology of Amazonia: vegetation and climate interactions. Wiley, New York, pp 175–222.
- Lawson, T., and Blatt, M. R. (2014). Stomatal size, speed and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiology*, 164: 1556–1570.
- Lawson, A. M. and Weir, J. T. (2014). Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, 17: 1427–1436.
- Leverenz, J. W., and Hinckley, T. M. (1990). Shoot structure, leaf area index, and productivity of evergreen conifer stands. *Tree Physiology*, 6: 135–149.
- Li, Q., Hou, J., He, N., Xu, L., and Zhang, Z. (2021). Changes in leaf stomatal traits of different aged temperate forest stands. *Journal of Forestry Research*, 32: 927–936.
- Lieberman, M., and Lieberman, D. (1994). Patterns of density and dispersion of forest trees. In: McDade, L. A., Bawa, K. S., Hespdenheide, H. A., and Hartshorn, G. S. (eds) Ecology and natural history of a tropical rainforest. University of Chicago Press, Chicago. Pp. 105–119.

- Lieberman, D., Lieberman, M., Hartshorn, G. S., and Peralta, R. (1985). Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology*, 1: 97–109.
- Lu, D., Moran, E., and Mausel, P. (2002). Linking Amazonian secondary forest growth to soil properties. *Land Degradation and Development*, 13: 331–343.
- Luomala, E. M., Laitinen, K., Sutinen, S., Kellomaki, S., and Vapaavuori, E. (2005). Stomatal density, anatomy and nutrient concentrations of Scots pine needles are affected by elevated CO₂ and temperature. *Plant, Cell and Environment*, 28: 733–749.
- Ma, X., Heal, K. V., Liu, A., and Jarvis, P. G. (2007). Nutrient cycling and distribution in different-aged plantations of Chinese fir in southern China. *Forest Ecology and Management*, 243: 61–74.
- Magnani, F., Bensada, A., Cinnirella, S., Ripullone, F., and Borghetti, M. (2008). Hydraulic limitations and water-use efficiency in *Pinus pinaster* along a chronosequence. *Canadian Journal of Forest Research*, 38: 73–81.
- Maguire, B. and Ashton, P.S. (1980). *Pakaraimaea* - Dipterocarpaceae 2. *Taxon* 29: 225–231.
- Makana, J., Hart, T. B., Liengola, I., Ewango, C., Hart, J. A., and Condit, R. (2004). Ituri forest dynamics plots, Democratic republic of Congo. Tropical forest diversity and dynamism: Findings from a large- scale plot network. 107–108.
- Malaysian Timber Council. (2021). Annual report 2020. Kuala Lumpur, MTC. [Accessed May 24th 2022].
- Marschner, H. (1995). Mineral nutrition of higher plants. Academic Press, London.
- Martin, C., and Glover, B. J. (2007). Functional aspects of cell patterning in aerial epidermis. *Current Opinion in Plant Biology*, 10(1): 70–82.
- Martínez-Vilalta, J., Vanderklein, D., and Mencuccini, M. (2007). Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia*, 150: 529–544.
- Matzner, S. L., Rice, K. J., and Richards, J. H. (2003). Patterns of stomatal conductance among blue oak (*Quercus douglasii*) size classes and populations: implications for seedling establishment. *Tree Physiology*, 23: 777–784.
- Maury, L. G., and Curtet, L. (1998) Biogeography and evolutionary systematic of family Dipterocarpaceae. In A Review of Dipterocarps: Taxonomy, Ecology and Silviculture (pp. 5–44). Center for International Forestry Research, Indonesia.
- McDonald, M. S. (2003). Photobiology of Higher Plants. Wiley, Chichester.

- McNamara, S., Tinh, D. V., Erskine, P. D., Lamb, D., Yates, D., and Brown, R. (2006). Rehabilitating degraded forest land in central Vietnam with mixed native species plantings. *Forest Ecology and Management*, 233(2): 358–365.
- Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., and Woodruff, D. R. (2009). Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, 23(5): 922–930.
- Meldau, S., M., Zeunert, L. U., Govind, G., Bartram, S., and Baldwin, I. T. (2012). MAPK-dependent JA and SA signalling in *Nicotiana attenuata* affects plant growth and fitness during competition with conspecifics. *BMC Plant Biology*, 12 (213). <http://www.biomedcentral.com/1471-2229/12/213>[Accessed July 22th 2019].
- Mencuccini, M., Höltä, T., and Martinez-Vilalta, J. (2011). Comparative criteria for models of the vascular transport systems of tall trees. In: Meinzer, F.C., Lachenbruch, B., and Dawson, T. E. (eds.) Size- and age-related changes in tree structure and function. Springer, Dordrecht, pp 309–339.
- Meng, L. Z., Zhang, J. L., Cao, K. F., and Xu, Z. F. (2005). Diurnal changes of photosynthetic characteristics and chlorophyll fluorescence in canopy leaves of four dipterocarp species under ex-situ conservation. *Acta Ecologica Sinica*, 29: 976–984.
- Mengel, K., and Kirkby, E. A. (1987). Principles of plant nutrition, 559–572. Bern: International Potash Institute.
- Merilo, E., Tulva, I., Räm, O., Kükit, A., Sellin, A., and Kull, O. (2009). Changes in needle nitrogen partitioning and photosynthesis during 80 years of tree ontogeny in *Picea abies*. *Trees*, 23:951–958.
- Mishra, S. R. (2004). Morphology of plants. Discovery Publishing House, New Delhi.
- Miyawaki, A. (1999). Creative Ecology. *Plant Biotechnology*, 16(1): 15–25.
- Miyawaki, A., and Box, E. O. (2006). The healing power of forests. The philosophy behind restoring Earth's balance with native trees. Kosei Publishing Co. Tokyo. ed.
- Mongabay. (2016a). Tropics' tallest tree found in Malaysia. <https://news.mongabay.com/2016/06/tropics-tallest-tree-found-in-malaysia/> [Accessed August 24th 2019].
- Mongabay. (2016b). World's tallest tropical tree discovered, along with nearly 50 other record-breakers. <https://news.mongabay.com/2016/11/worlds-tallest-tropical-tree-discovered-along-with-nearly-50-other-record-breakers/>[Accessed August 24th 2019].

- Mullin, L. P., Sillett, S. C., Koch, G. W., Tu, K. P., and Antoine, M. E. (2009). Physiological consequences of height related morphological variation in *Sequoia sempervirens* foliage. *Tree Physiology*, 29: 999–1010.
- Nabeshima, E., and Hiura, T. (2004). Size dependency of photosynthetic water- and nitrogen-use efficiency and hydraulic limitation in *Acer mono*. *Tree Physiology*, 24: 745–752.
- Nabeshima, E., and Hiura, T. (2008). Size-dependency in hydraulic and photosynthetic properties of three *Acer* species having different maximum sizes. *Ecological Research*, 23(2): 281–288.
- Newman, M. F., Burgess, P. F., and Whitmore, T. C. (1996). *Manual of Dipterocarps for Foresters: Borneo Island Light Hardwood* (Edinburgh: CIFOR and Royal Botanic Garden).
- Ng, F. S. P. (1977). Gregarious flowering of dipterocarps in Kepong 1976. *Malaysian Forester*, 40: 126–137.
- Nicola, S. (1998). Understanding Root Systems to Improve, Seedling Quality. *Horticulture Technology*, 8(4): 1–6.
- Niinemets, Ü. (2002). Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology*, 22: 515–535.
- Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, 25: 693–714.
- Niinemets, Ü., and Kull, O. (1995). Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in needle morphology. *Tree Physiology*, 15: 307–315.
- Niinemets, Ü., Díaz-Espejo, A., Flexas, J., Galmés, J., Warren, C. R. (2009). Role of mesophyll diffusion conductance in constraining potential photosynthetic productivity in the field. *Journal of Experimental Botany*, 60: 2249–2270.
- Niinemets, Ü., Kenan, T. F., and Hallik, L. (2015) A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist*, 205: 973–993.
- Niinemets, Ü., Kull, O., and Tenhunen, J. D. (1999). Variability in leaf morphology and chemical composition as a function of canopy light environment in co-existing trees. *International Journal of Plant Sciences*, 160: 837–848.
- Niklas, K. J. (2007). Maximum plant height and the biophysical factors that limit it. *Tree Physiology*, 27: 433–440.
- Nobuchi, T., and Sahri, M. H. (2008). The formation of wood in tropical forest tree. A challenge from the perspective of functional wood anatomy. Serdang: UPM Press.

- Ohashi, S., Okada, N., Nobuchi, T., Siripatanadilok, S., and Veenin, T. (2009). Detecting invisible growth rings of trees in seasonally dry forests in Thailand: isotopic and wood anatomical approaches. *Trees - Structure and Function*, 23: 813–822.
- Okuda, T., Manokaran, N., Matsumoto, Y., Niiyama, K., Thomas, S. C., and Ashton, P. S. (2013). *Pasoh: Ecology of a lowland rain forest in Southeast Asia*. London: Springer.
- Pallardy, S. G. (2010). *Physiology of Woody Plants*. Cambridge: Academic Press.
- Paoli, G. D., Curran, I. M., and Zak, D. Z. (2006). Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology*, 94: 157–170.
- Parresol, B. R., and Devall, M. S. (2013). Patterns of diametric growth in stem-analyzed laurel trees (*Cordia alliodora*) in a Panamanian forest. *The Southwestern Naturalist*, 58(2): 170–178.
- Peli, M., Husni, A., and Ibrahim, M. Y. (1984). Report and map of the detailed soil survey of UPM Farm, Bintulu Campus, and Sarawak. *UPM Sarawak Campus Technical Paper*, 1: 73.
- Perry, D., Ram, O., and Stephen, H. (2008). *Forest Ecosystems*. The John Hopkins University Press, Baltimore.
- Pons, T. L., and Percy, R. W. (1994). Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiologia Plantarum*, 92: 636–644.
- Powell, G. R. (2009). *Lives of conifers*. The Johns Hopkins University Press, Baltimore, 276 p.
- Powell, A. E., and Lenhard, M. (2012). Control of organ size in plants. *Current Biology*, 22(9): 360–367.
- Pretzsch, T., Rotzer, R., Matyssek, T. E. E., Grams, K.H., et al. (2014). Mixed Norway spruce (*Picea abies* L. Karst) and European beech (*Fagus sylvatica* L.) stands under drought: from reaction pattern to mechanism. *Trees*, 28(5): 1305–1321.
- Primack, R. B., Ashton, P. S., Chai, P., and Lee, H. S. (1985). Growth rates and population structure of Moraceae trees in Sarawak, East Malaysia. *Ecology*, 66: 577–588.
- Purwaningsih, and Kintamani, E. (2018). The diversity of *Shorea* spp. (*Meranti*) at some habitats in Indonesia. *IOP Conference Series: Earth and Environmental Science*, 197: 012034.
- Rebbeck, J., Jensen, K. F., and Greenwood, M. S. (1993). Ozone effects on grafted mature and juvenile red spruce: photosynthesis, stomatal conductance, and chlorophyll concentration. *Canadian Journal of Forest Research*, 23: 450–456.

- Reich, A., Holbrook, N. M., and Ewel, J. J. (2004). Developmental and physiological correlates of leaf size in *Hyeronima alchorneoides* (Euphorbiaceae). *American Journal of Botany*, 91: 582–589.
- Richardson, A. D., Berlyn, G. P., Ashton, P. M. S., Thadani, R., and Cameron, I. R. (2000). Foliar plasticity of hybrid spruce in relation to crown position and stand age. *Canadian Journal of Botany*, 78: 305–317.
- Rijkers, T., Pons, T. L., and Bongers, F. (2000). The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Functional Ecology*, 14:77–86.
- Roelfsema, M. R. G. and Hedrich, R. (2005). In the light of stomatal opening: new insights into ‘the Watergate’. *New Phytologist*, 167: 665–691.
- Rozendaal, D., and Zuidema, P. A. (2011). Dendroecology in the tropics. *Trees*, 25(1): 3–16.
- Rust, S., and Roloff, A. (2002). Reduced photosynthesis in old oak (*Quercus robur*): the impact of crown and hydraulic architecture. *Tree Physiology*, 22(8): 597–601.
- Ryan, M. G., and Waring, R. H. (1992). Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology*, 73: 2100–2108.
- Ryan, M. G., and Yoder, B. J. (1997). Hydraulic limits to tree height and tree growth. *Biosciences*, 47(4): 235–242.
- Ryan, M. G., Binkley, D., and Fownes, J. H. (1997). Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research*, 27: 213–262.
- Ryan, M. G., Phillips, N., and Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell and Environment*, 29(3): 367–381.
- Sakai, S., Harrison, R. D., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., Chong, L., and Nakashizuka, T. (2006). Irregular droughts trigger mass flowering in a seasonal tropical forests in Asia. *American Journal of Botany*, 93(8): 1134–1139.
- Sakai, S., Momose, K., Yumoto, T., and Kato, M. (1999). Beetle pollination of *Shorea parvifolia* (Section Mutica, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia. *American Journal of Botany*, 86(1): 62–69.
- Sanches, M. C., Ribeiro, S. P., Dalvi, V. C., da Silva Junior, M. B., de Sousa, H. C., and de Lemos-Filho, J. P. (2010). Differential leaf traits of a neotropical tree *Cariniana legalis* (Mart.) Kuntze (Lecythidaceae): comparing saplings and emergent trees. *Trees*, 24: 79–88.
- Saw, L. G., and Sam, Y. Y. (2000). Conservation of Dipterocarpaceae in Peninsular Malaysia. *Journal of Tropical Forest Science*, 593–615.
- Schoettle, A. W. (1994). Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiology*, 14: 1055–1068.

- Schulte, A., and Schone, D. (1996). Dipterocarp forest ecosystems: towards sustainable management. Hong Kong: World Scientific.
- Schwarzwaller, W., Chai, F. Y. C., and Hahn-Schilling, B. (1999). Growth characteristics and response to illumination of some *Shorea* species in the logged-over mixed dipterocarp forest of Sarawak, Malaysia. *Journal of Tropical Forest Science*, 11: 554–569.
- Sendall, K. M., and Reich, P. B. (2013). Variation in leaf and twig CO₂ flux as a function of plant size: a comparison of seedlings, saplings and trees. *Tree Physiology*, 33: 1338–1353.
- Serna, L., and Fenoll, C. (1997). Tracing the ontogeny of stomatal clusters in *Arabidopsis* with molecular markers. *The Plant Journal*, 12: 747–755.
- Sharma, G., Sharma, R., and Sharma, E. (2009). Impact of stand age on soil C, N and P dynamics in a 40-year chronosequence of alder-cardamom agroforestry stands of the Sikkim Himalaya. *Pedobiologia*, 52: 401–414.
- Sharma, H. R. and Shasrma, E. (1997). Mountain agricultural transformation processes and sustainability in the Sikkim Himalayas, India, Discussion Paper Series No.MFS 97/2. ICIMOD, Kathmandu, Nepal.
- Shenkin, A., Chandler, C. J., Boyd, D. S., Jackson, T. et al. (2019). The world's tallest tropical tree in three dimensions. *Frontiers in Forests and Global Change*, 32 (2): 1–5.
- Shimazaki, K. I., Michio, D., Assmann, S. M., and Kinoshita, T. (2007). Light Regulation of Stomatal Movement. *Annual Review of Plant Biology*, 58:219–247.
- Shiva, M. P., and Jantan, I. (1998). Non-Timber Forest Products from Dipterocarps. In: Apannah, S., and Turnbull, J. M. (eds.) *A Review of Dipterocarps: Taxonomy, Ecology and Sylviculture* (Bogor: CIFOR) pp: 187–198.
- Silk, J. W., Paoli, G., McGuire, K., Amaral, I. Barroso, J. et al. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, 22: 1261–1271.
- Sivak, M. N., and Walker, D. A. (1986). Photosynthesis in vivo can be limited by phosphate supply. *The New Phytologist*, 102: 499–512.
- Soares, A. S., Driscoll, S. P., Olmos, E., Harbinson, J., Arrabac, M. C., and Foyer, C. H. (2008). Adaxial/abaxial specification in the regulation of photosynthesis and stomatal opening with respect to light orientation and growth with CO₂ enrichment in the C₄ species.
- Soepadmo, E., Saw, L. G., and Chung, R. C. K. (2004). *Tree Flora of Sabah and Sarawak*, Volume 5. Sabah Forestry Department, Forest Research Institute Malaysia (FRIM), Sarawak Forestry Department, Malaysia. pp. 528.

- Souza, A. F., Martins, F. R., and Bernacci, L. C. (2003). Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*: An ontogenetic approach. *Canadian Journal of Botany*, 81: 101–112.
- Srivastava, A. K. (1993). Changes in physical and chemical properties of soil in irrigated Eucalyptus plantation in Gujarat state. *Indian Forester*, 119: 227–231.
- Stang, C. (2014). Role of submerged vegetation in the retention processes of three plant protection products in flow-through stream. *Chemosphere*, 107: 13–22.
- Steele, R., Amo, S. F., and Geier-Hayes, K. (1989). The Douglas-fir / ninebark habitat type in central Idaho: succession and management. United States Department of Agriculture Forest Service Intermountain Research Station, Ogden, Utah, USA. General Technical Report INT-252.
- Steeves, T. A., and Sussex, I. M. (1989). Patterns in plant development. Cambridge University Press, Cambridge.
- Steppe, K., Niinemets, U., and Teskey, R. O. (2011). Tree size- and age- related changes in leaf physiology and their influence on carbon gain. In *Size- and Age-related Changes in Tree Structure and Function*. London: Springer.
- Su, H., Li, Y., Liu, W., Xu, H., and Sun, O. J. (2013). Changes in water use with growth in *Ulmus pumila* in semiarid sandy land of northern China. *Trees*, 28: 41–52.
- Sukri, R. S. H., Wahab, R. A., Salim, K. A., and Burslem, D. F. R. P. (2012). Habitat associations and community structure of dipterocarps in response to environmental and soil conditions in Brunei Darussalam, northwest Borneo. *Biotropica*, 44: 595–605.
- Symington, C. F. (1943). Forester's manual of dipterocarps. Malaysian Forest Record 16, Penerbit Universiti, Kuala Lumpur, Malaya, p. 242.
- Symington, C. F., Ashton, P. S., and S Appanah, S. (2004). Foresters' manual of Dipterocarps, Malayan Forest Records 16. Forest Research Institute Malaysia and Malaysian Nature Society, Kuala Lumpur.
- Tan, K. H. (2005). Soil Sampling, Preparation, and Analysis. CRC press.
- Terashima, I., Miyazawa, S., and Hanba, T. Y. (2001). Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO₂ diffusion in the leaf. *Journal of Plant Research*, 114: 93–105.
- Thomas, S. C. (2011). Age-related changes in tree growth and functional biology: the role of reproduction. In: Meinzer, F.C., Lachenbruch, B., and Dawson, T. E. (eds.) *Size- and age-related changes in tree structure and function*. Springer, Dordrecht, pp 33–64.
- Van Kleunen, M., Weber, E., and Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13: 235–245.

- Veneklaas, E. J., and Poorter, L. (1998). Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In: Lambers, H., Poorter, H., and Van Vuren, M. M. I. (eds.) *Inherent variation in plant growth. physiological mechanisms and ecological consequences*, Backhuys Publishers, Leiden. pp. 337–355.
- Verdcourt, B. (1989). *Flora of tropical East Africa - Dipterocarpaceae*. Balkeman A.A., Rotterdam. p. 11.
- Visser, M. D., Bruijning, M., Wright, S. J., Muller-Landau, H. C., Jongejans, E., Comita, L. S., and de Kroon, H. (2016). Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology*, 30: 168–180.
- Walters, M. B., Kruger, E. L., and Reich, P. B. (1993). Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. *Oecologia*, 96: 219–231.
- Wang, J. R., Zhong, A. L., Simard, S. W., and Kimmins, J. P. (1996). Aboveground biomass and nutrient accumulation in an age sequence of paper birch (*Betula papyrifera*) in the Interior Cedar Hemlock zone, British Columbia. *Forest Ecology and Management*, 83: 27–38.
- Weatherbase, (2013). Seligman, Missouri. <http://www.weatherbase.com/weather/weather.php3?s=5546732&cityname=Seligman-Missouri>. [Accessed December 21st 2019.]
- Weiskittel, A. R., Hann, D. W., Kershaw Jr, J. A., and Vanclay, J. K. (2011). *Forest Growth and Yield Modeling*. New York: John Wiley and Sons.
- Whitmore, T. C. (1999). Arguments on the forest frontier. *Biodiversity and Conservation*, 8: 865–868.
- Wilkinson, S., Welch, R., Mayland, H., and Grunes, D. (1990). Magnesium in plants: uptake, distribution, function and utilization by man and animals. *Metal Ions in Biological Systems*, 26: 33–56.
- Wolfe, J. A. (1993). A method of obtaining climatic parameters from leaf assemblages. *United States Geological Survey Bulletin*, 2040: 1–71.
- Wong, S. C., Cowan, I. R., and Farquhar, G. D. (1985). Leaf conductance in relation to rate of CO₂ assimilation. III. Influences of water stress and photoinhibition. *Plant Physiology*, 78: 830–834.
- Woodruff, D. R., Bond, B. J., and Meinzer, F. C. (2004). Does turgor limit growth in tall trees? *Plant, Cell and Environment*, 27: 229–236.
- Woodruff, D. R., Meinzer, F. C., Lachenbruch, B., and Johnson, D. M. (2009). Coordination of leaf structure and gas exchange along a height gradient in a tall conifer. *Tree Physiology*, 29: 261–272.

- Worbes, M. (1992). Occurrence of seasonal climate and tree ring research in the tropics. *Lundqua Report*, 34: 338–342.
- Worbes, M. (2002). Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. Cambridge University Press, Cambridge.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z. et al. (2004). The world-wide leaf economics spectrum. *Nature*, 428: 821–827.
- Wright, S. J., Kitajima, K., Kraft, N. J., Reich, P. B., Wright, I. J., Bunker, D. E., et al. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91: 3664–3674.
- Wu, H., Xiang, W., Chen, L., Ouyang, S., Xiao, W., Li, S., Forrester, D. I. et al. (2020). Soil phosphorus bioavailability and recycling increased with stand age in Chinese Fir plantations. *Ecosystems*, 23: 973–988.
- Wyatt-Smith, J. (1963). Manual of Malayan silviculture. Malayan Forest Records No. 23.
- Xie, S., and Luo, X. (2003). Effect of leaf position and age on anatomical structure, photosynthesis, stomatal conductance and transpiration of Asian pear. *Botanical Bulletin of Academia Sinica*, 44.
- Yin, X., Zhao, L., Fang, Q., Ding, G. (2021). Differences in soil physicochemical properties in different-aged *Pinus massoniana* plantations in southwest China. *Forests*, 12: 987.
- Yoder, B. J., Ryan, M. G., Waring, R. H., Schoettle, A. W., and Kaufmann, M. R. (1994). Evidence of reduced photosynthetic rates in old trees. *Forest Science*, 40(3): 513–527.
- Yong, W.S.Y., Chua, L.S.L., Suhaida, M., and Aslina, B. (2011). Forest Research Institute Malaysia: A Sanctuary for Threatened Trees, Issue/No. 130. Forest Research Institute Malaysia (FRIM), Malaysia. pp. 91.
- Zhao, C., Chen, L., Ma, F., Yao, B., and Liu, J. (2008). Altitudinal differences in the leaf fitness of juvenile and mature alpine spruce trees (*Picea crassifolia*). *Tree Physiology*, 28:133–141.
- Zhou, Y., Schaub, M., Shi, L., Guo, Z., Fan, A., Yan, C., Wang, X., Wang, C., et al. (2012). Non-linear response of stomata in *Pinus koraiensis* to tree age and elevation. *Trees*, 26: 1389–1396.