

Optimising the Recovery of Degraded Tropical Rainforest Logging Estates

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I asked the root of a tree, what is your purpose?

*And the root of the tree replied, I draw the princely gifts of water and nutrients to feed the stem
which feeds the branches which feeds the leaves and fruits and, in turn, all life on earth...*

Julian Matthews, Malaysian Poet

STATEMENT OF ORIGINALITY

I declare that the research contained in this thesis is the product of my own work. Ideas or research from other people, published or otherwise, is duly acknowledged following standard referencing procedure.

This thesis has received input to specific chapters from other researchers listed below.

Robert Ewers provided detailed comments on multiple earlier versions of each chapter.

For Chapter 3, Francis Windram developed the Node Joining Algorithm (NJA) to my specifications for testing root system architecture. Development of the NJA formed a chapter of his own PhD thesis.

Chapter 4, David Orme helped with the coding of the draft biomass recovery simulation in R.

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For Janet

and for Jean

and for Rita

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Abstract

Tropical forests comprise 40% of the Earth's terrestrial carbon sink, converting carbon dioxide into biomass. The natural flux of carbon in forests is controlled by growth and decomposition of biomass; processes which can be influenced by human activity. Southeast Asia's history of intensive commercial logging has interrupted these natural processes, with 70% of extant forests now degraded. Despite their prevalence, logged forests are not studied as widely as primary forests. Data on belowground biomass and root systems is particularly scarce. Malaysian Borneo has been a global hotspot for timber production over the past century, often at greater rates than were considered sustainable. This casts doubt on whether heavily degraded forests will regenerate naturally within the expected timeframe of approximately 60-80 years. This thesis aims to fill these knowledge gaps by investigating the above and belowground biomass of Bornean forests along a degradation gradient, from highly degraded salvage-logged forests, to lightly logged forest, through to pristine primary forests. First, we trialled LiDAR and photogrammetry for generating 3D imagery of tree root systems using low-cost, handheld technology. We then used this technique to digitally capture the root system architecture of *Macaranga* trees excavated in Borneo and determined the biomass root:shoot ratio. Finally, we used data from an eight-year vegetation census across the degradation gradient to parameterise a simulation of biomass regeneration in logged forests. We found that the pioneer species in regenerating forests have a higher root:shoot ratio than is found in a primary forest and that *Macaranga* tree roots form complex networks by inosculating with their neighbours. Our simulation indicates that by 2050, most salvage-logged forests will remain degraded. We also showed that primary forests can continue to gain large amounts of biomass year-on-year. The outputs from this research can support restoration activities, advise sustainable logging, and improve local carbon accounting.

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Glossary

AGB – Aboveground Biomass. Living vegetation above the soil, including stem, stump, branches, bark, seeds, and foliage (Tyrrell et al., 2012). Usually measured in Mg ha^{-1} , (metric tonnes or 1000kg per hectare).

Basal area – The average amount of an area occupied by tree stems. It is defined as the total cross-sectional area of all stems in a stand measured at breast height, and expressed as per unit of land area (typically square feet per acre).

Basal Node – The vertex of a root system that is closest to the base of the tree trunk.

BGB – Belowground Biomass. Belowground biomass is defined as the entire biomass of all live roots, although fine roots less than 2 mm in diameter are often excluded because these cannot easily be distinguished empirically from soil organic matter (Ravindranath & Ostwald, 2008).

Binary Map – An image representing the presence or absence of a condition across a space. Presence is usually represented by a white pixel, and absence is represented by a black pixel.

Dbh – diameter (of a tree trunk) at breast height.

Edge – A link between two vertices in a network.

Extraction Rates – The amount of commercial timber removed from a site during logging operations, usually recorded by volume, such as cubic metres (m^3).

LiDAR – Light Detection and *Ranging*. A remote sensing method that uses light in the form of a pulsed laser to measure variable distances from the scanner to the object of interest, generating precise, three-dimensional information about the object's shape and surface characteristics.

NJA – Node-joining algorithm for digitising binary images of physical networks into their graph representation.

REDD⁺ – Reducing emissions from deforestation and forest degradation in developing countries.

RSR – Root:shoot Ratio. The ratio of belowground biomass to aboveground biomass, which is the parameter that most directly reflects biomass allocation by plants (Qi et al. 2019).

Topology – The hierarchical structure of branches, in this case of forming a tree

DTP – Digital Terrestrial Photogrammetry is a technique of representing and measuring 3D objects using data stored on 2D photographs, in this case taken from ground level.

Chapter 1) Introduction

The Global Context of Degraded Forests

Tropical forests provide a range of ecosystem services, including influencing the world's hydrological and carbon cycles (Brown, 1993; Phillips et al., 1998). By converting carbon dioxide to biomass, they comprise 40% of the planet's terrestrial carbon sink (Malhi, 2010; Ciais et al., 2013), but anthropogenic impacts can compromise the integrity of this sink (Hubau et al., 2020) and even shift these forests into carbon sources (Riutta et al., 2018; Mills et al., 2023). Compared to pre-industrial levels, approximately 30% of the world's forests have been lost (Potapov et al., 2008). This land-use change constitutes 13-21% of yearly anthropogenic CO₂ emissions (Nabuurs et al., 2023). Forest loss and degradation are also key threats driving biodiversity loss across the tropics (Sodhi et al., 2004; Harris et al., 2012). Of the forests that remain today, 70% are degraded, mainly due to selective logging (Potapov et al., 2008). Despite their global prevalence, logged forests have not been studied as widely as old-growth forests or those subject to other degradation phenomena such as fragmentation, especially in Southeast Asia (Estoque et al., 2019). Malaysian Borneo is a hotspot for deforestation, with the region acting as a centre for logging and oil palm industries (Sodhi et al., 2004; Bryan et al., 2013; Wilcove et al., 2013; Asner et al., 2018).

For all the threats that the forests of Borneo face, they also bear opportunities for restoration. The island hosts globally important levels of biodiversity and carbon storage (Berry et al., 2010; De Bruyn et al., 2014; Alamgir et al., 2020) - a hectare of intact forest in Sabah may have an aboveground biomass (AGB) 60% higher than the forests of the Amazon (Slik et al., 2013). Yet the biomass of logged forests is significantly lower than that of intact forests, particularly due to the removal of the largest trees, which contribute to the greatest biomass increases year-on-year (Slik et al., 2013; Pfeifer et al., 2016). Forest degradation can be considered as a reduction in biomass, although many other ecosystem services, such as hydrological and biodiversity services, are also subject to alteration (Sasaki & Putz, 2009; Sasaki et al., 2011; Thompson et al., 2013; Nabuurs et al., 2023). AGB may recover after 60-80 years in lightly logged forests, though in more heavily degraded areas, the timescale is likely over 100 years (Poorter et al., 2021). Accurately predicting AGB recovery rates can provide valuable insights for restoration strategies and sustainable logging rotations, but first, we must fully understand the reasons behind the degradation. In this thesis, I focus on the logged forests of Sabah,

the northeastern state of Malaysian Borneo, which has an expansive and well-documented logging history spanning more than a century.

The Logging History of Sabah

Pre-industrial (1880 - 1948)

The territory of North Borneo, modern-day Sabah, was established in 1878 under the administration of the British North Borneo Company and was made a British Crown Protectorate in 1888. Timber for export was earmarked as the primary economic resource for the territory, with migration schemes created to support the industry as the existing population was too small to match these ambitions. The first official number for annual timber extraction was 36,000 m³, recorded in 1917 (Matthews, 1917). Prior to this, some export figures are available as far back as 1902, and in 1910, ‘sawn wood was being exported to European ports by nearly every steamer for transshipment at Singapore,’ mainly from concessions on the east coast of modern-day Sabah, while wood was also in demand for construction of the railway line, firewood, and housing on the west coast (Lovegrove, 1912). The majority of the timber felled and exported was destined for colonial markets (Matthews, 1917). Annual timber production peaked at around 200,000 m³ until WWII when Japanese forces occupied the territory. The occupation led to economic devastation for the North Borneo Company, and in 1946, ownership of North Borneo - and its forest stocks - was transferred to the Crown. The first Crown Colony report states that by 1947, two large European-owned sawmills were ‘awaiting modern equipment’, each with a daily output of 14 m³ operating in the state and 15 small mills with outputs less than half that size (Colonial Office, 1947).

Industrialisation and boom (1949 – 1984)

November 1950 marked the advent of mechanical timber extraction, with one European company using three tractors, one logging arch, and three skid pans (Colonial Office, 1951). The preliminary performance of this equipment proved promising for expanding operations to locations and conditions where hand logging was not practical, and as a result, the other European company proposed to start utilising mechanical extraction the following year. Exports of timber and other forest products were profitable, but slow equipment deliveries and labour shortages limited the saw-milling facilities. European rearmament continued to delay machinery imports for the next three years. Small mills expanded, and some new, larger ones began operating, but labour shortages reduced this impact. Ten trained elephants were imported to Tawau in 1951, with little success, while an employee of the British

North Borneo Timber Company studied tractor and high lead logging in the Philippines intending to bring the practices to Sabah (Colonial Office, 1952).

In 1952, forest management was described to be in its infancy, with the objective of:

“sustained yield based on natural regeneration by a series of silvicultural operations. In Crown land working, attempts are always made to set aside sufficient forest to supply the mill for at least 15-20 years” (Colonial Office, 1953),

a timeframe that would coincidentally align with Malaysian independence. This year also saw the timber contract of the monopoly-holder British Borneo Timber Company terminated three years early and new 21-year concessions granted to four new major groups. Silvicultural prescriptions encouraging natural regeneration comprised climber cutting and poison girdling using sodium arsenite; 5,215 acres were treated that year (Colonial Office, 1953).

In 1953, increased mechanisation occurred by creating railways and road infrastructure and importing stone-crushing equipment, heavy tractors, road graders, and other machinery (Colonial Office, 1954). Over 11,000 acres annually received silvicultural treatments of climber removal and poison girdling (Colonial Office, 1954). By 1957, logging by tractor had become the primary method of production, with high lead yarding methods employed in hilly areas (Colonial Office, 1955). The sawmill industry expanded slightly during the year, with the number of mills rising to 54. At this point in time, 80% of Sabah remained under forest (Colonial Office, 1955).

In 1959, all but one forest concession was designated a Forest Reserve, a designation under which felling was carried out to an eight-feet obligatory upper girth limit with no lower limit. Trials of a less toxic alternative to sodium arsenite for poison girdling were underway in remote areas, but in 1961, they were discontinued due to the high cost, despite the danger to human life. Poison girdling had, by this point, increased to 27,075 acres annually (Colonial Office, 1960). The timber industry collectively imported 103 tractors in 1961, in addition to 108 in 1960 (Colonial Office, 1961).

Forest records for 1962 show that hand logging was, by now, limited to small, accessible pockets of forest on the west coast. High-lead cable yarding was implemented more widely as additional operators moved to steeper, harder-to-reach areas. Across the state, 457 tractors were in use, and 86 sawmills were licenced (Colonial Office, 1963). Though 80% of the land area remained under forest, under half was considered productive or potentially productive. Concerns over the ability of the forests to regenerate from industrial-scale extraction had arisen by 1962, as at this point, experiments on

mortality and recruitment of dipterocarp seedlings were starting, and plantations of conifers and other exotic species were also ordered (Colonial Office, 1963). The 1960s also saw the introduction of the chainsaw, which increased the rate at which trees could be felled. By the 1980s, when production was sustained at an extremely high rate, it is estimated that there were 1500 chainsaws in use across Sabah (Ibbotson, 2014). Following East Malaysian independence in 1963, the government opened new areas of forest to increase state income. Approximately half of the increased production resulted from forest reserves; the rest was sourced from areas cleared for agricultural production or on non-designated state land. Plantation development began in earnest from 1974, with high-lead yarding proving the most effective means of timber removal. However, softwood plantations did not become economically viable until chip mills were introduced in the 1990s (Ibbotson, 2014).

Gradual decline (1985 – 2024)

Production at these rates of over 10 million m³ yr⁻¹ could not continue indefinitely. By 1990, the beginning of the end of Sabah's timber boom, just 500,000 ha or around 1/5th of Sabah's primary lowland forest remained intact. By the millennium, production rates had fallen to levels comparable to the early 1960s. Agricultural expansion was largely complete at this point, with over 18% of the land area under oil palm (Ibbotson, 2014). The subsequent late-stage revival of timber production can be attributed to a 1998 deal which would require the creation of a pulpwood plantation of 250,000 ha (Reynolds et al., 2011), necessitating salvage logging of selectively logged forests that were in the process of recovering. Despite the plantation plans falling through in 2001, re-logging continued due to contractual obligations, sealing the fate of these areas as heavily degraded forests (Ibbotson, 2014). This policy is the reason for the slight resurgence in production between 2000 and 2010. These areas (Class II forest reserves) represent approximately one-third of Sabah's total land area (Reynolds et al., 2011), and are degraded to the point where their ability to regenerate is in serious doubt.

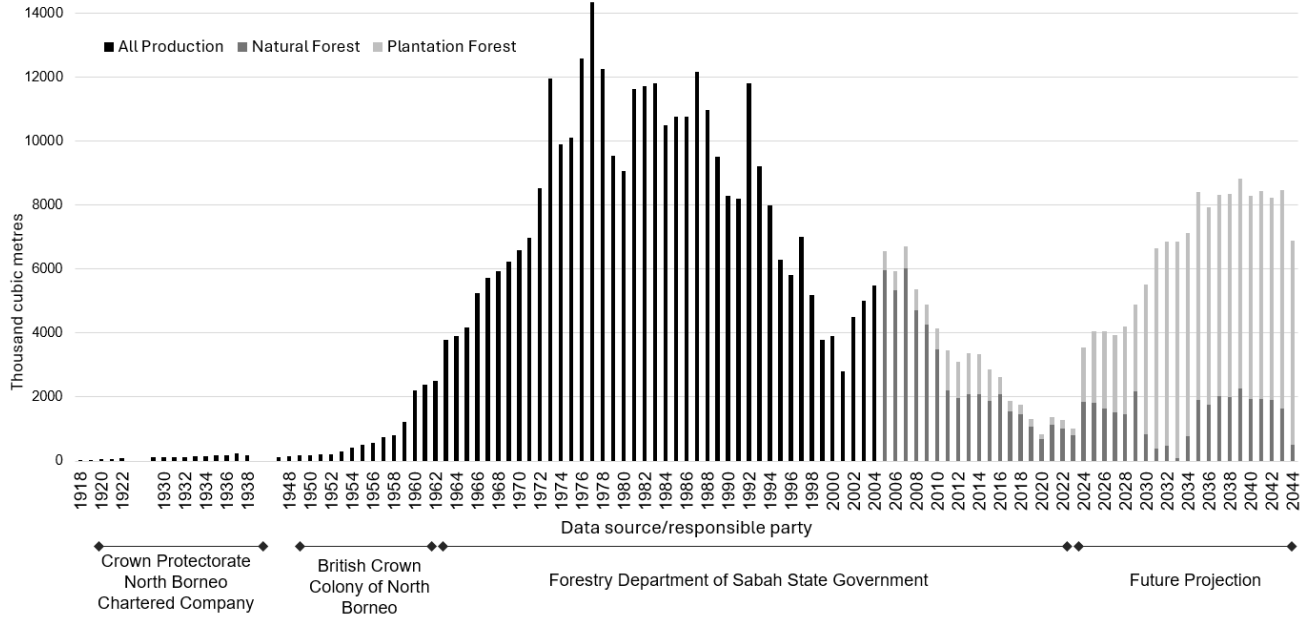


Figure 1) Extraction rates of timber in present-day Sabah from 1918-2023, and projected extraction from 2024-2044. Extraction rates are presented in thousand m³ and are split between natural and plantation forests where this data exists. Data is collated from the North Borneo Annual Forest Reports, Colony of North Borneo Annual Reports; Reynolds et al., 2011; Ong et al., 2023; Sabah Forestry Department Annual Reports.

Study Sites

The SAFE Project area (Ewers et al., 2011) is an excellent example of a selectively logged forest that endured additional rounds of salvage logging in the 1990s and early 2000s rather than being allowed to regenerate as per the original 60-year rotation prescribed (Riutta et al., 2018). In some of the plots, extraction restrictions were removed during the second round, and the forest was salvage-logged, resulting in heavily degraded stands (Struebig et al., 2013). These salvage-logged (A-F) plots are earmarked for conversion into a fragmented oil palm landscape (Pfeifer et al., 2015). Nearby control plots in old-growth and lightly logged areas (Figure 2) (OG1, OG2, OG3) form a continuum of forest quality.

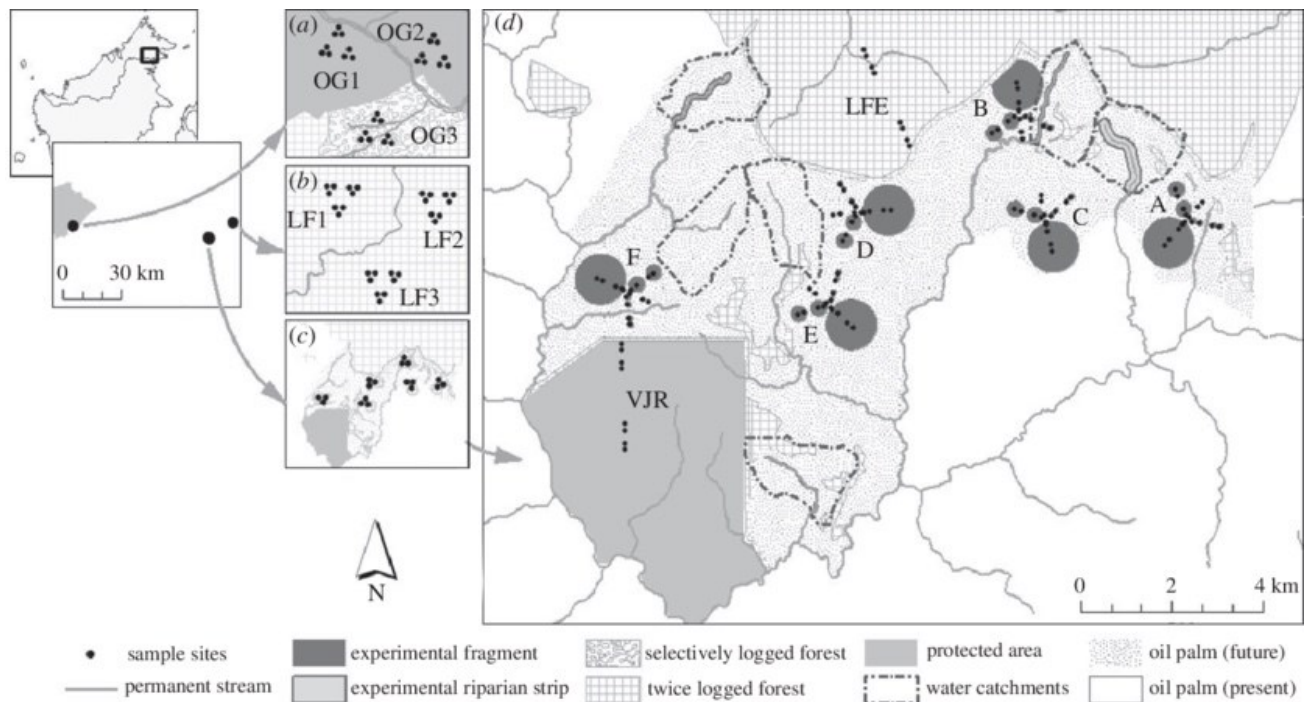


Figure 2) Map of the SAFE Project area in Sabah, Malaysian Borneo, which forms a gradient of forest modification encompassing (a) old-growth and lightly logged forest; (b) continuous, twice-logged forest; (c) twice-logged and fragmented forest. (Adapted from Ewers et al., 2011)

Understanding degradation and regeneration

Aboveground biomass recovery

Within the limited number of studies concerning logged forests in Southeast Asia, there is a strong bias toward understanding what is happening above the ground (Yuen, Fung & Ziegler, 2016). The trunk and canopy are readily accessible, and thanks to satellite and airborne imaging and spectroscopy, are getting easier to study across a large spatial scale (Rose et al., 2015; Swinfield et al., 2020). These measures do not accurately account for what is happening in the parts of the tree that can't be easily studied, like the roots (Sinacore et al., 2017; Sochacki et al., 2017; Waring & Powers, 2017). In many cases, this has resulted in studies quantifying forest carbon stocks that rely solely on aboveground biomass (AGB) equations (Berry et al., 2010; Cavanaugh et al., 2014; Sullivan et al., 2017; Asner et al., 2018; Deere et al., 2018; Jucker et al., 2018). Few also include belowground biomass (BGB).

Belowground

Root systems can comprise up to 40% of a tree's total biomass (Mokany, Raison & Prokushkin, 2006; Brunner & Godbold, 2007; Finér et al., 2011), but are repeatedly omitted from forestry studies (Vogt et al., 1995; Sinacore et al., 2017; Sochacki et al., 2017; Waring & Powers, 2017). In the instances where root biomass is considered, it is generally calculated from allometric root:shoot ratios (RSRs)

based on the AGB which have not been calibrated using local empirical data (Cairns et al., 1997; Aalde et al., 2006; Sochacki et al., 2017). Several studies acknowledge the need to consider belowground carbon when assessing carbon stocks and planning for restoration (Draper et al., 2014; Sullivan et al., 2017; McCulloch et al., 2024) and when monitoring emissions from forest degradation (Vargas, Paz & de Jong, 2013). Research shows that forests in Borneo subject to edge effects also have the potential to become a carbon source, though this data is based only on AGB measurements and that "data are lacking on belowground changes in Southeast Asian forests" (Qie et al., 2017).

Riutta et al., 2021 provide an estimate of belowground carbon stocks across the SAFE Project area, in which coarse root biomass is calculated from the diameter at breast height (dbh) of trees and an RSR of 0.18 developed from root excavations of dipterocarp forest in peninsular Malaysia (Niiyama et al., 2010). Niiyama et al. (2010) state that their equation may be useful "in other stands of old-growth dipterocarp forests". Its application to logged sites of SAFE and other degraded forest areas is therefore speculative, due to differing species composition and possible changes to growth patterns after logging disturbance, which may not respond in a manner linear to the aboveground changes identified by Riutta et al. (2018). A recently published study into above- and belowground biomass recovery post-logging also assumes an RSR of 0.18 (Miyamoto et al., 2024). It has been suggested that tropical stands with higher overall biomass, such as the forest measured in Niiyama et al. 2010 ($\text{AGB} > 500 \text{ Mg Ha}^{-1}$), have a lower RSR than those in low biomass forests, casting further doubt on the ability of the Niiyama et al. (2010) equation to represent both old-growth and logged forests. This relationship can be witnessed on a global scale, with high-biomass tropical forests displaying average RSRs of around 0.2, while in lower-biomass boreal regions, it is closer to 0.4 (Huang et al., 2021). Whether this inverse relationship between AGB and RSR persists on a landscape scale has not been investigated; understanding the recovery of BGB in secondary forests is urgently required (Waring & Powers, 2017; McCulloch et al., 2024). The sheer prevalence of logged forests means that if the equations used to quantify their biomass and recovery are off by even a small degree, this could have huge consequences for regional estimates.

To fully appreciate how tree root systems are involved in post-logging recovery, their structure should be considered in addition to their biomass. Root system architecture (RSA) has a functional significance, both influencing and being influenced by soil nutrients and uptake (Fitter, 1987). Water-related variables are strong predictors of the RSR, and temperature also has an effect (Huang et al., 2021), building a case for microclimatic impacts on root growth in disturbed regions. Soil chemistry

also impacts root growth, potentially due to the toxicity of low pH on fine roots (Meng et al., 2019). RSA influences how effectively a tree can access soil resources and the ability to adapt when these are suboptimal (Lynch, 1995). It follows to reason that the changes to soil which occur following logging may favour a different rooting strategy to that which persisted in the old-growth forest, in turn affecting the ability of trees to survive extreme events such as drought. Root systems and their architecture also provide stability for the organism (Resh et al., 2003; Osmont, Sibout & Hardtke, 2007) and the soil they grow in (Osman & Barakbah, 2011; Zhu et al., 2017; Alani & Lantini, 2020).

Deadwood

Deadwood is another component of the forest carbon pool not given adequate attention, despite the Intergovernmental Panel on Climate Change recommending it be included in carbon accounting exercises for many years (Watson et al., 2000). AGB calculations are generally synonymous with 'live' AGB, with deadwood overlooked. This is particularly problematic for disturbed forests, where deadwood carbon stocks may constitute more than half of aboveground carbon stocks (Pfeifer et al., 2015), compared to under 15% in undisturbed forests (Delaney et al., 1998; Saner et al., 2012). This disequilibrium results from a reduction in living biomass through timber extraction and associated damage to vegetation, and an increase in dead biomass present in the system, both above and belowground. In logged forests, around 25% of felled stems are abandoned in situ and left to decompose; over half (58%) of all logging emissions come from decomposing deadwood produced by collateral mortality (41%) and abandoned stems (16%) (Griscom et al., 2019). In some tropical forests, logged plots can remain carbon sources for around a decade due to the decomposition of above and belowground woody debris left in situ and disturbances to the soil carbon pool (Blanc et al., 2009a; Pfeifer et al., 2015; Mills et al., 2023).

In a natural system, aboveground deadwood is produced through tree mortality and branchfall. Trees naturally shed branches over time through self-pruning or wind damage, commonly comprising the largest route of biomass loss in a forest (Clark et al., 2001a). Despite the size of this pool, it can be challenging to monitor in the field due to the density of vegetation cover on the forest floor, high spatial variance and the episodic nature of the phenomenon (Wessman, 1992; Clark et al., 2001b).

Addressing the knowledge gap

Aims and Objectives

This thesis will address the knowledge gap regarding how long it takes for the above and belowground biomass of logged forests in Sabah to regenerate to the level of their undisturbed counterparts. We define the following key research objectives:

A) Determine whether the inbuilt LiDAR scanner in iPhone 12 Pro, when used in conjunction with Polycam's LiDAR and Photogrammetry features, can achieve a similar level of resolution as those boasted by more expensive, purpose-built LiDAR technology when capturing tree branching structures.

B) Use a combination of low-cost manual and digital methods to investigate the structure of root systems of seven pioneer *Macaranga* sp. trees in a regenerating logged forest in Malaysian Borneo.

C) Build a simulation to determine the regeneration trajectory for the SAFE project area in Sabah.

In the following paragraphs, I summarise how each chapter has met these objectives.

Thesis Chapter Outline

In Chapter 2, I test the ability of an iPhone 12 Pro in conjunction with the Polycam app to capture high-resolution 3D imagery of a leafless tree crown and an excavated root system. Firstly, I trial LiDAR and photogrammetry methods on an ornamental *Cornus nuttallii* specimen at Silwood Park to generate 3D models of the tree. I also measure the length and diameter of all branches up to the third branching order of the tree in situ, to be compared to those generated by the 3D model. I then excavate the root system of a small (7.6 cm dbh) *Acer pseudoplatnus* and use the most successful of the two imaging methods to create a 3D model of the root system. I use water displacement to find the volume of the above and belowground portions of the tree and compare these to the volumes predicted by TreeQSM for the 3D model and the volumes predicted by traditional allometric methods.

In Chapter 3, I use the photogrammetry methods trialled in Chapter 2 to generate 3D images of the root systems of seven *Macaranga* sp. specimens excavated from a regenerating logged forest in Borneo. I will measure the volume of the above and belowground parts of the tree and calculate the root:shoot ratios (RSR) of these trees, to be compared with the RSR found previously in a large-scale, multi-species experiment in a primary forest in West Malaysia. I investigate whether this partitioning of biomass varies with tree size. I compare metrics of branching complexity with various environmental

factors such as plot AGB, tree dbh, and slope gradient. I also present quantitative evidence of grafting between *Macaranga* tree roots originating from the same tree and roots from neighbouring trees.

In Chapter 4, I create a simulation to predict the regeneration of woody biomass in forest plots after 30 to 70 years since their initial logging disturbance. I parameterise the simulation with models of tree growth, recruitment, mortality and decomposition using census data for 172 forest plots spanning a degradation gradient from highly damaged salvage-logged areas to never-logged primary forests. I compare the plot biomass in 2011 across the degradation gradient and project each plot forward to 2050. I used the root:shoot ratio from Chapter 3 to include belowground biomass in this simulation.

Chapter 2) As above, so below? Applying low-cost 3D methods for describing tree crown topology to root systems.

Abstract

For several years, 3D imaging has been successfully used to capture the structure of tree crowns and stems, yet it is rarely applied to roots, which form complex 3D networks that play a pivotal role in terrestrial biogeochemical cycles. In tropical soils where GPR is ineffective, alternative methods of imaging must be used. LiDAR offers a promising means of gathering high-resolution imagery of complex structures. Its use in mapping aboveground structures, including trees, is the subject of many recent studies, and the process should be applicable to the exposed root systems in the same way. The main limitation of this technology is that dedicated LiDAR scanners are very expensive, cumbersome, and require training to use. In this study, we test the ability of an iPhone 12 Pro, in conjunction with the Polycam app, to capture 3D imagery of a tree crown and a root system. We test both the LiDAR and photogrammetry capabilities of the app. We find that these methods represent a low-cost, handheld alternative to dedicated 3D scanners without compromising on scan quality in branches down to 18 mm diameter. Photogrammetry was more accurate than LiDAR in reconstructing small branches, while LiDAR is effective for branches over 50 mm in diameter. We also show that these methods can be applied to excavated tree root systems to create a reconstruction which can be examined in perpetuity. These scans can then be interrogated further using quantitative structural models or other quantitative analyses to derive data on tree growth patterns in relation to their environment.

1.0 - Introduction

As we approach the midpoint of the UN's Decade on Ecosystem Restoration, international demand for effective forest restoration is experiencing an all-time high. Between 1990 and 2020, 420 million ha of forest were lost, with more than 90% occurring in the tropics (IPCC, 2023). The *Guide to Identifying Priorities and Indicators for Monitoring Forest and Landscape Restoration* produced by the Food and Agriculture Organisation and World Resources Institute recognises that root systems are critical to restoring chemical and biological soil health, primarily in the context of enhancing agricultural production and increasing food security (Buckingham et al., 2019). Despite this promising inclusion, belowground processes are massively understudied and underrepresented in the ecological theory associated with restoration efforts (Waring & Powers, 2017; Werden et al., 2022; McCulloch et al., 2024). Roots form complex 3D networks which play a pivotal role in terrestrial biogeochemical cycles, particularly the hydrological (Neumann & Cardon, 2012) and carbon cycles (Rasse, Rumpel & Dignac, 2005; Craig et al., 2018), which in turn affect the survival of entire forests (Werden et al., 2022).

Neglecting to consider key aspects of ecological theory, including belowground factors such as root biomass and structural traits, can lead to the failure of restoration projects (Lindenmayer, 2020).

Obtaining data on these hidden networks is easier said than done. In temperate zones, it is possible to investigate tree root stems using Ground Penetrating Radar (GPR), which provides information on rooting area and depth of coarse roots (Guo et al., 2013). The success of this technique relies on high soil conductivity, and is not applicable to areas with high water and clay contents, such as the tropical soils of Borneo (Butnor et al., 2003). Instead, destructive excavations are required, which are time-consuming, expensive and physically demanding (Alani & Lantini, 2020).

Once excavated, 3D image capture enables the exposed root system to be digitised so that it may be studied in perpetuity without the need for physical storage space of large biological samples. Coarse roots are generally considered to be all those above 2 mm diameter (Zhang & Wang, 2015); over the past two decades there have been many methods trialled with the goal of capturing this level of detail, to varying degrees of success. Light Detection and Ranging (LiDAR) is a remote sensing method that can provide high-resolution data on the three-dimensional structure of objects and surfaces (Vierling et al., 2008). The LiDAR unit emits laser pulses which travel to the receiving surface. The time it takes for the light to reach this surface and bounce back to the sensor provides information on the distance travelled, which can then be used to build point cloud datasets. Ground-to-ground LiDAR setups are commonly known as TLS (Terrestrial Laser Scanning), and have been used in multiple studies to capture the structure of tree branches and estimate biomass, with resolutions as high as millimetres (Disney, 2019), e.g. (Othmani et al., 2011; Disney et al., 2018; Lau et al., 2018; Fan et al., 2020). While TLS provides a fast and efficient means of generating point cloud data, it comes with a high equipment cost and the complication of personnel training. A low-end professional handheld unit (such as the Artec Eva Lite) costs in the region of £6000 (artec3d.com), with popular mounted models such as the RIEGL VZ-400 (RiEGL Laser Measurement Systems GmbH, Horn, Austria, riegl.com), costing from £75,000 - £150,000 depending on the model and accessories (as used in Disney *et al.*, 2018 and Lau *et al.*, 2018). These can achieve resolutions down to the millimetre level at a distance of up to 700 m (Disney et al., 2018), but the price is prohibitive for many prospective users. Advances have been made in more affordable, handheld units. Tomaščík et al., 2017 investigated the accuracy and feasibility of Google's 'Tango' technology, released summer 2016, which used a combination of a depth map and inertial sensors and visual Simultaneous Localisation and Mapping to create 3D images from a handheld platform

(Matney, 2017). An accuracy of 2 cm RMSE was reported for dbh measurements, and the study concluded that the Tango platform could be an accurate and cost-effective means of gathering forestry point clouds. However, the Tango project was discontinued in March 2018 in favour of developing software that can provide the same service without needing dedicated hardware (Matney, 2017).

In October 2020, Apple released the iPhone 12 Pro, which includes a LiDAR scanner. The in-built LiDAR capabilities of the iPhone 12 Pro and later editions provide a relatively low-cost way to access LiDAR technology (£999 for iPhone 15, apple.com/uk/iphone). The handheld nature of a smartphone makes it lightweight and portable, and the screen allows the user to check the progress of the scan in real-time. Branches which have been missed can easily be identified and rectified. A handful of free and paid apps exist which make use of the 3D scanning capabilities of the LiDAR cameras, including Polycam (poly.cam/), SiteScape (sitescape.ai), Scaniverse (scaniverse.com), Scandy Pro (scandy.co/apps/scandy-pro), and ForestScanner (Tatsumi, Yamaguchi & Furuya, 2023), which is a recently released iPhone app designed specifically for completing forest inventories using LiDAR, but is currently restricted to capturing dbh measurements.

Another alternative to using expensive LiDAR equipment lies in photogrammetry; the process of using multiple overlapping images taken from different positions and angles to generate 3D models of the subject. Photogrammetry is generally a cheaper option than LiDAR because it can be done with any high-resolution digital photography assuming there is sufficient overlap between images, though it requires significant storage and processing power. Digital Terrestrial Photogrammetry (DTP) has served as a solution for the aboveground portion of trees (e.g. (Gatziolis et al., 2015; Mokroš et al., 2018; Mulverhill et al., 2019) to varying degrees of accuracy, so the same should theoretically be achievable for root systems, which somewhat resemble the crown of a tree in a leafless condition.

In this study, we create 3D models of a tree crown and a root system using an iPhone 12 Pro in conjunction with the Polycam app, which allows users to generate point cloud data using either LiDAR or photogrammetry. In addition to its versatility, we chose Polycam for its efficiency and purported 1 mm accuracy, which earned it the acclaim of the ‘world’s most popular 3D app’ and an App Store rating of 4.7 out of 5 from 6300 reviews (May 2024). The app interface is simple and allows users to process scans without requiring detailed knowledge of the workflow. It allows users to work in remote areas with unreliable access to the internet, as a connection is not required to

complete a scan, only to process it. Polycam's LiDAR function allows fast capture and processing of spaces and large objects, which is ideal for reconstructing trunks and crowns during leaf-bearing months, and the scans can be exported from Polycam in a wide variety of file formats including point clouds and meshes. Polycam also has capabilities for photogrammetry, with a hands-off capture function which will take up to 250 photos with just one press of a button. The app automatically determines when to take photos based on internal algorithms that detect the optimal amount of image overlap, without this decision falling to the user. The image processing pipeline is designed to reconstruct thin geometries down to 1 mm.

This study aims to determine whether the iPhone 12 Pro, when used in conjunction with Polycam's LiDAR and Photogrammetry features, can achieve a similar level of resolution as those boasted by more expensive, purpose-built LiDAR technology when capturing tree branching systems. The methodology was first tested on a small tree crown in a leafless condition, with the intention to apply both the imaging and analysis methodologies to root systems.

For this study, we have three main objectives: (1) To devise a simple, effective method for successful capture of above and belowground branch networks using 3D images collected with iPhone and Polycam; (2) To validate length and diameter attributes of virtual tree branches using measurements taken using standard forestry methods; (3) To calculate the volume of the 3D tree and compare to the biomass estimates available from allometric equations, including root:shoot ratios (RSRs) and from water displacement experiments.

2.0 - Methods

2.1 - Study site

All field data were collected from two trees at Silwood Park in Ascot (51.4091 N, -0.6395 E). To test the ability of iPhone-based LiDAR and photogrammetry to accurately reconstruct the 3D features of a tree, we selected a *Cornus nuttallii* specimen planted in 1988 (Figure 1a). We chose this tree for its accessibility, the low, flat, root-like spread of its branches, and the height of < 4 m, which is within the maximum LiDAR scanning range of 5 m. The trunk bifurcates at 108 cm, so we measured the diameter below the swell of the bifurcation (11.5 cm) and considered this to be the dbh. This tree was not appropriate for destructive harvesting, so for the second part of our study – applying the most accurate of the above methods to a root system – we selected a 7.6 cm dbh *Acer pseudoplatanus* in the oak woodland on the same site as the first tree. This *A.*

pseudoplatanus leaned heavily in a south-westerly direction (Figure 1b) and is surrounded by oak woodland planted in 1950.

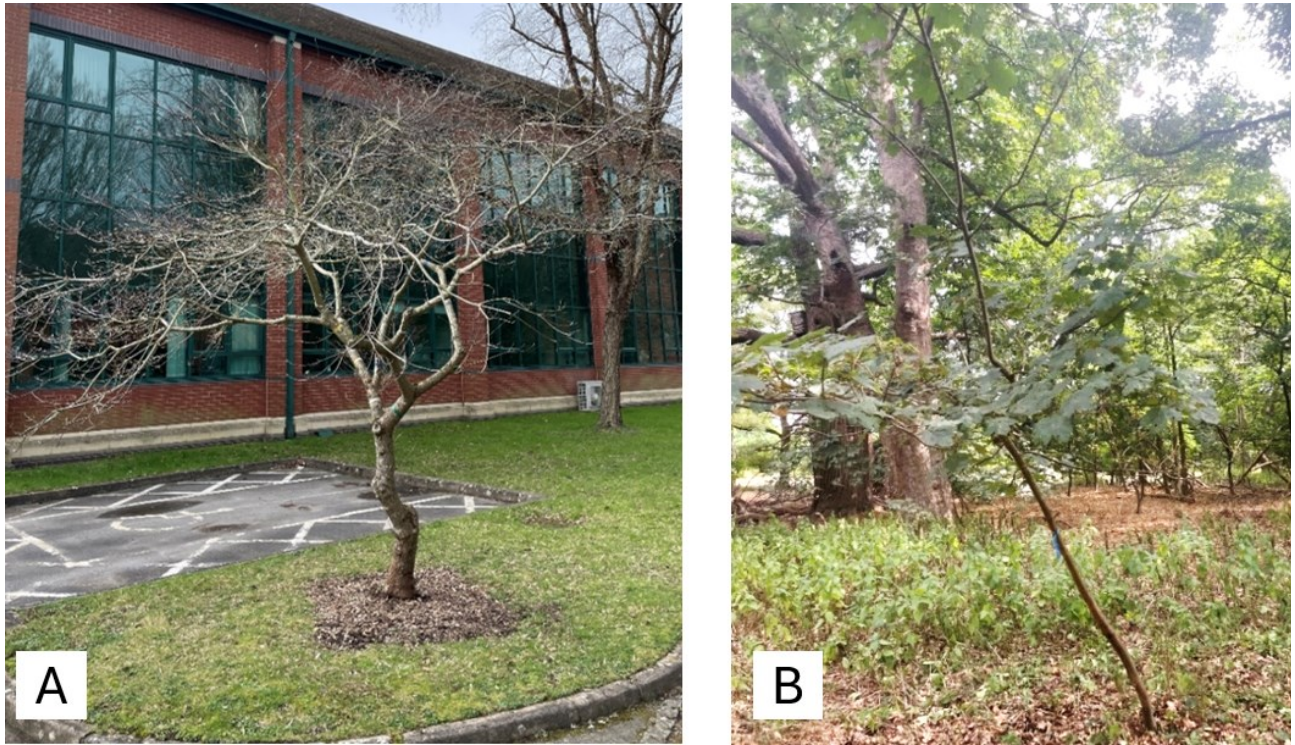


Figure 1a) Sample trees for 3D imaging: an 11 cm diameter pacific dogwood *Cornus nuttallii* at Silwood Park b) 7.6 cm sycamore *Acer pseudoplatanus* at Silwood Park prior to felling and excavation, taken facing northeast.

2.2 - Manual measurements – aboveground

Following the methodology outlined by Lau et al. (2018), we define a ‘branch segment’ as a region of branch between a point of furcation and a point of termination (Figure 2). The diameter at the point of furcation and termination of each branch segment up to the fifth branching order, and the length of the branch between these points, were measured to the nearest 1 mm using forestry tape. The diameter measurement points at furcation and termination were marked with red 3 mm tape, and each branch segment was given a unique Branch ID and marked using a unique, colour-coded tape combination to enable identification and matching in the 3D imagery. In total, 20 branch segments were measured up the fourth branching order, ranging from diameters of 18 mm to 65 mm. Length measurements were taken from the furcation point to the termination point. The ornamental *C. nuttallii* tree had undergone pruning and/or damage at several points throughout its life, resulting in some points of furcation producing only one measurable daughter branch segment. In these cases, only the surviving daughter branch segment was measured.

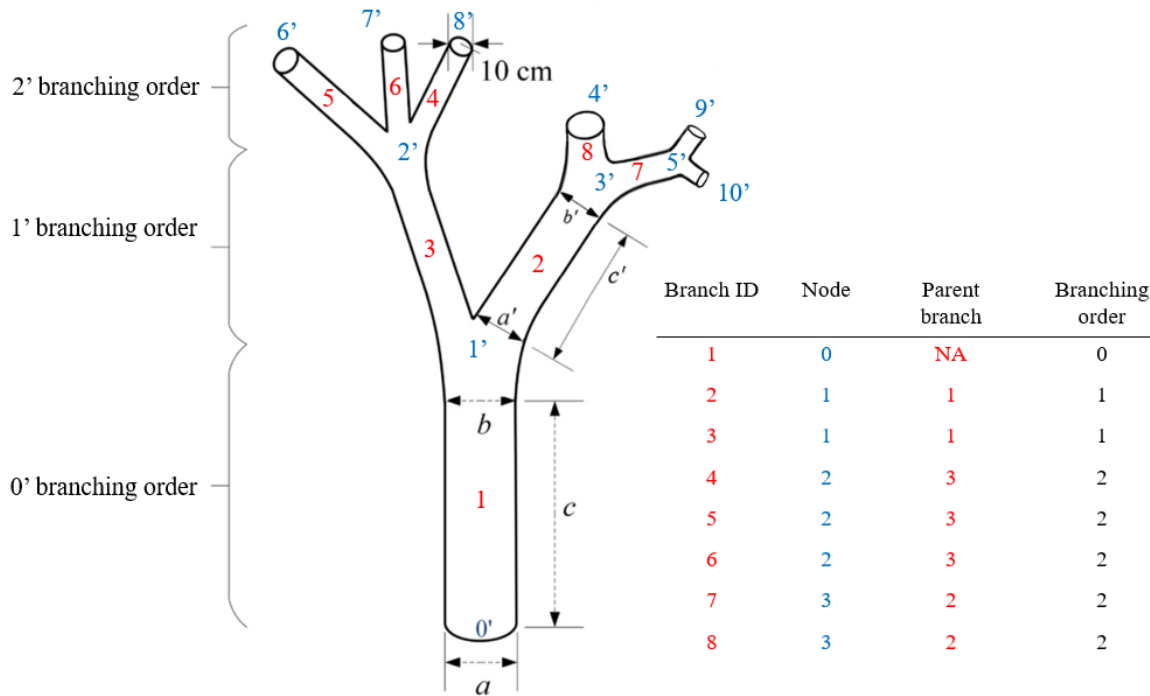


Figure 2) Diagram of manual tree branch measurements, adapted from Lau et al., 2018. A “branch node” (blue) is the furcation point over a tree segment where another tree segment originates (e.g. 0’, 1’, 2’). A “branch segment” describes what originates from a furcation point and terminates either: when the tree segment begins to widen into another furcation point (1’) or when the tree segment ends or is broken (4’, 10’). “Branch length” is defined as the distance between the base furcation point and the termination point of the branch (c and c') and “branch diameter” as the average of the diameter taken over the furcation point (a and a') and the diameter taken below the termination point of the branch segment (b and b'). A unique Branch ID (red) was assigned to each branch for identification. The branching order was determined relative to the main stem (Branch ID 1).

2.3 - 3D data acquisition

DTP and LiDAR data were acquired with an iPhone 12 Pro using the Polycam app (poly.cam/). The iPhone was attached to a 6’6” telescopic pole using adhesive-backed Velcro to extend the reach of the scannable area.

2.3.1 - Digital Terrestrial Photogrammetry (Rear camera of iPhone 12 pro)

Polycam’s ‘video’ function was enabled so pictures would be taken automatically when the camera had moved enough to ensure the appropriate level of overlap between pictures, with no need to interrupt the scanning process. A maximum of 250 images were captured in each scan. The scanning trajectory combined the ‘stacked circle’ and ‘spiral’ approaches (Gatzliolis et al., 2015); a lap of the tree was first completed with the iPhone held at around 1.3 m from ground level, and on completion of the circle, the telescopic pole was extended by 0.4 m. Another lap was completed, then raised another 0.4 m. Finally, a circle at the height of the top of the crown was completed, with the camera facing down into the crown. Two complete scans were accomplished, one focussing more thoroughly

on the left and right side of the tree respectively, while both capture the trunk to ensure there is enough overlap to enable successful reconstruction.

2.3.2 - Handheld mobile terrestrial laser scanner (LiDAR)

Scanning trajectory using LiDAR differed slightly from the DTP, as the app interface displays which areas have been successfully captured and which require further attention. We found that the best method to ensure a successful capture was to use the stacked spiral method as before, followed by an over-the-top ‘spring hemisphere’ approach (Gatziolis et al., 2015). The resulting scans were processed with a depth range of 4.9 m, a minimum voxel size of 20 mm and a simplification of 0 %, chosen to ensure the highest resolution possible. An in-app processing time of approximately three minutes produced a point cloud with 165.6k vertices, 163.4 MB, ready for export.

2.4 - 3D Tree Reconstruction

The ‘cloud processing’ feature of Polycam enables a 3D model to be created with little effort on the user’s part, making it suitable for use without specialist training. The ‘RAW’ processing setting with the highest geometry and texture size was selected, which includes only albedo textures. This was chosen to minimise occlusion as all branches could be viewed from all angles. The LiDAR scan (165.6k) was considered complete at this point and is henceforth referred to as the ‘LiDAR model’ (figure 3b). The two DTP scans (82.4 and 217.1k vertices) were imported to the open-source 3D point cloud processing software CloudCompare (Version 2.6.3) (danielgm.net/cc/) and placed in the same orientation. The point cloud registration tool was used to align the scans, which were merged into one composite. There is no need for scaling correction, as the app automatically applies this. The finest twigs that could not be separated from the sky were removed manually using the ‘Scissor’ tool. We refer to this clean, composite 3D model as the ‘DTP model’ (Figure 3a). Diameters and lengths of individual branches were also measured from the red tape tie points on the model by computing the Euclidean distance between selected points. We measured segment diameter at three view angles 120° apart and took the mean.

To approximate the volume of the reconstructed LiDAR and DTP models, we used TreeQSM V2.4.1, a quantitative structural model that fits cylinders to individual branch segments to enable volumetric calculations (Raumonen & Åkerblom, 2022). This QSM method circumvents the issues associated with attempting to triangulate volume from a complex 3D structure such as tree branches (Fan et al., 2020). We set TreeQSM to generate eight reconstructions of the sample tree, cycling through the standard PatchDiam and BallRad parameter array (Raumonen & Åkerblom, 2022). As

we were not able to destructively measure the *C. nuttallii* to verify the computed volume, we estimated the volume and biomass using traditional allometric equations for comparison with the TreeQSM results. Conversion between volume and biomass uses wood density; two numbers are published for *C. nuttallii* and we used both to capture variation arising from uncertainty in this parameter. Firstly, we use 0.57 g/cm³, the average of the ‘pooled hardwood’ species used by Lutz 2012 and Jenkins 2001, and 0.79 g/cm³, which is the value quoted for *Cornus sp.* in McGraw-Hill Encyclopaedia 2006.



Figure 3) Point clouds of 11 cm dbh *Cornus nuttallii* specimen generated using (left) photogrammetry (DTP model), reconstructed from two scans each of 250 photos and (right) LiDAR (LiDAR model) and the Polycam app on an iPhone 12 Pro, placed side-by-side in CloudCompare. Scale bar shown in metres.

2.5 - Statistical Analysis

To assess the accuracy of the LiDAR model and Photogrammetry model in capturing the measurements of the *C. nuttallii* specimen, the difference between the manually measured diameters and lengths and those gathered from the generated point clouds was investigated using root mean square error (RMSE), relative root mean square error (RRMSE), and the coefficient of determination (r^2). We also used linear regression to determine the effect of log-transformed branch segment diameter on the percentage error of the generated 3D models. All statistical analyses were conducted in R 4.3.3 (R Core Team, 2024), with the significance level set to $p < 0.05$.

2.6 - Belowground

After determining the most effective method for obtaining an accurate aboveground 3D model, we applied this technique to the root system of the *A. pseudoplanatus*. Prior to excavation, we felled the tree and cut it into sections of $< 40\text{cm}$ length which were retained for volume assessment. We excavated the root system by hand using small garden trowels and stainless steel widgers, starting at the trunk and radiating outwards, following the line of roots as they became exposed. The excavation was considered complete when all roots $> 2\text{ mm}$ were freed from the surrounding soil and labelled with tape to aid the registration of point clouds. If roots were accidentally severed, they were reconnected in their original position using electrical tape. Once fully excavated, the root system was scanned using Polycam's photogrammetry feature. Eight runs of 200 images were required to capture the full extent of the root system, which Polycam processed into eight point clouds that were combined and cleaned as for the *C. Nuttallii* specimen. The main difference was that rather than cleaning 'sky' pixels, it was soil that required manual removal. After scanning, the root system was disassembled and taken to the lab where volume was measured using water displacement, along with the stem and branches. The above and belowground components were stored separately to enable the parameterisation of a root:shoot ratio (RSR). The volume of all roots was combined to give belowground volume, and all trunk and branch pieces were combined to give an aboveground volume for each tree, which we compared to the values computed by TreeQSM. These volumes were combined with the species-specific wood density of 0.55 (Wagenführ, 2007) to estimate biomass.

3.0 - Results

3.1 Aboveground Accuracy Assessment

Both the DTP model and LiDAR model succeeded in generating a fair reconstruction of the *C. nuttallii* tree up to the 4th branching order, and in the case of the DTP model, beyond this (Figure 3). Of the branches up to the 4th branching order, the DTP model accurately reconstructed branches to the observed diameter with an RMSE of 2.51 cm, an RRMSE of 4.4%, and an R^2 of 0.99. The LiDAR model was less reliable, with an RMSE of 14.57 cm, an RRMSE of 25.77% and an R^2 of 0.75 when the reconstructed diameter was compared to the observed diameters, largely driven by two failures

where 4th order branches were entirely missing from the reconstruction (Table I, SI). Both methods were more effective at reconstructing branch segments with larger diameters (Figure 3c).

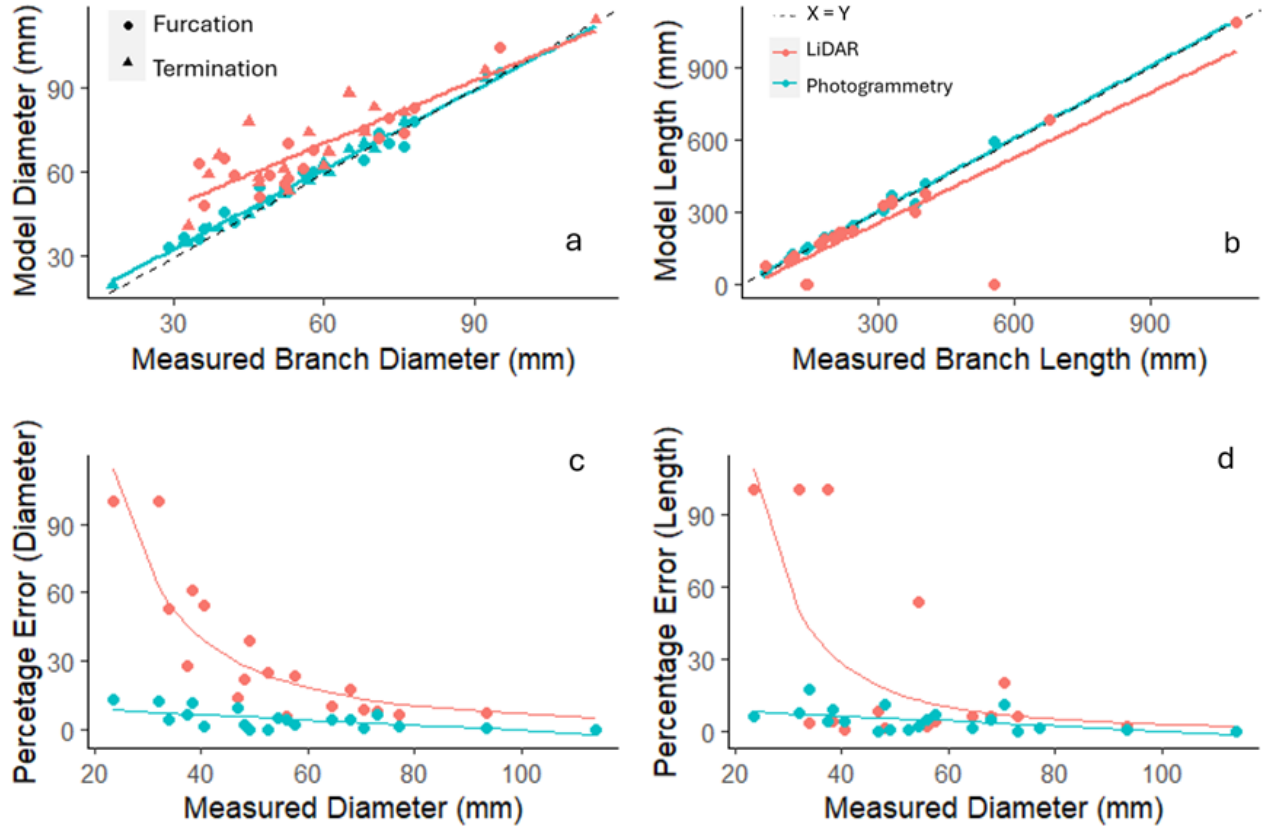


Figure 4) Comparison of observed diameter and length measurements with measurements captured from photogrammetric and LiDAR-generated images. (a) diameter at branch furcation and termination points measured from the DTP and LiDAR models against the observed branch diameter. (b) branch segment length measured from the DTP and LiDAR models plotted against the observed branch segment length. (c) The percentage error in average branch segment diameter and (d) branch segment length plotted against the observed average diameter of each branch segment. Percentage error includes over- and under-estimations. The dashed line shows $x = y$, solid lines show regression lines fit using OLS with the Measured Diameter variable log-transformed.

Branches with a field-measured diameter of > 50 mm (average of furcation and termination diameters) were overestimated by an average of 0.57 % (mean $\pm$ 3.39 SD) by the Photogrammetry model, and 10.49 % (Mean $\pm$ 7.98 SD) by the LiDAR model. Branches < 50 mm were overestimated by an average of 6.77 % (Mean $\pm$ 5.06 SD) by the DTP model. The LiDAR model overestimated most branches < 50 mm ($38.68\% \pm 18.68$ SD) and failed to reconstruct two branches entirely (Table S1). The minimum branch diameter reconstructed by the DTP model was 18 mm (error $< 12\%$), while LiDAR could only accurately capture branches over 34 mm, with substantial associated error ($> 21\%$).

Generally, the length of branch segments reconstructed by both the LiDAR model and DTP model were very close to the tape-measured length, with the DTP model performing slightly better (Figure

4b). There was no significant relationship between the length of a branch segment and the accuracy of its reconstruction either model. In the three instances where the LiDAR model scored 100% error in length comparisons, it was again due to the small branch diameter. The percentage error in both modelled diameter and modelled length follow the same patterns when plotted against tape-measured diameter (Figure 4c, 4d). In the LiDAR model, analysis of percentage errors in both length and diameter shows exacerbation as branch segment diameter decreases. As average branch diameter decreases with increasing branching order ($Diameter = 118.022 - 15.967 \times Branch\ Order$) ($R^2 = 0.80$, $F(1, 18) = 70.51$, $p < .001$, adj. $R^2 = 0.79$), the accuracy of the imaging can be considered to reduce in accuracy with distance from the trunk.

3.2 - Volume and mass

The average volume of the *C. nuttallii* specimen computed by the eight iterations of TreeQSM was estimated as: LiDAR model (40,658 cm³, SD = 0.3) and DTP model (51,477 cm³, SD = 1.6). The improved resolution of the DTP model enabled TreeQSM to apply additional cylinders to higher branching orders, resulting in a greater overall volume, but the increased complexity resulted in a greater variation between the eight iterations. This trade-off with increasing complexity (i.e. maximum and median number of branches identified) became even more extreme with the *Acer* root system (19.3, SD = 6.1).

Table 1) Volume and mass calculations for sample trees, calculated using species-specific wood density. References for wood density: a) Lutz 2012/Jenkins 2001, b) McGraw-Hill, 2006, c) Wagenführ, 2007. References for methods: 1) TreeQSM, 2) Chave et al., 2014, (height calculated using height-diameter model), 3) Konôpka et al., 2010 (dbh-based RSR for broadleaf trees in European woodland, 0.6). *Calculated using water displacement AGB volume.

Tree	Method	Volume (cm ³)	Wood Density (g/cm ³)	Mass (kg)	Reference
Cornus nuttallii	LiDARmodel TreeQSM	40,658	0.57	23.18	a, 1
			0.79	32.12	b, 1
	DTP-model TreeQSM	51,477	0.57	29.34	a, 1
			0.79	40.67	a, 1
Sycamore	DBH-height allometry	22,424	0.57	12.78	a, 2
			0.79	17.58	b, 2
	AGB	12,781	0.55	7.03	c, 2
			0.55	5.18	c
	BGB	9,327	0.55	5.13	c, 1
			0.55	3.11	c, 3
	R:S ratio*	5,655	0.55	3.11	c, 3
			0.55	1.80	c

3.3 - Belowground

Upon excavating the roots of the *A. pseudoplatanus*, we found that the spread of the roots reflected the crown position, with most branches and roots on the side to which the trunk leaned (Figure 5b), a south-westerly direction. The volume of the entire tree, as calculated by water displacement, was 12,705 cm³, with a root volume of 3,280 cm³, giving an RSR of 0.35. The average root volume calculated by TreeQSM was over three times too high at 10,441 cm³, with the closest iteration (PatchDiam1 = 0.12, PatchDiam2Max = 0.07, PatchDiam2Min = 0.03) computing the volume at 4,305 cm³ (+ 31%) (Table, SI).

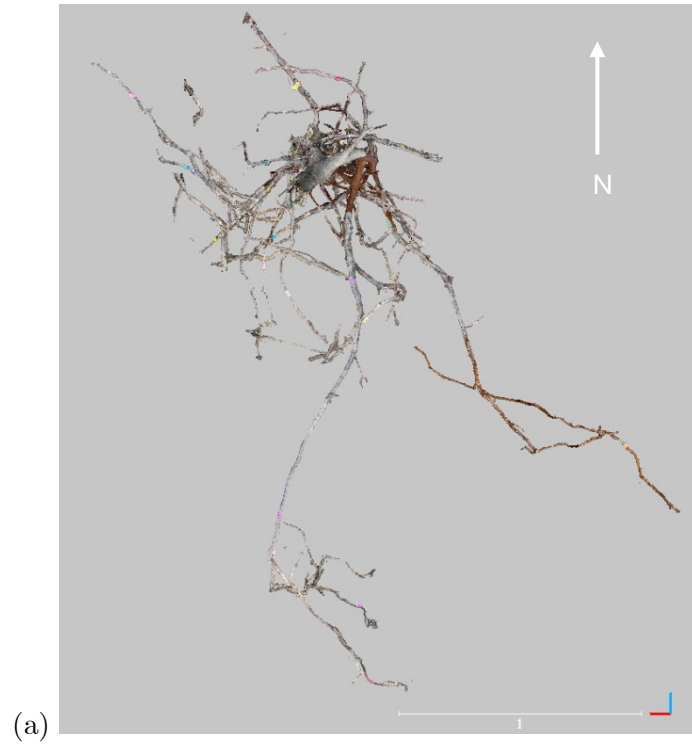


Figure 5) (a) top-down view of an excavated *Acer pseudoplatanus* root system (b) side view of the *A. pseudoplatanus* root system, showing lean of trunk and concentration of roots in a south-westerly direction. Both images are point clouds generated from photogrammetry using an iPhone 12 Pro and the Polycam app. The scale bar is in metres.

4.0 - Discussion

This study presents a simple, effective method of using an iPhone 12 Pro, in conjunction with the Polycam app, to capture highly accurate 3D imagery of a leafless tree crown. Our LiDAR method saw a sharp decrease in accuracy when reconstructing branches below 50 mm diameter, so it would be better suited to trees with thicker branches, though the maximum depth range of 5 m limits the height

of trees it can be used on. This would not be an issue with root systems which, once excavated, are more easily accessible. The DTP model improved upon the performance of the LiDAR model, with a 100% success rate in reconstructing branches less than 10 cm, with a maximum error of 12.8%. The smallest branch segment that the DTP model reconstructed was 18 mm at the point of termination, so we cannot say for certain whether this method can reach resolutions to the same level as GPR, which can reliably detect branches or roots as small as 10 mm (Borden et al., 2014). Due to the advertised 1 mm accuracy of Polycam’s processing capabilities, we feel that the 18 mm resolution achieved here does not represent the smallest possible branch that the method could capture. The lack of confounding factors such as clouds and sky when scanning root systems instead of tree crowns may aid this improvement, as well as being able to get closer to the subject, though the Polycam developers do provide the caveat that ‘fine, hair-like structures’ may not be reconstructed to this high degree of accuracy. As approximately 75% of coarse root biomass is made up of roots > 20 mm diameter (Resh et al., 2003), and over 85% is > 10 mm diameter, we can confidently say that the methods we utilise here are capable of capturing the vast majority of coarse root biomass. In root systems with particularly thick central root boles, researchers may wish to combine the two methods – to complete an initial scan of the central root bole and low branching orders using LiDAR for a fast, low-data option, then complete scans of thinner roots of higher branching orders using photogrammetry. The point clouds generated by either method are compatible when stitched together.

The ability of both the DTP and LiDAR methods to reconstruct branches of less than 10 cm diameter is a marked improvement compared to that shown by Lau *et al.* (2018) with a more expensive, less portable dedicated LiDAR scanner. They were able to reconstruct less than 56% of branches < 10 cm diameter, for LiDAR, we succeeded in reconstructing 90% of branches, with an average error of just 22%, comparable to the accuracy they achieved for branches > 30 cm diameter. One caveat when comparing the accuracy of our method to that of Lau *et al.* is that the measurements they report are from their fitted QSM rather than directly from the point cloud, which will likely add additional error, as seen in our attempts to generate QSMs of our trees.

The volumes calculated by TreeQSM for both the DTP model and the LiDAR model of the *C. nuttallii* were far higher than the values predicted by the allometric equations. Although the LiDAR model was closer to the volume predicted by the (Chave et al., 2014) height-diameter allometric equation, these seem likely to be underpredictions, as branch segments higher than the 4th order are not present in the LiDAR scan and are therefore cannot be assigned cylinders by the QSM. In the *A.*

pseudoplatanus, the dbh-height allometry method (C) overestimated the observed shoot volume by 36%. The DTP TreeQSM clearly overestimated the volume, as it was almost triple that (284%) of the volume observed by water displacement. Therefore, we can assume that both methods also overestimate the true biomass of the *C. nuttallii* specimen. Using the error from the *A. pseudoplatanus*, the *C. nuttallii* may be around 18,108 cm³ (from TreeQSM error) or 14,351 cm³ (from dbh-height allometry error). While the tree cannot be harvested to verify this assumption, there are additional methods of estimating volume from 3D scans that were outside the scope of this study, and may provide a better means of estimating volume than TreeQSM. Methods such as voxelisation, encapsulation/triangulation (e.g. Disney *et al.*, 2018) and improved slicing could be applied, but can be extremely labour and data-intensive (Wang *et al.*, 2023; Melo, 2024). Outside of fields such as medicine where high precision of volume calculations is critical (Ferrante & Paragios, 2017), continuing to improve existing allometric equations by gathering more data may be a better use of time and resources.

The DTP method that we trialled on the *C. nuttallii* crown appeared successful in reconstructing a visually similar representation of an excavated root system of a small *A. pseudoplatanus*. The scans proved simple to recombine; the tape tie points were effective for roughly aligning the individual scans in CloudCompare, and the automated ‘align scans’ feature handled the fine registration. Manual cleaning was somewhat time-consuming, but not technically difficult. Despite the roots and the surrounding soil being the same colour, the depth of field made removing those soil pixels easy, unlike in 2D images where segmentation of fine linear structures from complex backgrounds presents a significant challenge (Holtzman-Gazit *et al.*, 2006; Sandberg & Brega, 2007).

The RSR of 0.35 calculated from water displacement varied from the best available published value of 0.6 for mixed deciduous woodland. Despite being appropriate for temperate broadleaved trees of this diameter, it was generated using oak and beech, not *A. pseudoplatanus*. We could not find a more appropriate species-specific RSR, and therefore expected there to be a difference between the observed and estimated RSR. *Acer. sp* are fast-growing and can be considered a pioneer species, unlike the slower-growing beech and oak, and RSR differ even between species of the same guild (Sinacore *et al.*, 2017).

Alternatively, it may be that the root structure of this particular *A. pseudoplatanus* specimen is not indicative of the wider species; it lacked the characteristic strong, deep root system. This, and the extreme lean, may be explained by the conditions in which the seedling grew. *Acer pseudoplatanus*

seedlings that grow under closed canopies develop a characteristic morphology, including an etiolated stem with low mechanical strength often not rigid enough to prevent bending under its own weight (Hein et al., 2009). *A. pseudoplatanus* seedlings > 1m height that have developed under deep shade are often not able to take advantage of canopy openings because they cannot recover the mechanical stability necessary to start rapid height growth (Hein et al., 2009). This tree leans into the prevailing wind (South-Westerly) and the roots are also concentrated on this side. The greater distribution of second and third-order roots on the windward side of the tree follows expectations for tree responses to wind-loading stress (Stokes, Fitter & Courts, 1995), though the direction in which the trunk leans defies this expectation. Instead, it is likely a phototropic response triggered by insufficient light due to growing in shady conditions, common in *A. pseudoplatanus* (Hein et al., 2009; Tischler, Michalzik & Lotze, 2020). Future work might focus on defining a measure of root asymmetry that can be applied to trees such as this that have grown in stressful conditions, such as under heavy prevailing winds, on slopes, or after damage. Improving methods for digitally estimating the volume of complex 3D networks should also be a focus and would be valuable for calculating root biomass.

In this study, we have presented a simple, low-cost method of capturing 3D imagery the branches and root systems of single trees, to a resolution comparable with dedicated LiDAR scanners, using an iPhone 12 Pro and the Polycam app. In addition to potential applications for root system studies, the small branch diameters captured using this method could be applied to tasks such as monitoring the growth of small trees over time and in response to environmental change, or in other fields entirely, such as mechanical engineering and medicine.

Supplementary Information

Table S1) Comparison of analogue branch length and diameter measurements using forestry tape and measurements taken from the point clouds generated using LiDAR (LiDAR model) and photogrammetry (DTP model).

Branch segment	Node	Branch order	Branch segment length (mm)					Branch segment diameter (average of termination and furcation) (mm)				
			Tape	DTP model	LiDAR model	P % error	L % error	Tape average	DTP model average	LiDAR model average	DTP model % error	LiDAR model % error
1	1	1	220	216	216	-1.82	-1.82	77	78	82	1.30	6.49
2	1	1	212	213	216	0.47	1.89	93.5	94	100	0.53	6.95
3	2	2	380	338	302	-11.05	-20.53	70.5	70	76.5	-0.71	8.51
4	2	2	168	169	167	0.60	-0.60	52.5	52.5	65.5	0.00	24.76
6	3	2	310	309	330	-0.32	6.45	73	68.5	78.5	-6.16	7.53
7	3	2	329	335	350	1.82	6.38	64.5	62	71	-3.88	10.08
8	4	3	103	108	101	4.85	-1.94	56	58.5	59	4.46	5.36
9	5	3	330	368	334	11.52	1.21	48	49	58.5	2.08	21.88
10	6	3	678	683	685	0.74	1.03	49	49	68	0.00	38.78
11	7	3	402	421	376	4.73	-6.47	68	71	80	4.41	17.65
12	7	3	242	242	221	0.00	-8.68	47	51.5	53.5	9.57	13.83
13	8	4	52	51	80	-1.92	53.85	54.5	57	57	4.59	4.59
14	9	4	144	155	0	7.64	100	32	36	0	12.50	100.00
15	9	4	140	146	0	4.29	100	37.5	40	48	6.67	28.00
16	10	4	182	198	190	8.79	4.340	38.5	43	62	11.69	61.04
17	10	4	109	128	113	17.43	3.67	34	35.5	52	4.41	52.94
18	11	4	197	206	199	4.57	1.02	40.5	41	62.5	1.23	54.32
19	11	4	553	590	0	6.69	100	23.5	26.5	0	12.77	100.00
20	12	4	114	122	119	7.02	4.39	57.5	58.5	71	1.74	23.48

Chapter 3) Root Systems of Tropical Pioneer Trees Form Complex Networks

Abstract

Tree roots comprise up to 25% of a tropical forest's biomass, but studies on belowground biomass are rare, particularly in logged forests, despite their global prevalence. The species composition of logged forests differs from their primary counterparts, with early successional pioneer species forming a higher proportion of the population. This difference in species composition, along with physical changes to the surrounding environment caused by logging pressures, may result in a difference in the ratio of biomass partitioning and in the topological structure of the root systems. Despite this, the lack of root excavations in logged tropical forests leads to variables such as root to shoot ratios (RSRs) from primary forests being applied to calculations of biomass in logged forests, along with other assumptions of root structure. In this study, we excavated the coarse roots of seven *Macaranga sp.* trees in a regenerating logged forest in Malaysian Borneo to determine the ratio of biomass partitioning (RSR) and quantify the complexity of the root system. Here we show that the RSR of pioneers in a regenerating logged forest in Sabah is significantly higher than the average RSR of trees in a primary mixed dipterocarp forest in Peninsular Malaysia. We also present the first quantitative evidence of root graft prevalence in *Macaranga* species, with some inosculation forming between trees of different species. These findings highlight the importance of early successional pioneer species sequestering carbon belowground in regenerating forests, and in contributing to restoration more widely. Root systems that form complex networks increase slope stability, and the grafts may have some contribution to allowing the post-logging vegetation to flourish as a community.

1.0 Introduction

Growing attention towards the potential of reforestation to mitigate climate change and biodiversity loss necessitates robust models of forest growth and succession, yet belowground aspects are rarely included, reducing their contribution towards effective conservation (Waring & Powers, 2017; McCulloch et al., 2024). Historically, forest stock calculations have used allometric equations to estimate the harvestable volume of timber from simple metrics such as basal area or diameter at breast height (dbh) and estimated tree height (e.g. (Higuchi & Ramm, 1985; Malhi et al., 2006; Berry et al., 2010; Yahya, Ahmad Zuhaidi, & Albert Ikau, A, 2016). With modern technologies such as satellite imagery, Digital Terrestrial Photogrammetry, and LiDAR, accurate biomass and topological measurements for the visible part of the tree are easily accessible, from individual to stand level (e.g. (Korpela, 2004; Tangki & Chappell, 2008; Asner et al., 2018; Disney et al., 2018; O'Sullivan et al., 2021). But as the demands upon forest inventories shift from anticipating timber production volumes to supporting nature-based solutions such as carbon offsets and REDD+ certifications, accurate biomass assessments for the whole tree are required, including the belowground components (Stover

et al., 2007). Root systems can represent 20 - 40% of a tree's total biomass, depending on the region (Sochacki et al., 2017), though suitably quantitative data on coarse root systems remains elusive (Cairns et al., 1997; Herrero et al., 2014), particularly in degraded forests.

Root:shoot ratios (RSRs) are a preferred method of estimating belowground biomass as they reduce the need for costly excavations. RSRs enable the biomass of a tree to be estimated from easy-to-measure aboveground variables such as stem dbh, sometimes in conjunction with wood density, stem height, or in some cases, stump basal area, assuming a suitable equation has already been parameterised for trees of that type, in a comparable habitat (Waring & Powers, 2017). In their review of allometric equations for various land cover types in Southeast Asia, Yuen et al. found 54 allometric equations suitable for logged forests compared to 98 in primary forests, with just 14 of these logged forest equations including belowground biomass, none of which were from the Bornean rainforest (Yuen et al., 2013). Previously (e.g. Saner et al., 2012; Riutta et al., 2021), this gap has been addressed by using allometric equations ($RSR = 0.18$) developed in the Pasoh Forest Reserve in Peninsular Malaysia (Niiyama et al., 2010). This is a multi-species study based on 54 excavated trees of various size classes, establishing multiple equations depending on dbh, but includes very few pioneers. Regenerating forests are known to differ from their predecessors in terms of aboveground biomass (AGB) and species composition (Hayward et al., 2021). In the early successional stages, they are colonised by fast-growing, short-lived pioneer trees with low wood density such as *Macaranga* species, eventually giving way to slower-growing hardwood species that have been hypothesised to invest more energy into root growth than younger forest stands (Ferry Slik, Kekler & van Welzen, 2003; Waring & Powers, 2017). Niiyama et al. (2010) note that for this reason, their equations should only be applied to old-growth primary forests, but a lack of alternatives has led to them being used in logged forests (e.g. (Saner et al., 2012; Riutta et al., 2018). In these cases, a subset of trees from the study site should be excavated to validate the equation, though this is rarely implemented (Thant et al., 2012; Yuen et al., 2013). 65-70% of Southeast Asia's extant forests have been degraded by logging pressures (Estoque et al., 2019), highlighting the critical nature of this knowledge gap. Forest inventory models accounting only for AGB generally predict rapid growth in regenerating stands (Poorter et al., 2016; Philipson et al., 2020), but other studies show that when the belowground component is added, it can shift a system from a sink to a source of carbon (Mills et al., 2023), making it a critical parameter in ecosystem carbon models (Stover et al., 2007; Yuen et al., 2013).

Unlike in dry, temperate soils where ground-penetrating radar can be used to measure root systems without breaking ground (Zhu et al., 2014), studying coarse roots in tropical environments requires costly excavations. The extremely time and labour-intensive nature of root excavations of mature trees are the main reasons for the lack of BGB equations compared to AGB (Yuen et al., 2013), especially in clay soils where removing the entire root bole by force is ineffective due to the high chance of root breakage. Previous tropical root excavations done by hand have taken over 100 hours per tree (Sinacore, personal communication, 2021). To maximise the value of these costly excavations, it is prudent to measure topological metrics of the exposed root system prior to the harvest and destruction required for accurate biomass calculations.

Root system architecture is indirectly linked to biomass formation and carbon storage as it determines the functioning of a tree, and consequently the entire forest community. The topology of the root system dictates nutrient and water acquisition, and the mechanical stability of both the tree and the surrounding soil (Alani & Lantini, 2020). Slopes and root systems are intrinsically linked – slopes can affect root growth, and roots, in turn, affect slope stability. Pioneer tree growth has been shown to increase slope stability and speed up the regeneration of disturbed systems (Osman & Barakbah, 2011); in particular, roots that cross the slip surface are vital in decreasing landslide risk (Reubens et al., 2007). For this reason, the root system architecture of plant species used in restoration efforts must be considered (Thomas & Pollen-Bankhead, 2010).

Another aspect of root system architecture that is understudied yet could have massive implications for afforestation is the presence and purpose of root grafts. These grafts vary in their level of tissue integration. We define two levels: superficial grafts where only bark is attached, and true inosculation where the bark has been eroded and the cortexes of multiple roots is completely integrated, potentially including xylem and phloem. Both graft types can occur between roots of the same tree or the roots of neighbouring trees. In some cases, they exist between trees of different species. *Macaranga* have previously been observed to form self-grafts, while grafts between neighbours were ‘not frequent’, though quantitative data was not collected (Kenzo et al., 2009). Elsewhere, reports exist of inosculation between neighbours. A forest restoration study in the Ivory Coast (Dosso, Guillaumet & Hadley, 1981) noted that *Macaranga hurifolia* formed intra-specific root grafts, and one study traced the movement of radioactive phosphorus (P32) from small to large and dead to living individuals in grafted pairs ($n = 2$) (Khan, 1978). Most studies on terrestrial inosculation focus on conifers in Europe and North America, specifically in silviculturally important conifer species (e.g. (Yli-Vakkuri, 1953;

Stokes et al., 2005; Tarroux & DesRochers, 2010). However, there exist anecdotal accounts of inosculation in tropical trees going back many years, such as the living stumps in the Malayan rubber plantations (Anon, 1950, in B. F. Graham & Bormann, 1966), and in 1952, a North American botanist visiting Puerto Rico postulated that root grafting may be more abundant in tropical trees than in temperate regions (LaRue, 1952). These inosculations may represent intraspecific competition or a cooperative community where the benefits of connection outweigh the increased risk of disease transmission (Graham and Bormann, 1966).

Various methods exist to describe root system architecture, from greenhouse studies on seedlings (Kutschera, 1960) to mature trees in their natural environment (Pagès et al., 2004; Fitter, 2008; Sinacore et al., 2017). The advent of 3D modelling has improved our ability to describe tree branching systems in quantitative terms (Othmani et al., 2011; Lau et al., 2018). LiDAR is an effective method of capturing 3D point cloud data quickly, but high-quality equipment is expensive, requires specialist training to use, and can be difficult to carry and power in remote field sites (e.g. the RIEGL VZ-400i cf. Lau et al., 2018, costing up to £96,000). Photogrammetry provides a simple, affordable alternative when used at close ranges, and can be captured using any device capable of producing high-quality photographs (Korpela, 2004). As shown in the previous chapter, using an iPhone 12 Pro (cost £999) in conjunction with the Polycam app (£49.99 pa) creates 3D models down to at least 25 mm resolution, and the resulting 3D imagery can be processed and analysed using a multitude of methods.

In this paper, we use a combination of low-cost manual and digital methods to investigate the structure of root systems of seven pioneer trees (genus: *Macaranga*, local name: Mahang) in the Danum Valley-Ulu Segama Forest Reserve in Sabah, a regenerating logged forest in Malaysian Borneo. The seven trees (dbh 10-20 cm) are pioneer species from recruitment following selective logging in 1988 (Reynolds et al., 2011). As individuals of *Macaranga sp.* commonly grow in highly disturbed areas such as roadsides, studying this genus provides a valuable opportunity to study the role of slope on root growth. Terrain topography can also be captured using photogrammetry, negating the need for clinometers. We focus on the following questions: (1) is the RSR of pioneer trees in a regenerating logged forest comparable to the equations (Niiyama et al., 2010) parameterised in the primary dipterocarp forest that preceded it? (2) how does root system complexity vary with tree size, and environmental factors such as slope grade and the AGB of the surrounding area (3) the extent to which Bornean *Macaranga* species form root grafts. We then conclude with some possible implications of our findings in relation to forest restoration activities.

2.0 Methods

2.1 Study area

The study area is located within the West Bole region of the Danum Valley-Ulu Segama Forest Reserve complex (4.9618 N, 117.6892 E), a lowland dipterocarp forest with a rugged, hilly topography (Tangki & Chappell, 2008) of approximately 300 m elevation above sea level. Soils in this area are orthic Acrisol and dystic Cambisol, with parent materials of mudstone, sandstone, tuff, and chert (Ordnance Survey, 1974). Annual rainfall is approximately 2700 mm yr⁻¹ (Keller et al., 2023), and the average daily temperature is 26.7°C. Predominant tree species composition is from the families *Dipterocarpaceae* and *Euphorbiaceae* (Newbery et al., 1992). The study area falls into logging coupes from 1988 and 1989, during which time the forest was selectively logged using predominantly high lead logging, with some tractor usage in coupe 1988 (Tangki & Chappell, 2008). Commercial trees with a diameter at breast height (dbh) of over 60 cm were felled, with an area of approximately 20 ha surrounding each spar-pole left with few or no trees (Tangki & Chappell, 2008), representing an annual timber production volume of around 100 m³ ha⁻¹ (Moura-Costa and Karolus, 1992). On completion of logging operations, the area was left to regenerate naturally.

2.2 Study sites and sampling design

We arbitrarily identified our sample trees according to a pre-determined set of criteria. The number of potential candidates was limited by low population density in this area, so single-stemmed, healthy trees of genus *Macaranga* between c.10 and 20 cm dbh that were within visual distance of road access were selected. All suitable *Macaranga* specimens grew on slopes of 27 to 97% incline (15° to 44°), grades which are characteristic of this area (Walsh et al., 2011).

2.3 Excavations

We first raked the area surrounding each sample tree clear of litter and understorey vegetation to improve access to the soil. To improve site safety, we felled the tree using a chainsaw or machete leaving a trunk of no more than 1 m height. The trunk and branches were cut into sections of less than 40 cm in length and retained for volume measurements. A team of four worked on excavating each tree by hand, starting at the bole and radiating outwards following the line of roots as they became exposed. We used shovels and hand hoes to remove the top layer of organic matter, then hand trowels and stainless steel widders for excavating around roots. Displaced soil was moved downhill or carried away from the site using buckets. Where roots from neighbouring trees entered the network

of the sample tree, they were removed using a sharp saw. The exposed end was covered in petroleum jelly to prevent infection of living tissues. At the end of each working day, we covered the exposed roots and soil with tarpaulins to prevent flooding.

Excavation was considered complete when all roots > 2 mm were freed from the surrounding soil. We marked all roots up to the third branching order with tapes and a unique ID to enable identification. If roots broke, we fixed them with a combination of plastic raffia string and duct tape before returning them to their original position. Additional peripheral roots were also marked with tapes in primary colours to aid in the registration of point clouds.

2.4 3D imaging

DTP and LiDAR Data were acquired with an iPhone 12 Pro using the Polycam app (poly.cam/). Between clearing the ground and beginning excavation, we scanned the area surrounding the tree using LiDAR to form a slope profile. After excavation, roots were scanned using the photogrammetry application. We used the ‘video’ function so pictures were taken automatically when the camera position had moved enough to ensure the appropriate level of overlap between pictures, with no need to interrupt the scanning process. A maximum of 250 images were captured in each scan. The first scan focused on capturing the central portion of the root bole along with the first-order branches. Subsequent scans then focused on the extent of each first-order branch and its daughters in turn. We processed the scans within Polycam using the ‘full’ detail setting, and exported them with high point density to CloudCompare 2.13.1 (danielgm.net/cc/) for post-processing. We calculated the slope grade using a ‘rise over run’ method and the maximum extent of the root network. Then, we manually removed the non-root parts of the capture and combined multiple scans to create a single scan per sample tree. Firstly, scans were roughly aligned by eye, using the coloured tapes for reference. Following this, we used the automatic ‘fine registration’ tool to complete the scan alignment process.

2.5 Manual measurements

Measurements of root branches were taken following the methodology outlined by Lau et al. (2018), which defines a ‘branch’ as a segment between a point of furcation and a point of termination, henceforth referred to as a ‘branch segment’. We measured the diameter at the point of furcation and termination of each branch segment up to the third branching order (Lau et al., 2018), and the length of the branch between these points, to the nearest 1 mm using forestry tape. Instances of grafting were recorded as part of this process. These manual measurements were only completed up to the third branching order because they are extremely time-consuming. Due to previous environmental

disturbances such as animal foraging, some roots had become damaged, resulting in furcations producing only one measurable daughter branch segment. In these cases, we did our best to identify bifurcation points and retain as much data as possible by measuring the remaining daughter branch segment. We also measured each sample tree's maximum Euclidean root depth and root length. In addition to measurements of the sample trees, we inventoried the surrounding standing woody biomass of the surrounding 20 x 20 m plot to enable verification of our study area's resemblance to Sabah's wider logged forest habitat.

2.6 Volume and biomass calculations

Once all measurements were complete, we disassembled the root system using hand saws and removed it to the lab. The volume of the sample trees was measured by water displacement from 20 l plastic bins, measured to 1 mm³ precision. The volume of all roots was combined to give belowground volume, and all trunk and branch pieces were combined to give an aboveground volume for each tree. These volumes were combined with the species-specific wood density to estimate biomass (*M. gigantea* 0.29, *M. Hypoleuca* 0.27, *M. Pruinosa* 0.31 (g cm⁻³), (Zanne et al., 2009)). The same value was used for root and shoot, as is acceptable for tropical trees without visible growth rings (Amoah, Appiah-Yeboah & Okai, 2012; Schuldt et al., 2013; Nakagawa et al., 2016).

2.7 Analysis

We used a simple linear model to determine the allometric relationship between stem diameter (dbh) and the volume of the entire woody component (TB) of each of the seven sample trees (whole tree biomass). We began by fitting a fully factorial linear model to describe the relationship between above- and belowground biomass and various predictor variables, including dbh, slope grade, AGB/BGB partitioning, and the interactions between these effects (biomass ~ dbh * slope grade * biomass partitioning) and followed model simplification processes to find the minimum adequate model. We used a Welch Two-Sample T-Test to determine whether the RSRs of our *Macaranga sp.* specimens was statistically significantly different from the stand average RSR presented by (Niiyama et al., 2010).

2.7.1 3D structural analysis (manual)

We used Spearman's rank tests to investigate the relationship between tree dbh and the various root system complexity measures at the first, second and third branching order (total number of nodes, branches, and grafts). We used Pearson's correlation to examine the relationship between maximum

root depth and the dbh of the tree and slope grade. As branching is considered to follow a power-law relationship (Kassab, 2006), we fitted a log-log linear model to predict the increase in the number of branches with each branching order up to the third, moving out from the central node (Figure 3).

We employed linear models to determine the effects of various variables (dbh, number of branches, surrounding plot AGB) on the frequency of grafts present in the system. We categorised each root as growing in one of four directions- upslope (U), downhill (D), perpendicular to slope incline (P), and sinking (growing straight down into soil) (S). We then performed a simple linear regression to determine the effect of slope grade on the root growth direction.

2.7.2 Structural analysis (digital)

To keep processing times short and file sizes small so they might be sent over unstable, rural internet connections while in the field, we chose to collapse our 3D imagery into 2D binary images from different planes of view (Figure 4a). We developed the Node-Joining Algorithm (NJA) (Windram and Folkard-Tapp, in progress) to skeletonise our root images for structural analysis (Figure 4b). The first step in image pre-processing for the NJA requires capturing 2D binary silhouettes of the 3D photogrammetric data, with pixels being ‘on’ if they represent root tissue or ‘off’ if they are void space (Figure 3). We generated three images for each tree; one ‘overhead’ image that captures the radial spread of the roots, and two side views at a 45° angle from the other. The node closest to the centroid of the area with the highest density of ‘on’ pixels is designated the basal node. We used the binary map of the ‘overhead’ view to investigate the proportion of roots that grew uphill versus downhill. The slope direction was marked on the binary map, and a perpendicular line was added through the basal node to divide the image into upslope and downslope segments. We counted the number of ‘on’ pixels in each of these segments and determined the upslope-to-downslope ratio.

We chose to analyse our photogrammetry data in this way to maximise the accessibility of our methodology. Binary images are much smaller than point clouds and, therefore, require less data to send and receive from remote locations with unstable internet connection, as is the case at many tropical field sites. We tested the accuracy of the NJA in reproducing the root system by comparing the maximum rooting distance measured in the field to the computed Euclidean maximum distance. The NJA was then used to calculate the maximum root order (Lau et al., 2018) for each of the images. Starting from the basal node, every ‘edge’ connected to that node is assigned an order of one, and the next edge connected to that one is assigned an order of two, repeating with increasing root order until there no unassigned edges remain. This results in the formation of a skeletonised map (Figure S2).

We then calculated the branching factor to describe the average number of daughters that a node has, i.e. the ‘bushiness’ of the root. Branching order was calculated by dividing the number of nodes found in the network by the number of nodes connected to more than one edge. The NJA was also used to calculate two measures of distance; the Euclidean displacement, which draws a straight line from the root tip to the basal node, and the path distance, which calculates the distance by traversing the root skeleton. For the distance metric, we gather two summary statistics: the mean and maximum distances from all root tips to the basal node. The sinuosity of the longest root was calculated by dividing the path distance by the Euclidean distance.

3) Results

3.1) Biomass allocation

The AGB of the 20 x 20 m area surrounding the seven sampled trees ranged from 79 to 470 kg (1.98 to 11.75 Mg ha⁻¹). The seven sampled trees had a total volume ranging from 76 to 247 litres, of which an average of 22% was belowground (Table 1). The correlation coefficient between stem diameter and woody volume was $r = 0.89$ ($p < 0.008$), but converting woody volume to biomass using wood density increased the correlation coefficient to 0.93 ($P = < 0.003$; Figure 1), leading to a more explanatory allometric equation. Whole-tree woody biomass (TB) can therefore be calculated thus:

$$TB = 4.52 \pm 0.80 * dbh - 12.19 \pm 11.80$$

Table 1) Above and belowground woody biomass *Macaranga* trees in a regenerating logged forest. Volumes were measured using water displacement. Mass was calculated using species wood density (*M. gigantea* 0.29, *M. hypoleuca* 0.27, *M. pruinosa* 0.31 (g/cm³, (Zanne et al., 2009)). ‘Shoot’ includes stems and branches. Root % shows the amount of woody biomass stored belowground as coarse roots.

Species	(cm)		Kg Plot AGB	Volume (l)			Mass (kg)			
	dbh	Max depth		Shoot	Root	Total	Shoot	Root	Total	Root %
<i>M. pruinosa</i>	9.8	61	137.93	58.15	17.95	76.10	18.03	5.56	23.59	23.59
<i>M. hypoleuca</i>	12.5	72	123.85	167.05	32.65	199.7	45.10	8.82	53.92	16.35
<i>M. hypoleuca</i>	12.8	57	266.86	129.75	49.70	179.45	35.03	13.42	48.45	27.70
<i>M. pruinosa</i>	14.4	93	291.32	129.30	41.85	171.15	40.08	12.97	53.06	24.45
<i>M. hypoleuca</i>	15.3	72	284.05	186.90	27.80	214.7	50.46	7.51	57.97	12.95
<i>M. hypoleuca</i>	17.3	81	78.62	186.55	47.80	234.35	50.37	12.91	63.27	20.40
<i>M. gigantea</i>	19	138	469.34	175.10	72.05	247.15	50.78	20.89	71.67	29.15

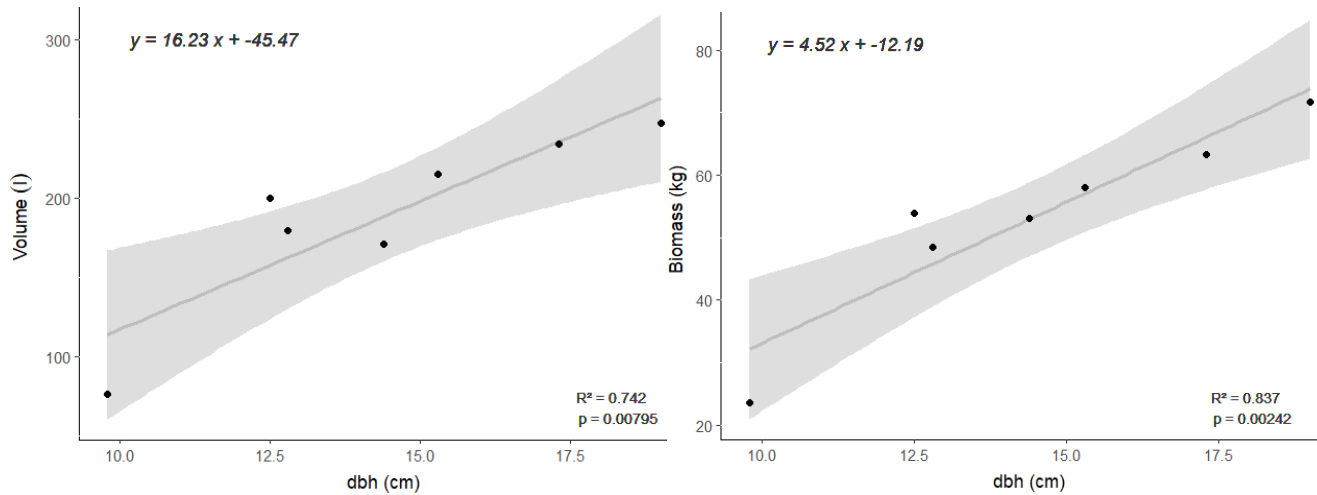


Figure 1) Whole-tree volume (left) and biomass (right) of seven excavated *Macaranga* individuals scale linearly with increasing dbh. Converting woody volume to biomass using wood density (*M. gigantea* 0.29, *M. hypoleuca* 0.27, *M. pruinosa* 0.31 (g/cm³, (Zanne et al., 2009)) improves the explanatory power of the allometric equation. Grey shading shows 95% confidence intervals.

In addition to whole-tree biomass (TB), we parameterised equations which independently calculate AGB from dbh (Figure 2). Though we started with a variety of explanatory variables and interaction effects, model simplification only retained a single slope for both AGB and BGB, with different intercepts (adjusted R-squared: 0.88 F-statistic: 48.49 on 2 and 11 DF, p-value: 3.501e-06), with only dbh as a significant explanatory variable (Figure 2).

These models support a simple continuous relationship between biomass and dbh. Therefore, a single RSR may be applied to all trees of these species and within these diameter classes and slope grades. The ratio of this biomass stored belowground versus aboveground ranged from 0.13 to 0.29 (mean = 0.22, median = 0.24). In cases where BGB is to be estimated from AGB, the mean (0.22) may be used. A Welch Two-Sample t-test shows that this value is statistically significantly different ($t(6.0185) = -3.0602$, $p = 0.02213$, 95% CI: [-0.1991, -0.0222]) from the mean value of 0.18 presented by Niiyama *et al.* (2010).

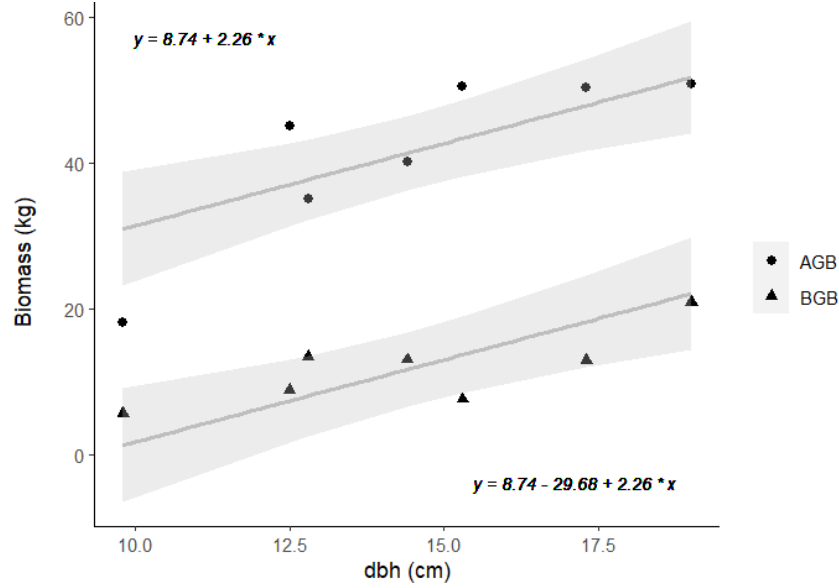


Figure 2) Tree biomass (kg) increases with dbh (cm), across both partitions of of aboveground (circles) and belowground biomass (triangles) of seven *Macaranga* specimens. Grey lines represent minimum adequate models, points show actual values. Shaded ribbons show 95% confidence intervals.

3.2) Root System Architecture

3.2.1 - 3D structural analysis (manual)

The maximum rooting depth of the trees was fairly shallow, ranging from 57 to 138 cm. The maximum depth had a strong positive correlation with the dbh of the tree (Pearson's correlation, $r = 0.79$, $p = 0.04$). Examining the branch traits (segment length, diameter at furcation, diameter at termination) of the sample trees up to the third branching order resulted in measurements of 450 root branches stemming from 165 nodes (Table 2). There was only a weak positive correlation between tree dbh and the number of branches in the first three branching orders. On fitting linear models, the effect of plot AGB was not significant ($R^2 = 0.51$, $p = 0.071$, adj. $R^2 = 0.41$) while the effect of dbh was statistically not significant and explained only a weak proportion of variance ($R^2 = 0.10$, $p = 0.479$, adj. $R^2 = -0.07$).

Of the 450 branches, 86 displayed grafts, either self-grafts ($n = 70$) or inosculation with a neighbour ($n = 16$). Inter-tree inosculation was restricted to the three sample trees growing in the highest AGB surroundings, but all individuals showed extensive self-grafting, affecting almost 20% of all measured branch segments across all branching orders 1-3 (range = 10 - 24%). We find no evidence (OLS logistic regression and GAM) that the likelihood of grafting changes with branching order or distance from the trunk. In Pearson's rank tests, indicators of graft prevalence were the number of branches present in the system ($R^2 = 0.58$, $F(1, 5) = 6.77$, $p = 0.048$, adj. $R^2 = 0.49$), and the AGB of the surrounding

area ($R^2 = 0.73$, $F(1, 5) = 13.60$, $p = 0.014$, $\text{adj. } R^2 = 0.68$). If the inter-tree inosculations are removed from these models, the effects become non-significant.

Table 2) Manually measured root system architecture features from 1st to 3rd branching order, radiating out from the central root bole.

Trunk dbh (cm)	Branches				Nodes				Grafts			
	B1	B2	B3	Total	B1	B2	B3	Total	B1	B2	B3	Total
9.8	9	20	32	61	1	9	15	25	2	5	7	14
12.5	8	21	34	63	1	7	15	23	2	2	2	6
12.8	6	19	46	71	1	6	16	23	0	3	10	13
14.4	6	13	27	46	1	6	10	17	3	5	3	11
15.3	5	19	44	68	1	5	18	24	0	2	12	14
17.3	5	12	31	48	1	5	12	18	1	4	3	8
19	11	30	52	93	1	11	23	35	4	9	7	20
Total	50	134	266	450	7	49	109	165	12	30	44	86

The model predicting the increase in the number of branches with branching order explains a statistically significant and substantial proportion of variance ($R^2 = 0.87$, $F(1, 19) = 126.60$, $p < .001$, $\text{adj. } R^2 = 0.86$) (Figure 3).

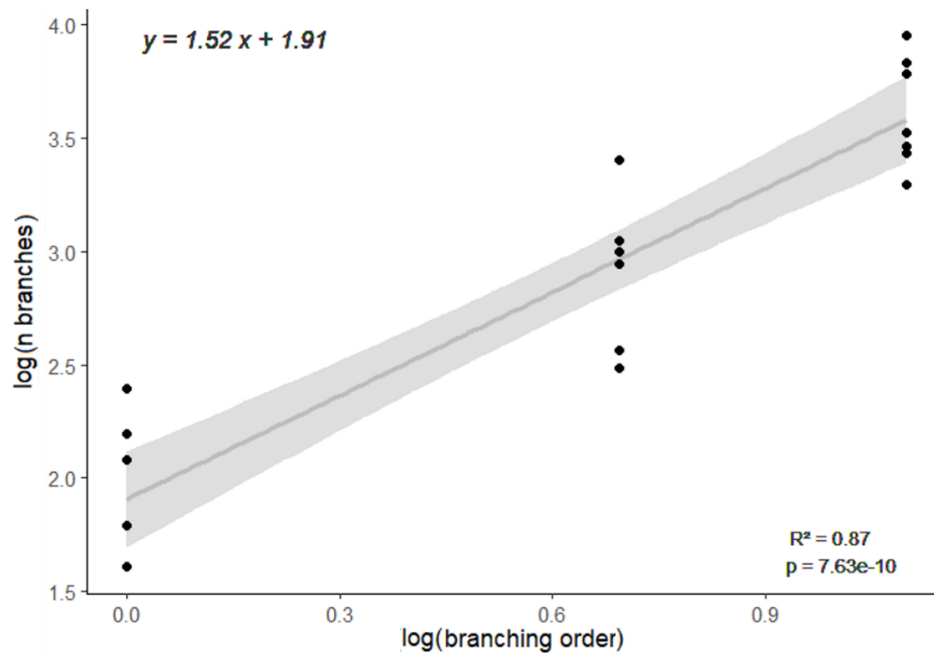


Figure 3) Linear relationship between $\log_{10}\text{-}\log_{10}$ transformed branching order (1-3) and the number of branches in each of branching orders for the seven sample *Macaranga sp.* trees. Scatter plots of $\log_{10}\text{-}\log_{10}$ transformed data illustrate the relationship between branching order (1-3) and the number of branches in that order for each of the seven sample trees. Linear models support a power-law relationship with branch numbers increasing with each subsequent branching order. 95% confidence interval is shaded grey.

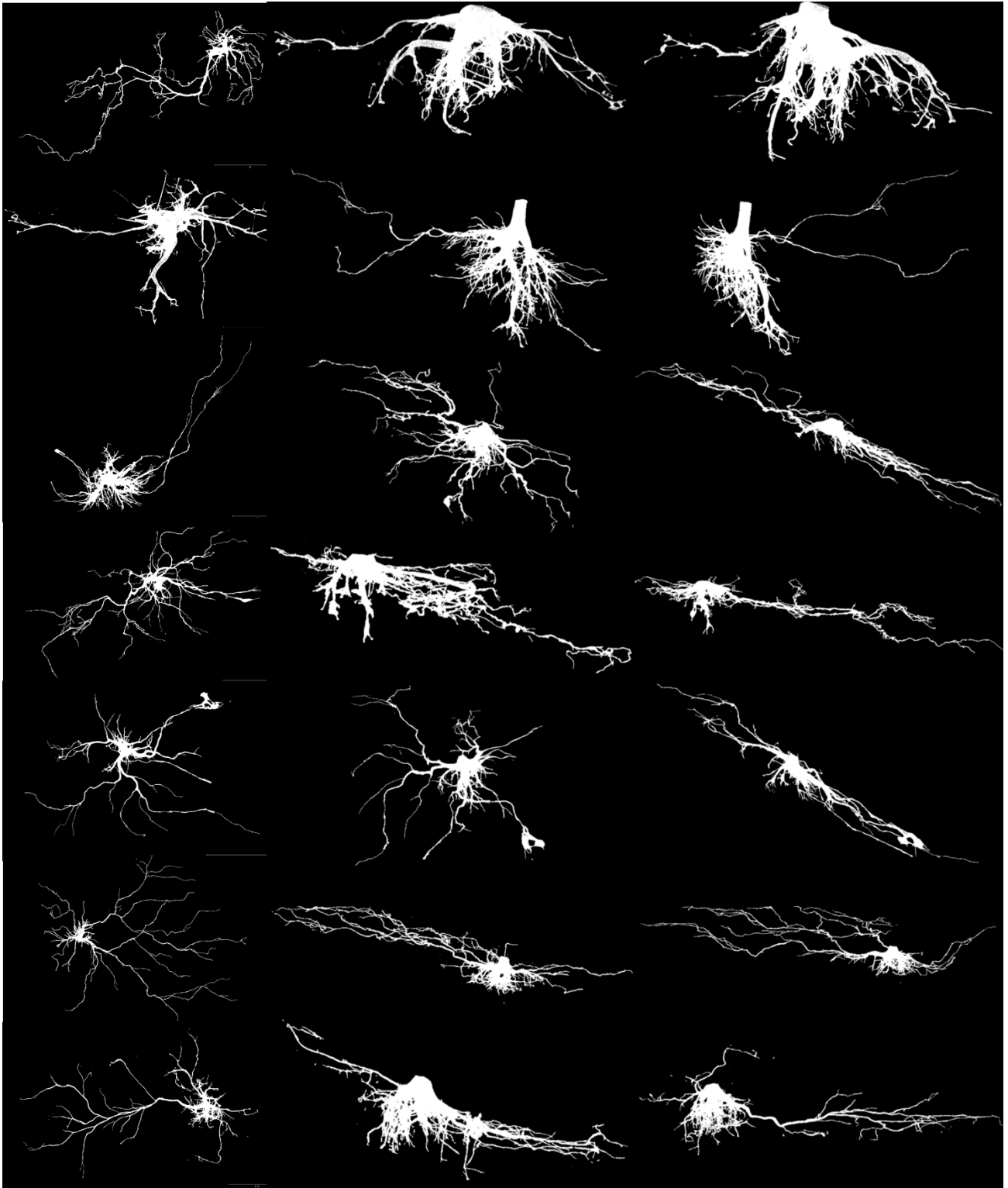


Figure 4) Binary maps images of the excavated root systems of seven *Macaranga sp.* specimens. Images on the left show a top-down view, the middle column shows the 'front' view, and on the right is the 'side' view. The scale varies for each image.

Of the variables investigated (slope, species, dbh, root biomass, plot AGB), slope interactions had the greatest impact on root system architecture. We found that steeper slopes favour more cross-slope root growth. Regression analysis between slope grade (G) and the proportion of roots growing crosswise (C) to the slope direction (P and S combined) shows a significant positive relationship [$C = 23.296 + 44.707 \cdot G$]. The model explains a significant amount of variance in rooting direction, $R^2 = 0.87$, $F(1,5) = 42.74$, $p < .001$. No significant correlation was found between slope grade and maximum rooting depth.

3.2.2 Structural analysis (digital)

Binary map analysis showed extensive asymmetrical radial root growth (Figure 4), though none of the metrics tested explained this variance. Three of the trees showed preferential uphill growth, three showed preferential downhill growth, and one showed an even distribution of pixels both up and downhill. Preference for branching upslope or downslope does not appear to be correlated with any of the metrics tested here.

The mean branching factor of our sample trees was 1.39; this did not differ between trees in relation to any of the environmental variables, except for the 12.5 cm diameter tree, which had a significantly higher branching factor (1.49) than any of the other trees (Table 3). The NJA proved over 90% accurate when computing the maximum Euclidean root length compared to the field-measured maximum (Figure 5). The mean percentage error was -8.65% ($SD \pm 7.17$), and includes any legacy errors resulting from the 3D digitisation as discussed in Chapter 2. Neither the size of the root system nor tree dbh affected the distribution of the residuals.

Table 3) Branching outputs (sinuosity, maximum branching order, and branching factor) from the Node-joining algorithm for the seven *Macaranga sp.* trees.

dbh (cm)	Sinuosity	Max. branching order	Branching factor
9.8	1.37	31	1.40
12.5	1.50	23	1.49
12.8	1.16	27	1.33
14.4	1.43	45	1.35
15.3	1.19	31	1.38
17.3	1.19	25	1.38
19	1.13	37	1.36

When looking for a correlation between tree dbh and root system extent (maximum Euclidean distance and average Euclidian root length) of all seven trees, we found no significant correlation. However, when the tree with multiple inoscultations was considered an outlier and removed, linear regression

revealed a positive relationship ($R^2 = 0.78$, $F(1, 4) = 14.22$, $p = 0.020$, adj. $R^2 = 0.78$) (Figure 5). If this tree was reinstated and the longest functionally grafted root (measured manually) was included in this analysis, then the relationship became even stronger ($R^2 = 0.83$, $F(1, 5) = 24.77$, $p = 0.004$, adj. $R^2 = 0.83$). In the trees that did not have active functional grafts, the maximum root length was three to five times longer than the average root length (mean = 4. SD = 1). Overall, roots had a low sinuosity index (mean = 1.13, SD = 0.13), which was not affected by dbh or any of the environmental factors. The sinuosity index of each tree's longest root was slightly higher at 1.31 (SD = 0.13, dbh 19 excluded from analysis).

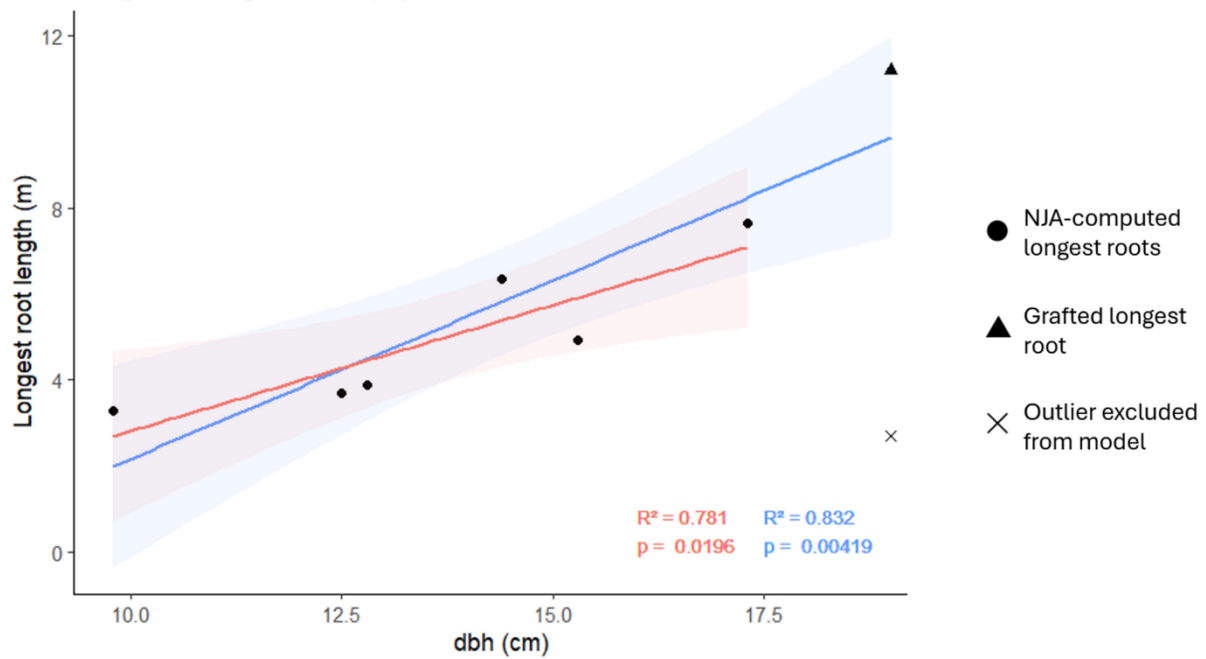


Figure 5) Linear models showing increasing maximum rooting distance with tree diameter. The model in red shows the relationship between the trees with reliable maximum root distances as captured by 3D modelling. The largest tree has been excluded from the model but is represented with 'X'. Blue line shows the improved model when the full extent of the largest tree's root system is accounted for (shown as triangle); considering the inosculated neighbour's root as part of the sample tree's root system.

4) Discussion

The RSR of 0.22 that we determined for these pioneer species in logged forests is significantly higher than the multi-species RSR of 0.18 developed in the primary forest of the Pasoh Forest Reserve in Peninsular Malaysia (Niiyama et al., 2010), but still lower than the global average of 0.25 (Huang et al., 2021). This finding supports the concerns of those authors that the primary forest equation should not be used to calculate the BGB of pioneer-dominated logged forests. It is impossible to know whether the difference in the RSRs is due to the difference in species composition, a direct response to logging

pressures, or more likely, some combination of the two. Further research into *Macaranga* in canopy gaps in primary forests and dipterocarps in secondary forests would aid in determining an answer to this. The size classes of the 54 trees used by Niiyama et al. to calculate the Pasoh RSR also differed from those in our study; theirs included trees from 2.5 cm to 67 cm dbh, while our smallest tree was just under 10 cm dbh and our largest just under 20 cm. Regardless, our higher RSR highlights the significant carbon stores that exist in the root networks of even short-lived tropical tree species. While there is evidence that in logged forests NPP investment shifts to favour woody biomass at the expense of leaf production and defence (Riutta et al., 2018), the partitioning between stem/branch and root growth appears to be isometric, at least among trees of this size within the genus *Macaranga*. However, as in the previous studies, these conclusions operate under the assumption that the wood density values published in the Global Wood Density Database (Zanne et al., 2009) are representative of the sample trees and that the wood density of individuals within a species is not affected by land use legacies (Alfaro-Sánchez et al., 2019). We could not empirically measure the wood density of our sample trees as the drying oven at Danum Valley was not functional.

While our sample size of seven exceeds the minimum considered acceptable by Yuen et al. (2016), it limits the power of statistical tests and increases the likelihood of Type I and Type II errors. The range of species included in our study also has benefits and trade-offs; while the overall RSR is more representative generally of logged forests containing *Macaranga sp.*, it impacts our ability to discern patterns within our results. The ecology of *M. gigantea* differs from the rest of the genus as it does not form the mutualistic relationship with ants that is otherwise characteristic. It follows that survival strategies are different between the myrmecophyte and non-myrmecophyte species (Fiala, Maschwitz & Yow Pong, 1991; Heil et al., 1999); differences in above/belowground resource allocation may be one of these adaptations.

The surprisingly high abundance of grafts found within the root systems of all sample trees offers important evidence towards a widespread presence of root grafts in tropical pioneer trees, which was previously hypothesised by LaRue (1952). While dbh did not have a significant effect on the number of grafts found within the first three branching orders, we generally observed inosculation between larger individuals, including the sample tree and the grafted neighbour. The biggest influence that we found on grafting, considering both self-grafts and true inosculations, was the biomass of the trees in the area immediately surrounding the sample tree. This supports the findings of Tarroux and DesRochers (2010) in their study of regenerating pine forests in North America, where stand density

was a significant factor in predicting graft rate, though proximity of trees was an even stronger predictor. In our study we did not measure the distance between the sample trees and the grafted neighbour, as in some cases it was impossible to determine the origin of these grafted roots, as they came from so far away. The rate of inosculation in our trees (0.57) was twice as high as that found in North American pines, a community considered especially likely to form grafts with neighbouring trees, at a similar stand density (Tarroux & DesRochers, 2010). This is a particularly interesting result considering that clay soils such as acrisol or ultisol should reduce the probability of grafts forming due to low friction between soil particles (Cook & Welch, 1956; Bormann & Graham, 1959).

Grafts ranged from superficial (attached only by the bark layer) to functional, where it was impossible to distinguish which functional tissues belonged to each tree (Figure S1). Superficial grafts increase stability and reduce the chance of windthrow (Stokes et al., 2005). True interspecific inosculation was confirmed only for the *M. gigantea* x *M. pearsonii* graft; the tree that the *M. hypoleuca* specimen had grafted with was too decayed to identify, and the *M. pruinosa*, while forming a structural graft with a neighbouring *M. pearsonii*, had not fully inosculated, with no fusion of the cortex. This was the smallest of the grafted sample trees; given more time, the graft may have fully inosculated, or the two species may have been incompatible. *M. gigantea* has been shown to hybridise with both *M. pruinosa* and *M. pearsonii* (Dixit et al., 2023), though there is not yet evidence of *M. pruinosa* x *pearsonii* hybrids, perhaps explaining why we did not see true inosculation in the root graft of this type. There is some evidence of gene and trait transmission between grafted trees of different species (Kadambi, 1954).

The propensity of these trees to inosculate may be an evolutionary alternative or supplement to relationships with mycorrhizal fungi in areas where the fungal community is reduced due to disturbance (van der Heijden et al., 2015). With the exception of *M. denticulata*, other members of the genus growing in disturbed areas do not appear to form important relationships with AM fungi (Ahmad, 1996; Turjaman et al., 2019); or at least, are able to establish in areas where the fungal community has been decimated (van Gardingen et al., 1998). This may be related to the mutualistic relationship with ants (except *M. Gigantea*) (Heil et al., 1999), or the physical grafts between roots may perform similar functions as mycorrhizal networks in providing additional moisture, carbohydrates, and minerals (Goltapeh et al., 2008). These grafts are hypothesised to be mutualistic, with larger trees preferentially grafting to smaller individuals (Fraser, Lieffers & Landhäusser, 2006). Carbohydrates preferentially travel from large to small trees within a graft, and this can offset the

effects of shading in smaller trees (Fraser, Lieffers & Landhäusser, 2006). Water direction is more dynamic, based on transpirational pull if both trees are alive (Wimmler et al., 2022). In the cases where one of the trees falls and leaves a living stump, the stump provides water to the tree and the tree provides sugars to the stump (Bader & Leuzinger, 2019), preserving living biomass for longer.

The effect of including the interspecific root graft in the dbh – maximum root length relationship further indicates the integral role of these inosculated roots in a tree’s root network. Where the sample tree forms a functional graft with a neighbour’s long root, it may not need to expend resources in creating one of its own. The NJA underestimated these longest roots by about 10%, an error caused primarily by the failure of the photogrammetry to accurately capture the thinnest parts of the root system. In the previous chapter, we showed that roots less than 25 mm were not accurately reconstructed. Even with this prematurely truncated root system, the roots we measured are longer than the previously reported maximum length for *Macaranga* trees, i.e. 5.5 m in an *M. gigantea* specimen of 24.5 cm dbh (Kenzo et al., 2009). Combining the measured 11.2 m of the *M. pearsonii* inosculated root with the 6 m distance from the graft to the parent tree, we found a maximum root length of 17.2 m for a tree of 60 cm dbh, showing the massive potential coverage of a mature *Macaranga* root system.

The low sinuosity index of the root networks in our *Macaranga* specimens enables each tree to explore a larger area of soil for a low carbon investment; a strategy that has previously been described for equivalent shallow-rooted pioneers in savannah ecosystems (O’Donnell et al., 2015). O’Donnell et al. hypothesized that this maximised a tree’s chances of finding soil uninhabited by other individuals, but considering the likely cooperative nature of root grafts, it may be a strategy which increases the chance of a root reaching a viable neighbour with which to inosculate. Our finding that trees without functional grafts displayed a maximum root length three to five times longer than the sample average root length would also support this theory. Both root grafts and sinuosity have also been linked to the concentration or diversion of water fluxes, which can have implications for subsurface flow and slope stability (Ghestem & Sidle, 2011); however, we found no significant relationship between either graft occurrence or sinuosity and slope grade.

Slope grade did have a significant effect on one aspect of root system architecture: the proportion of roots growing crosswise to the slope direction. Increased investment into lateral roots on steeper slopes, which supports the hypothesis of this strategy preventing a tree from slipping down a slope, may also help to prevent the slope from collapsing, increasing survival chances for the whole community (Zhu

et al., 2017). Preference for branching upslope or downslope does not appear to be correlated with any of the metrics we tested. The preferential gravitropism is instead likely dictated by nutrient gradients and soil physical properties, both mechanical and hydrological (Ghestem & Sidle, 2011). The placement of the tree along the slope profile (Zhu et al., 2017) can influence all these factors, so future studies should include this as an explanatory variable.

The number of branches in the first three branching orders did not increase significantly with dbh, implying that this number is settled early in a tree's development (i.e. at less than 10 cm dbh), or that increases in branch number are offset by the greater number of grafts as a tree ages, reducing the number of apparent individual branches. Though the branching factors provided by the NJA did not reveal any insights into how branching complexity varies between trees within a degraded landscape, we have provided a baseline against which future root systems can be studied using a simple methodology.

The advantage of collecting root data in high-quality point cloud format is that it is stored as a databank in perpetuity and can be analysed by ever more sophisticated methods as they become available. If, for example, a similar study is completed on *Macaranga* in primary forest, or on Dipterocarps in logged forest, then the root networks can be compared to the specimens collected in this study, despite the biological samples being long since destroyed.

As we found the RSR of *Macaranga* trees growing in secondary forests to be higher than the average RSR of a primary Dipterocarp forest, we advise that our new allometric equation is applied to pioneer species in regenerating forests. We showed that while the roots of *Macaranga sp.* are shallow, the lateral extent of their roots extends far further than previously reported. We also found interactions between the steepness of the growing surface and the proportion of roots growing perpendicular to the slope direction. Finally, we highlight the unexpected complexity of *Macaranga sp.* root systems in terms of their propensity to form grafts with neighbours, a factor that should be considered in restoration initiatives, particularly in areas with unstable slopes. Further research into the root system architecture and the RSRs of other early successional pioneer species should be a research priority not just to quantify existing carbon sinks, but to understand the role that these trees play in supporting and enhancing ecosystem regeneration.

Supplementary Information



Figure S1) Photographs of root grafts between neighbouring excavated *Macaranga* *sp.* trees. In the top row, there is full inosculation between the roots of a 19 cm *M. gigantea* (marked with purple tape) and a *M. personii*. In the bottom row, the sample *M. pruinosa* has grafted structurally with a neighbouring *M. personii* (red and white tape), but the cortices remain separated from each other.

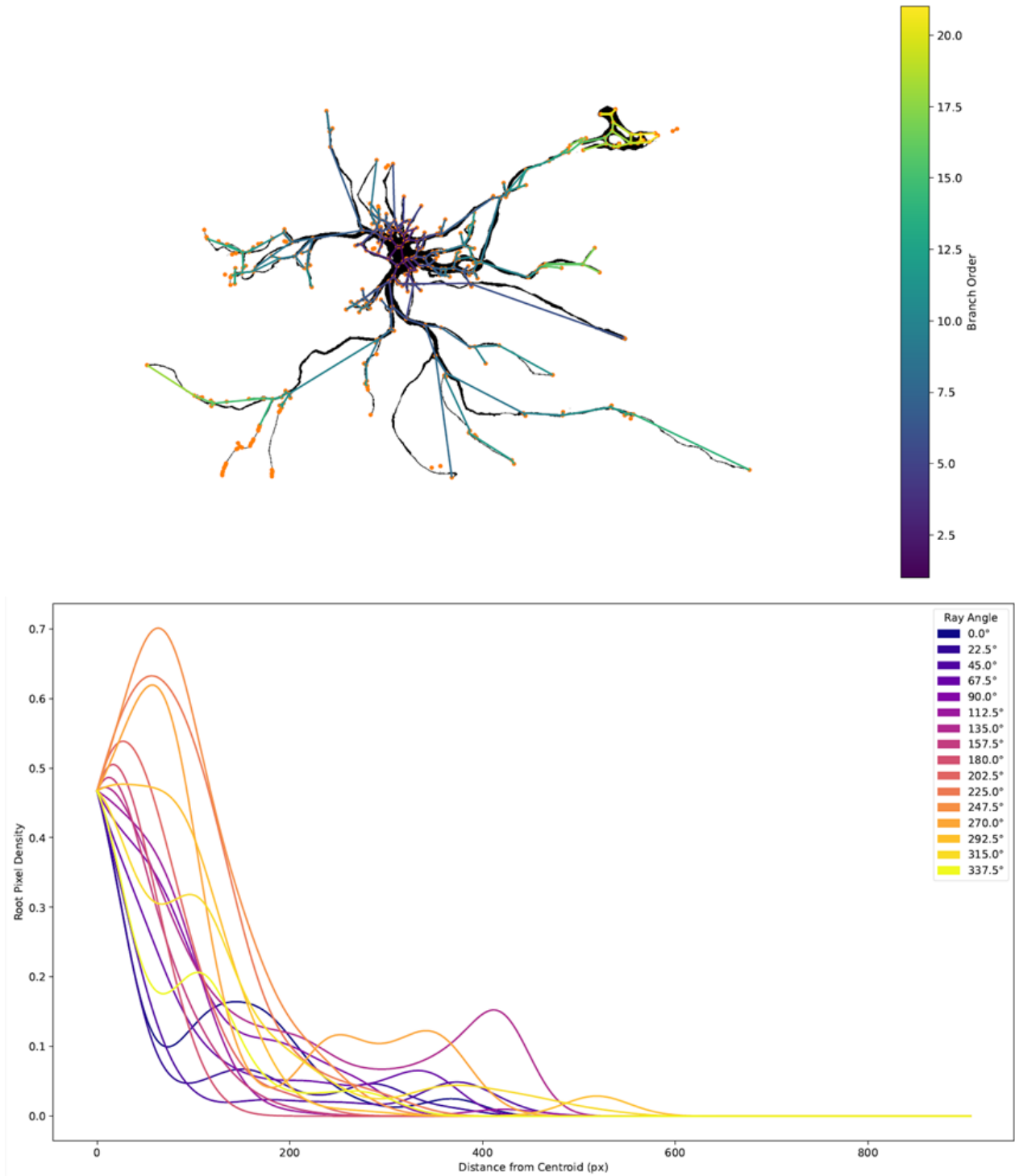


Figure S2) Example outputs from the NJA for the root system complexity metrics of the 12.5 cm dbh *Macaranga hypoleuca* tree. The top panel shows the skeletonized root network, with colours representing branching order. The bottom panel shows a measure of root eccentricity from rays cast out from the central node at 22.5° intervals.

Chapter 4) Growth trajectories of naturally regenerating logged forests in Sabah

Abstract

Much of the forests of Southeast Asia have been logged throughout the last 70 years. In many cases, these forests were left alone to regenerate naturally once the largest trees were removed. Under the originally prescribed extraction allowances and logging rotations, it was expected that it would take 60 years for the forests to regenerate to their original quality. In many cases, this advice was not followed, with forests suffering multiple rounds of salvage logging at higher-than-planned intensities, leaving them in states of extreme degradation. We use data from eight annual vegetation censuses across plots that span a degradation gradient to check on the recovery of these plots *c.* 30 years post-logging and build a simulation of growth, mortality, and recruitment to project this recovery forward to 2050. We found that at the start of our census, the majority of plots that experienced logging pressures remained significantly lower in aboveground woody biomass than their unlogged counterparts. We predict that by 2050, just 35% of the Salvage-logged plots with a historical extraction rate of 179 Mg ha⁻¹ will reach a threshold AGB comparable with unlogged forests. Forests that were logged twice with a lower historical extraction volume rate of 150 Mg ha⁻¹ fare slightly better with a 55% recovery rate. Our results show that passive regeneration is an extremely slow process in heavily logged plots, so active restoration may be the only hope of the worst affected areas recovering within the span of a human lifetime. We also show that the primary forest plots are still gaining significant amounts of biomass year-on-year (8.98 Mg ha⁻¹), the same as in the Salvage-logged plots, highlighting their persisting importance as a carbon sink.

1.0) Introduction

Borneo's rainforests are among the oldest, most biodiverse forests in the world, with up to 200 species of tree per hectare (Whitmore 1984, 1990; Richards 1996). These qualities, including a natural abundance of high-value heavy hardwoods in the *Dipterocarp* family, made them an ideal target for intensive and continuous timber production over the past century (Wyatt-Smith, 1963), with average annual extraction rates of over 150 m³ ha⁻¹ across the state of Sabah (Struebig et al., 2013). Approximately 70% of Sabah's forests are now degraded to varying degrees of severity, with the

majority of the degradation occurring in the 60 years between 1953 and 2013 (Matthews, 1917; Bryan et al., 2013; Estoque et al., 2019).

These degraded forests now exist in a state that is inherently out of equilibrium (Qie et al., 2017; Riutta et al., 2021). Large quantities of living biomass have been removed, and excessive amounts of necromass are now present, and in the worst cases, they no longer provide the same ecosystem services as a primary forest. As well as reduced plant and animal biodiversity (Saiful & Latiff, 2014; Costantini, Edwards & Simons, 2016), the carbon-sequestering properties of rainforests that earn them the title ‘lungs of the earth’ are called into question (Mills et al., 2023). The perception of these degraded forests as ‘less than’ their pristine counterparts leaves them vulnerable to land use change through shifting cultivation, such as soya or oil palm plantations.

The alternative is ecosystem restoration, which aims to remediate the damage caused by logging and other anthropogenic drivers of habitat degradation. The global ecological restoration market was worth around \$13 billion USD in 2021 and is projected to reach \$23 billion by 2031 (Business Research Insights, 2024; Ferwerda, 2024). The global Bonn Challenge (IUCN, 2020) aims to restore 350 million ha of forests on degraded and deforested land by 2030.

Forest restoration falls into two main subcategories; ‘passive’ (alternatively ‘natural’, ‘unassisted’ or ‘assisted natural’) and ‘active’ restoration. Passive restoration relies on the spontaneous recovery of native tree species in degraded areas, which may be complemented by interventions such as pest control, fire protection, and removal of grazing pressures (Zahawi, Reid & Holl, 2014). Active restoration involves accelerating the process or attempting to change the trajectory of succession, usually including some form of seedling planting (Vaughn et al., 2010).

The choice between passive and active restoration should be informed by the state of the landscape; active restoration is likely to be the only solution in areas where intensive and prolonged disturbance has caused a loss of seed banks, genetic diversity or nutrients. Where passive regeneration is possible, the results are more favourable in the long-term for a wider range of ecosystem services, and generally require a smaller financial investment (Crouzeilles et al., 2017). Active restoration is more expensive but can be seen as a ‘quick fix’ with results appearing rapidly, while regeneration may take over 100 years under more natural conditions (Blanc et al., 2009b; Veryard et al., 2023). Therefore, the decision between passive and active restoration often comes down to finances and the timeframe in which a ‘satisfactory’ result can be achieved, rather than being based on the underlying ecological processes (Lindenmayer, 2020).

To properly determine the most appropriate method of restoration, one must first establish a baseline of the current ecological state, understand the mechanisms of recruitment, growth, and mortality that drive habitat regeneration, and estimate the expected recovery rates under any planned treatments (Galante, Pinard & Mencuccini, 2018; Philipson et al., 2020). By these means, it then becomes possible to determine the level of degradation beyond which an ecosystem will not recover by itself, and active restoration becomes the only realistic path for restoration. Identifying this cutoff will allow resources to be allocated more efficiently; policymakers can decide whether to intervene and commit to active restoration or to allow these areas to be converted to alternative land uses, especially if the remaining funds could be diverted to areas with greater potential for restoration.

Sabah makes an ideal case study for these debates due to the extensive and well-documented logging history of the past 100 years. The introduction of mechanised logging practices in 1950, including tractors for lowland areas and high-lead logging for less accessible slopes, caused extraction rates to rise rapidly, peaking at over 14,000 m³ in the mid-1970s (Chapter 1). In addition to this reported removal of the target hardwood trees, these intensive logging strategies cause subsequent collateral damage to the ecosystem, including target trees bringing down neighbouring trees on their descent and the removal of trees to create skid trails and other infrastructure. This results in biomass loss of more than twice the reported extraction once felling damage, post-logging mortality, and the abandonment of non-commercial trees are accounted for (Pfeifer et al., 2016; Zuleta et al., 2023). Due to the height and density of trees in Southeast Asian forests, collateral logging loss was higher here than elsewhere in the tropics (Picard, Gourlet-Fleury & Forni, 2012), and up to 25 % of target trees intentionall felled were abandoned as they did not meet commercial standards (Griscom, Ellis & Putz, 2014).

Since this peak annual extraction in the 1970s, timber production has declined due to widespread regeneration failure of commercially desirable species such as *Dipterocarps* and a few notable heavy hardwoods such as belian, which represented 90% of all timber deliberately extracted (Qie et al., 2019). Historical silvicultural practices prescribed 60-year logging rotations alongside climber cutting and poison girdling of economically undesirable species (Berry et al., 2010; Philipson et al., 2020). The prescribed rotations were often not followed (Ewers et al., 2011), and these herbicidal treatments, alongside soil compaction, pollinator decline, and the loss of reproductive vigour due to seed removal and reduced genetic diversity, have all contributed to this failure of the forest to regenerate as expected.

Previous research indicates that the intensity of logging pressures, including the volume of timber extracted (Appanah et al., 1990; Gourlet-Fleury et al., 2013; Otani et al., 2018; de Avila et al., 2018; Roopsind et al., 2018; Hu et al., 2020) or the techniques and treatments used (Zimmerman et al., 1995; Pinard & Cropper, 2000; Susanty, 2021; Bedrij et al., 2022; Hayward et al., 2021) affect how long it takes vegetation to recover. Neotropical studies have shown that forests are resilient to low-intensity land use, with most forest attributes (78%) showing recovery to old-growth levels in just 20 years (Poorter et al., 2021) or 40 years (Aide et al., 2000). However, vegetation structure and species diversity are predicted to take up to 60 years, and over 120 years for biomass and species composition (Zimmerman et al., 1995; Pinard & Cropper, 2000; Poorter et al., 2021). In Sabah, most of the studies on forest regeneration come from well-managed, lightly logged areas where all extraction occurred within a single campaign. (e.g. (Hayward et al., 2021; Keller et al., 2023; Berry et al., 2010). The estimated regeneration timelines for these areas align with the 120-year predictions by (Pinard & Cropper, 2000), but for forests that have suffered the accumulated effects of multiple high-volume logging cycles, the timescale is likely even longer (Appanah et al., 1990; Hayward et al., 2021).

In this paper, we build a simulation to determine the regeneration trajectory for logged forest in Sabah. Specifically, we address the following questions: a) What was the above and belowground woody biomass of logged forest plots in 2011, in comparison to the baseline established for primary forest control plots, b) how many of these degraded forest plots can be expected to regenerate by 2050.

We use the network of sites to build a pseudo-chronosequence ‘space for time’ approach (Johnson & Miyanishi, 2008) where we assume that the climax community of a fully regenerated logged plot should have similar woody biomass to the neighbouring protected primary forest conservation areas at Danum Valley and Maliau Basin. The simulation outputs provide insights into the threshold level of logging degradation beyond which the Bornean rainforest is unlikely to regenerate naturally by 2050.

2.0) Methods

2.1) Site description

The data used to parameterise our simulation comes from annual vegetation censuses of trees > 1 cm diameter undertaken from 2011 to 2019 in the SAFE Project area in Sabah, Malaysian Borneo (Ewers et al., 2011). The data comprises 172 25 x 25 m plots spanning a logging gradient from Salvage-logged, fragmented forest to continuous, primary forest that has never been logged (Table 1). Commercial forests in and around the SAFE project were subject to selective logging in 1975, followed by additional

rounds of salvage logging in the 1990s. The original prescribed logging rotation was 60 years. Therefore, we have chosen 2050 as the target date for projected recovery.

Table 1) The land-use intensity gradient across the SAFE Project area, extending from salvage-logged forest through to primary forest.

Block(s)	N. plots	Logging Intensity	Fragmentation ^a	Forest quality range ^b	Notes
A, B, C, D E, F	100	Salvage	Fragmented	1 - 4	Logged multiple times, including salvage logging
LFE, LF1, LF2	33	Twice	Fragmented	2 - 4	Twice logged
VJR	8	Variable	Fragmented	2 - 5	Lightly logged 1970s and 1990s
OG3	9	Low	Continuous	3 - 5	Greater than 500 m from reserve boundary
OG1, OG2, MLA, DAN	22	Never	Continuous	3 - 5	OG1 >1 km from reserve boundary, OG2 >500 m from boundary.

^aContinuous forest cover means the block is in a contiguous forest management area of approximately one million ha.

^bAverage forest quality within each block. Quality is scored on a qualitative scale of 1 –5; (1) very poor, no standing trees, open canopy with ginger, vines or low scrub; (2) poor, open canopy with some small trees over a ginger and vine layer; (3) okay, small trees abundant and canopy at least partly closed; (4) good, lots of trees including some large trees and closed canopy; (5) very good, logging evidence, closed canopy with large trees.

In this study, we chose to measure ‘biomass’ rather than ‘carbon density’, to highlight that forest restoration success should be considered in broader terms than its carbon sequestration potential. Conversion between the two can be achieved simply by multiplying the biomass value by average carbon content (0.47), but an inclusive lexicon is important in ensuring good practice in nature-based solutions (Folkard-Tapp, Banks-Leite & Cavan, 2021; Welden, Chausson & Melanidis, 2021).

2.2) Biomass growth

We used census data from 18,965 trees that were measured on at least two occasions between 2011 and 2020 to calculate aboveground biomass (AGB) growth rates. Stem diameter at breast height (dbh) was measured at 1.3 m above ground level using the standardised RAINFOR protocol (Marthews et al., 2013). For multi-stemmed trees, a single diameter was calculated via a quadratic sum (Magarik et al., 2020). Of these, 8,693 trees were above 10 cm diameter, 10,271 trees were below 10 cm diameter. 14,265 trees had been identified to some level of taxonomy (family: 173, 5268: genus, 8824: species) and were assigned a wood density value based on average values within their highest classification (Zanne et al., 2009). Those that were not identified were assigned the plot-level average wood density.

We computed the above-ground biomass of these trees in each available census year using the ‘BIOMASS’ package (Réjou-Méchain et al. 2017); based on the following equation (Chave et al., 2014);

$$AGB = \exp(-2.024 - 0.896 * E + 0.920 * \log(Wd) + 2.795 * \log(D) - 0.0461 * (\log(D)^2))$$

where D is the stem diameter measured at 1.3 m, Wd is wood density, and the constant E is a measure of environmental stress estimated from the study site coordinates (Chave et al., 2014). Inclusion of E creates a localised height-diameter model that should function as a site-specific allometric equation.

For each plot, the biomass of all trees present in the first census was combined to generate a starting AGB and scaled to the hectare level. In plots where the first census year was delayed, eg. the first census for a certain plot took place in 2014, we backcast the calculated yearly growth (as calculated below) to estimate what the AGB may have been in 2011. For every tree, we calculated the change in AGB between the first and last year that the tree appeared in the census and divided this total change by the number of intervening years to get the average annual growth rate in Mg. To test whether these growth rates of individual trees followed the expected allometric scaling law, we plotted the growth of all trees against the AGB of the tree during its first census year.

We conducted an Analysis of Covariance (ANCOVA) to investigate potential differences in growth rates between trees > 10 cm and those < 10 cm diameter, considering an interaction effect. Although the slopes were not significantly different, the intercepts demonstrated statistical significance (Adjusted R-squared: 0.69, p-value: $< 2.2e-16$). Subsequently, we removed the interaction term, resulting in the following allometric equations:

$$(<10 \text{ cm}) \Delta AGB = -3.9478282 + 0.6841950 \times \log(AGB_{1st})$$

$$(>10 \text{ cm}) \Delta AGB = -3.5510274 + 0.6841950 \times \log(AGB_{1st})$$

To determine a single line which best described the growth of trees across both size classes, we took the mean of the intercepts and retained the slope.

$$(\text{All sizes}) \Delta AGB = -3.749428. + 0.6841950 \times \log(AGB_{1st})$$

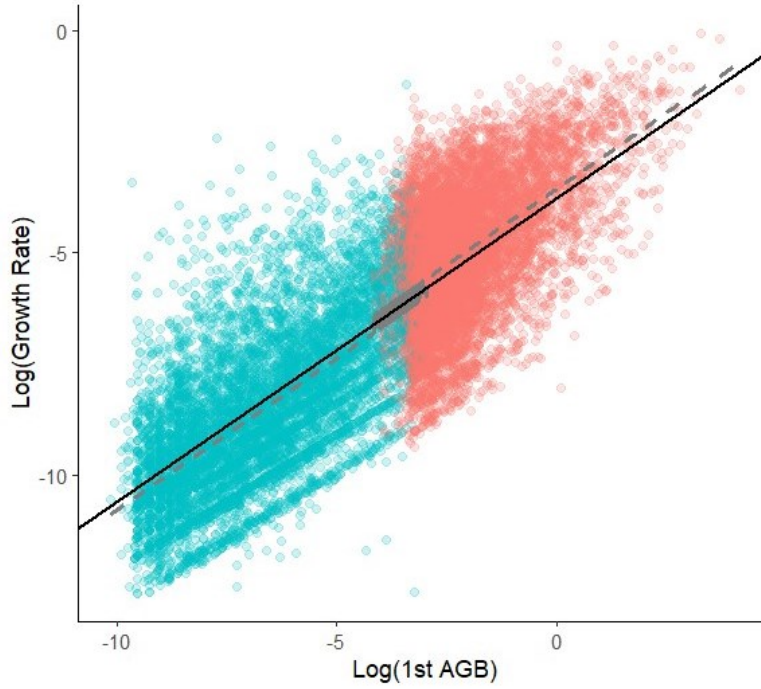


Figure 1) Allometric scaling relationship between the $\log(\text{AGB})$ of trees in 2011 and the average $\log(\text{annual AGB growth})$ of those trees. Trees < 10 cm diameter are shown in blue, trees > 10 cm are shown in red. Grey dashed lines show the fitted linear models for each size class of tree, with different intercept but same slope. The black solid line shows the average of the two intercepts, which is the model we chose to represent trees of both size classes.

To obtain a plot-level AGB growth estimate, we multiplied the plot-level average growth rate of trees by the number of trees present in that plot during its first census year and scaled this to the hectare level. We henceforth refer to this as the ‘average tree growth model’. The number of trees is only used at the first timestep to generate a growth vector for each plot. After that, recruitment, growth and mortality are modelled in terms of plot biomass rather than on a per-tree basis.

2.3) Recruitment

Modelling tree recruitment is more challenging than growth and mortality (Díaz-Yáñez et al., 2024), leading to this parameter often being omitted from classical forest regeneration models, e.g. (Pretzsch, Biber & Ďurský, 2002). In empirical distribution models, recruitment can be modelled as a constant value per hectare (Porté & Bartelink, 2002). For each plot, we summed the initial biomass of all trees flagged as new recruits ($n = 2,148$). We then divided this total by the number of years censused to approximate an annual recruitment rate in each plot. As recruitment was recorded in a subset of plots, we used a block-level average, an improvement upon simulations using only a constant value per hectare (e.g. Nakashizuka, 1991; Kolstrom, 1993; Hinssen, 1994 in Porté & Bartelink, 2002).

2.4) Mortality

We calculated deadwood production rates from trees classified as dead during the census period. We took the AGB from each tree's last living measurement and considered this to be the amount of deadwood produced. Tree mortality is a far more stochastic process than growth, but we estimate mean annual mortality rates as the total amount of deadwood produced in a plot across the census period divided by the number of intervening years.

In addition to whole tree biomass, we added a branchfall modifier to the total deadwood production in each plot. Branchfall was measured two to four times per year between 2014 and 2017 using $2\text{ m} \times 2\text{ m}$ quadrats on the ground ($n = 25$ per plot) in a limited subset of plots within the SAFE landscape spanning all logging intensities (Riutta et al., 2022). Branches $> 2\text{ cm}$ in diameter fallen from live trees were collected, dried, weighed and corrected for mass loss due to decay (Nunes et al., 2021). The first survey quantified stock; subsequent surveys measured turnover (Ewers, Pfeifer & Turner, 2018). A Welch's 2-Sample T-Test showed no significant difference in branch turnover between plots of different logging intensities ($t(7.52) = -0.40$, $p = 0.70$, 95% CI $[-0.57, 0.40]$), so we added the yearly branchfall production value of $1.45\text{ Mg ha yr}^{-1}$ for the whole landscape to every plot. The estimated initial pool of deadwood in each plot was sourced from Ewers, Pfeifer and Turner, 2018.

2.5) Decomposition

Deadwood decomposition data was sourced from a field experiment that ran from 2017 to 2019. Standing and fallen deadwood pieces greater than 10 cm in diameter, in plots that spanned the logging gradient, were given unique tags and measured for length and diameter. The diameter of standing deadwood was measured at 1.3 m height, and fallen deadwood was measured at both ends. Where logs were hollow, the diameter of the void was recorded. Wood density was measured from small volumetric samples using an increment borer and analysed in the lab, from the fresh volume and dry mass of the wood samples. All deadwood pieces were then resampled in 2019 to measure decay. We calculated the volume of each deadwood piece as a truncated cone, with the hollow volume removed where necessary. We combined this with density to give the mass, and halved the change in mass between the two years to obtain a yearly rate.

2.6) Model selection

2.6.1) AGB growth

To model the annual rates of biomass growth for the plots under each logging intensity as a function of the biomass in the preceding year, we estimated the line of best fit using standardised major axis (SMA) and major axis (MA) techniques. Linear regression is not appropriate for these analyses as one variable does not directly influence the other; instead, the model attempts to estimate an underlying line of best fit (Warton et al., 2006). When both axes are log-transformed, the relationship becomes approximately linear, as to be expected from an allometric relationship (Niklas, 1994; Francis et al., 2017). We used the “smatr” package (Warton et al., 2012) in R to generate several SMAs on log-transformed variables, fitted separately for each logging intensity ($\log(\text{growthrate}) \sim \log(\text{AGB1}) * \text{logging intensity}$). To account for the presence of outliers, we selected the ‘robust’ option.

The differences in slope between the models for each logging intensity were not significant, so we simplified the model ($\log(\text{growthrate}) \sim \log(\text{AGB1}) + \text{logging intensity}$) to fit a common slope but test for separate elevations for each level of the factor groups (Warton et al., 2006). This resulted in a significant difference in elevations ($p = < 0.001$), where the intercept was lower for higher logging intensities.

2.6.2) Recruitment

To model the recruitment rate, we fitted a log-log linear model to predict AGB recruitment from 2011 live biomass (Porté & Bartelink, 2002).

2.6.3) Mortality

The mechanisms behind tree mortality are more difficult to model than growth due to the inherently stochastic nature of tree deaths, especially in the largest trees that have the highest influence on total biomass loss (Blanc et al., 2009b; San-José et al., 2021). Despite this, species composition can be considered a good predictor of the likelihood of tree mortality, with pioneer-dominated forests experiencing faster turnover (Esquivel-Muelbert *et al.*, 2020, Yu *et al.*, 2022). Therefore, it is appropriate to consider logging intensity as a factor when fitting a model for plot-level mortality, as the logging intensities function as a pseudo-chronosequence of succession.

The ‘smatr’ package (Warton et al., 2012) was employed to generate robust SMAs on the log-transformed variables, fitted separately for each logging intensity ($\log(\text{deathrate}) \sim \log(\text{AGB1}) * \text{logging intensity}$).

2.6.4) Decomposition

We found no significant relationship between the change in mass with logging intensity or starting AGB, so we took the average decomposition across the entire logging gradient; resulting in an average annual decrease in mass of 25 %. We then calculated the decay constant, k , using the following equation:

$$-k = -\frac{\ln(\text{fraction remaining after one year})}{\text{time interval}}$$

We then used the resulting constant of ($k = 0.288$) to fit exponential decay models to describe the loss of necromass from the system (H  rault et al., 2010; Gora et al., 2019) (Figure 2d).

2.7) Belowground

To calculate the amount of belowground biomass in 2011, annual growth, and recruitment, we multiplied the output values for Logged forests by 0.22; the R:S calculated in Chapter 3, and the Low and Never-logged control plots by 0.18 (Niiyama et al., 2010) . For decomposition, we used an alternative decay constant ($k = 0.55$) better suited to belowground decomposition rates, from Ohashi et al., 2019.

2.8) Simulating biomass recovery

The statistical models were then used to define a deterministic statistical simulation of the fates of existing experimental plots. Given the initial plot AGB and logging status, we used the appropriate growth model coefficients to predict annual increase in AGB and then added AGB from the recruitment model and subtracted AGB resulting from the mortality model. We forecast the AGB in plots from their current state out to 2050 because for most plots, this represents around 60 years since the final round of logging, which was the original rotation prescribed in which the forest should be able to regenerate naturally. We also took initial deadwood estimates for each plot, removed deadwood biomass annually according to the decay model and added fresh mortality to provide a similar time series for plot deadwood.

2.9) Model validation and regeneration threshold

To test whether the simulated annual changes in biomass calculated from the average tree growth model followed the pattern observed on the ground, we compared the simulation's outputs after eight years to the observed data from the final census in 2019. We consider logged forest to be regenerated

when it meets a threshold value of AGB 489 Mg ha^{-1} , ($\text{AGB} + \text{BGB} = 577 \text{ Mg ha}^{-1}$), derived from the median biomass density of an unlogged forest observed by airborne LiDAR data (Ewers et al., 2024).

3) Results

3.1) Model parametrisation

3.1.1) AGB growth

In the smatr models generated for each logging intensity, the intercepts of ‘Salvage’ and ‘Twice’ logged plots differed from all other logging intensities ($p = < 0.001$ and 0.003 respectively). The three lowest logging intensity groups did not produce robust models and had similar intercepts, so we combined them into a single ‘Control’ group. The final output was three SMA lines with different intercepts (Salvage = -0.999 , Twice = -1.718 , Control = -2.154) and a single slope (0.757) (Figure 2a).

3.1.2) Recruitment

The recruitment model accounted for a substantial proportion of variance ($R^2 = 0.31$, $F(1, 12) = 5.49$, $p = 0.037$, adj. $R^2 = 0.26$). The model's intercept is at 2.31 (95% CI $[-1.79, 6.41]$, $t(12) = 1.23$, $p = 0.244$). $\text{Log}(2011\text{biomass})$ negatively affected recruitment ($\text{beta} = -0.86$, 95% CI $[-1.67, -0.06]$, $t(12) = -2.34$, $p = 0.037$; Std. $\text{beta} = -0.56$, 95% CI $[-1.08, -0.04]$) (Figure 2c).

3.1.3) Mortality

When we fitted smatr models for mortality data for each of the the logging intensity groups, only ‘Salvage’ logged plots showed a significant relationship ($p = 5.4648\text{e-}08$). Therefore, we fitted a SMA for this group separately, resulting in the following model: $\text{Log}(\text{death rate}) = -0.7404952 + 0.6243866 * \text{log}(2011 \text{ biomass})$. Due to the lack of relationship between the other logging intensity groups and AGB, we combined them into one group and fitted the model $\text{lm}(\text{LogDeathRate} \sim 1)$ (Figure 2b).

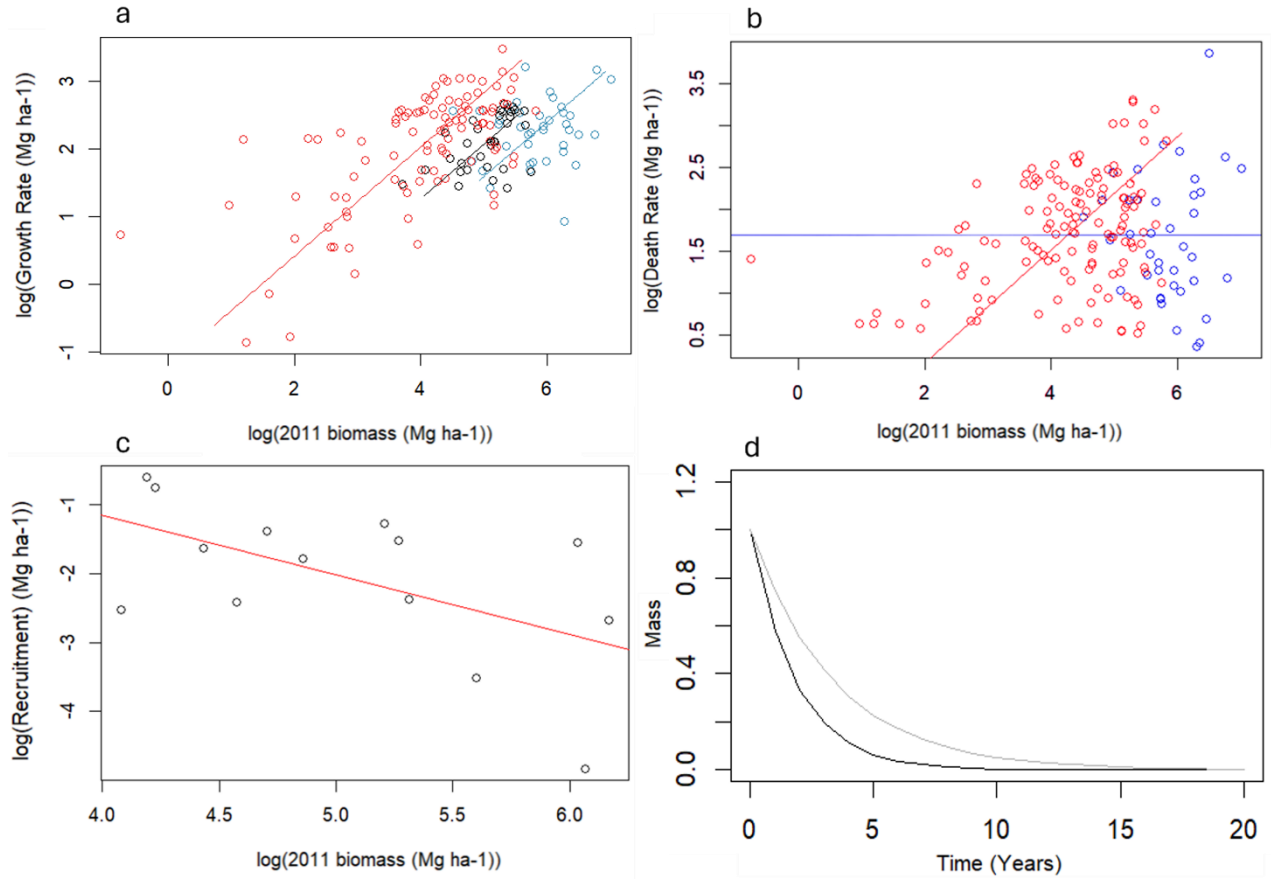


Figure 2) Models used to parameterise the forest regeneration simulation based on log-transformed vegetation census data. a) smatr models of biomass increase: red line shows salvage logged plots, black is twice logged, and blue contains all other plots as controls. b) red points and line shows Smatr model of increasing mortality with higher 2011 biomass in Salvage logged plots, blue shows intercept but no relationship between 2022 biomass and annual death rate. c) shows a single model of decreasing recruitment rate with increasing 2011 biomass across all logging intensities. d) shows wood decomposition rates using the constant k ; *grey line is aboveground decay rate, black line is belowground decay rate.*

3.2) Baseline and model verification

We found that the 2011 AGB baselines decreased along the degradation gradient from Never-logged pristine forest to Salvage-logged degraded forest (Figure 4). The median biomass for each logging intensity along the gradient ranged from 70.21 Mg ha⁻¹ (IQR = 87.82), Twice = 170.19 (IQR = 98.79), Variable = 237.62 (IQR = 90.92), Low = 380.81 (IQR = 251.69), to 380 Mg ha⁻¹ (IQR = 251.69) in the Never-logged plots. Results from an ANOVA and subsequent Tukey Post-Hoc test showed that the AGB of Salvage-logged plots (median = 70.21 Mg ha⁻¹, IQR = 87.82) was significantly lower than plots at all other logging intensities, as was the AGB of Twice-logged forest plots ($P = < 0.005$). None of these Salvage or Twice-logged plots exceeded the threshold value in 2011. 41% of the Never-logged control and 33% of Low-intensity plots exceeded the AGB threshold, while only one of the eight Variably-logged plots exceeded the threshold (Figure 4). When we tested the simulation outputs for

2019 against the subset of plot-level census data available for the same year ($n = 162$), the predicted plot biomass aligned closely with the observed values (Figure 3). The RMSE for observed vs predicted was 74.49 (range = 1183.02), NRMSE = 0.06, $R^2 = 0.85$.

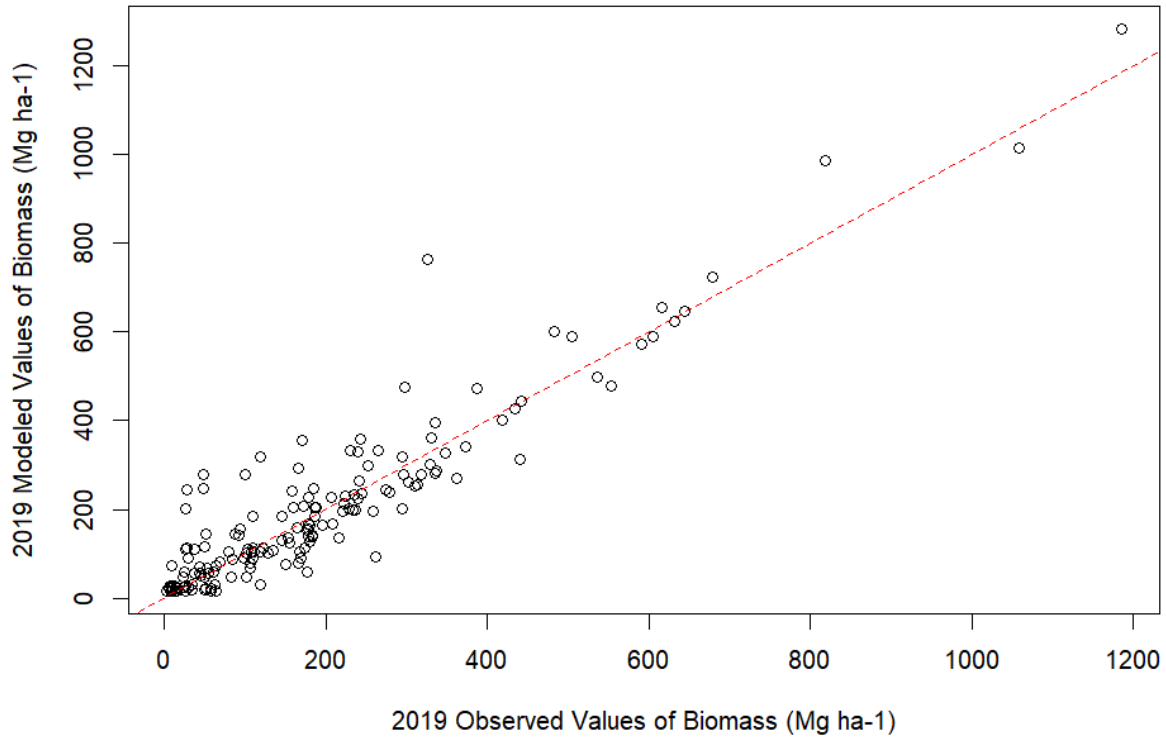


Figure 3) Observed and modelled aboveground biomass (AGB, Mg ha^{-1}) of all forest plots in 2019 ($n = 172$). The dashed red line shows $x = y$. Observed values come from a vegetation census undertaken in 2019. The modelled values show the result of the average-tree growth, mortality, and recruitment models after eight years of the simulation, based on 2011 starting values.

3.3) Forest regeneration

Our simulation predicted the live biomass recovery trajectory and deadwood stock balance for 172 individual forest plots across the degradation gradient (Figure S1 and S2, Supplementary Information). Most were predicted to increase in live biomass, though seven declined in biomass over time. These plots were Unlogged, Twice logged, or Variably logged plots with a low starting biomass ($\text{TB} = < 177 \text{ Mg ha}^{-1}$), where growth and recruitment did not balance the mortality rate of $5.31 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. The mean annual net biomass increase was the same for Never and Salvage-logged forests, at $8.98 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. In terms of percentage increase, this is 1.59% annually for Never-logged plots and 4.19% in Salvage-logged plots. The mean annual net increase in Low and Twice-logged plots was slightly lower at 8.6 and $7.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively. The smallest mean net annual growth was observed in the Variably logged plots at $3.91 \text{ Mg ha}^{-1} \text{ yr}^{-1}$.

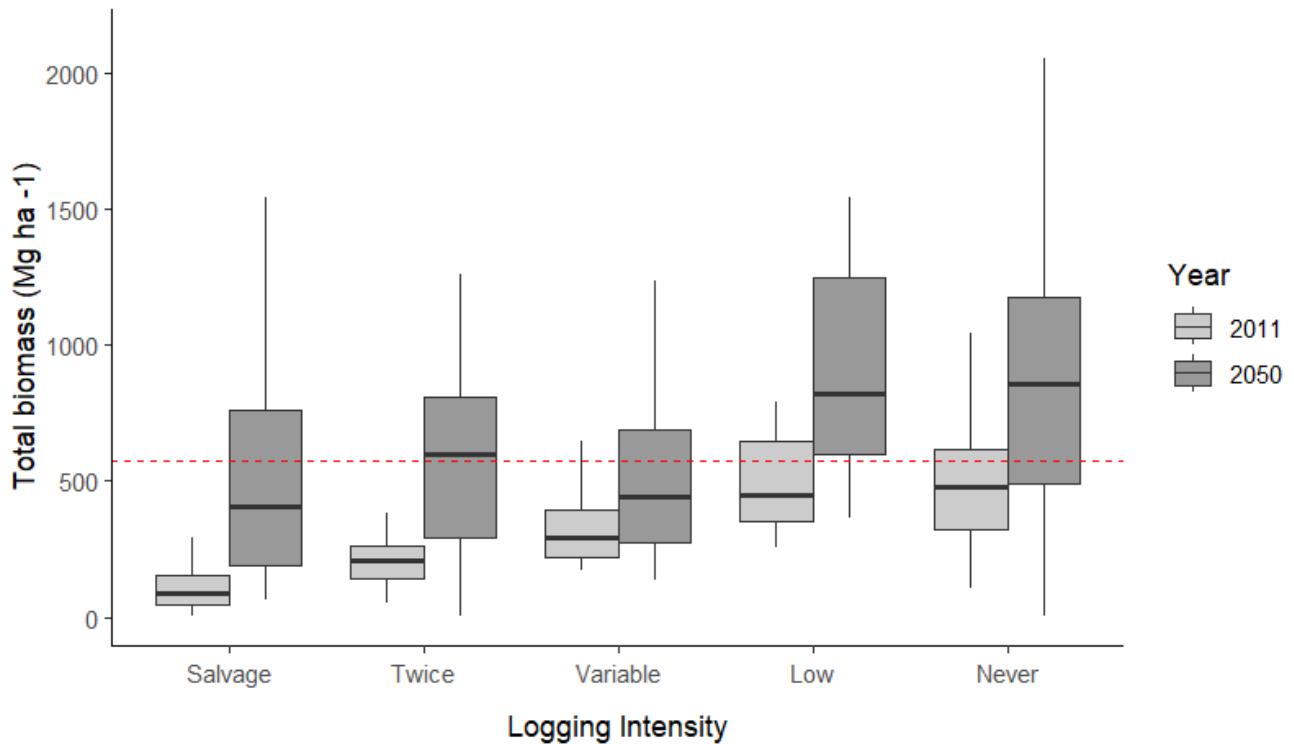


Figure 4) The total woody biomass (above and belowground) of 172 forest plots along a logging gradient from low-quality Salvage logged to pristine Never-logged forest in Sabah. Light grey bars show the measured biomass in 2011, and dark grey shows the simulated values after 40 years of (re)growth. The dashed red line shows the threshold of 577 Mg ha⁻¹ chosen to represent the forest in a natural state with no logging damage.

Of the 165 plots that increased in biomass, less than half (47 %) were projected to reach the threshold of 577 Mg ha⁻¹ by 2050. Regeneration failed in the plots with the lowest starting AGB. Just 35% of Salvage-logged plots were predicted to reach the recovery threshold within this timeframe, compared to 55% in Twice-logged plots (Figure 4). For Salvage-logged areas, plots with a 2011 AGB of below c.90 Mg ha⁻¹ failed to recover. For Twice-logged plots, regeneration failed in plots with a 2011 AGB below c.160 Mg ha⁻¹.

The biomass of plots in 2050 varied significantly with logging intensity (Figure 4). Plots categorised as Variably logged had a 38 % regeneration success rate. 78 % of the Low-logging level plots and 73 % of Never-logged plots exceeded the threshold by 2050. An ANOVA and subsequent Tukey HSD post hoc test showed that the 2050 biomass of Salvage-logged and Twice-logged was significantly different from that of Never-logged forests ($P = < 0.001$ and < 0.05 , respectively).

Our simulation showed a decline in deadwood stocks over time across all logging intensities (Figures S2 and S2). The initial median deadwood biomass in 2011 was: Salvage = 24.8, Twice = 23.34, Variable = 20.6, Low = 29.5, Never = 23.4 Mg ha⁻¹. An ANOVA showed no statistical difference in the starting deadwood between any of the logging intensities ($F(4, 167) = 0.395$, $p = 0.812$). The deadwood

biomass fell rapidly across all logging intensities but began to slowly increase again in the Salvage-logged plots after approximately five years. By 2050, median deadwood biomass stocks were 23.3 Mg ha⁻¹ in Salvage-logged plots and 7.0 Mg ha⁻¹ across all other logging intensities.

4.0) Discussion

In this study, we parameterised models of growth, mortality and recruitment to build a simulation predicting biomass recovery across a range of logged forests. Our results show that while some logged forest plots can recover from logging disturbance within the anticipated timeframe of *c.* 60 years, sites exposed to intensive and repeated extractions will take far longer to regenerate. Approximately 15-20 years after the final rounds of logging, in 2011, Salvage- and Twice-logged plots contained woody biomass significantly lower than their Low- and Never-logged plots, a trend that persisted into 2050 for the Salvage-logged plots. By 2050, the AGB of Twice-logged plots were no longer significantly different from Low-logging intensity plots but were from Never-logged forests. We also found a ‘shifting goalposts’ effect, where predicting recovery of logged forests against the 2011 baselines of primary forests may not be appropriate, as in some cases these ecosystems also appear to be gaining significant amounts of biomass year-on-year. When the change in biomass predicted by our simulation between 2011 and 2050 is averaged over those four decades, the resulting annual mean biomass increase of 8.43 Mg ha⁻¹ yr⁻¹ lies at the upper end of the range presented by other Bornean studies. For logged forests, previously published figures range from 2.8 to 10.5 Mg ha⁻¹ yr⁻¹ (trees > 10 cm) (Lawrence, 2005; Laing et al., 2021; Berry et al., 2010) for unlogged forests, and 0.6 to 9.2 Mg ha⁻¹ yr⁻¹ (Laing et al., 2021; Qie et al., 2017; Berry et al., 2010).

Our predicted regeneration rates show that repeated rounds of salvage logging have degraded these plots to a degree where the majority would fail to regenerate naturally by 2050. The Twice-logged plots fare slightly better, with the median AGB predicted for 2050 (599 Mg ha⁻¹) exceeding the threshold. The difference in timber extraction between these two logging intensities was relatively small (150 vs 179 Mg ha⁻¹), but the frequency of the logging was doubled in the salvage-logged plots. The twice-logged sites endured two rounds with reported extraction rates of 113 then 37 Mg ha⁻¹, whereas the salvage-logged sites went through multiple subsequent rounds (26, 22, 18 Mg ha⁻¹) after the initial 113 Mg ha⁻¹. Double the number of campaigns leads to a greater density of access roads and skid trails, and more opportunities for associated collateral damage, particularly to emergent trees (Struebig et al., 2013). More comprehensive road networks increase habitat fragmentation and the

associated edge effects (Nunes et al., 2021), and also lead to more illegal logging (Kleinschroth & Healey, 2017; Thompson & Magrath, 2021). The Variably-logged forests of the Virgin Jungle Reserve have primarily been exposed to illegal logging, meaning that the extraction rates vary greatly within the class and were not recorded, making comparisons to other areas difficult. They do appear to have been exposed to less degradation than the Twice-logged forest, but more than the Low-logging intensity forests. Though extraction rates in the Low-logging intensity plots at Maliau Basin are not published, they appear to have been sustainable in their amount and methods, allowing more than three quarters of these plots to exceed the threshold by 2050. The 2011 AGB of these low-logging intensity plots (Median = 380.81 Mg ha⁻¹) is comparable to the biomass of once-logged plots in the Ulu-Segama reserve (358.58 Mg ha⁻¹), where 96 - 100 m³ of timber was extracted per hectare (Phua et al., 2016), providing some insight into reasonable extraction estimates at Maliau.

The variation in the fate of the Never-logged control plots is an interesting result of our simulation. The fact that some plots decline over time, with a few crashing completely, is at first glance counter-intuitive to the preconceptions of a ‘pristine’ forest. The level of degradation in the protected VJR makes it possible to believe that perhaps there may have been some unauthorised extraction in Maliau, causing lower-than-expected woody biomass, though a far more likely explanation is natural disturbances. Many of the plots at Maliau Basin are located on extremely steep slopes. These geological features protected the area from becoming a commercially viable logging site, but also leave them vulnerable to landslides and other hazards. These areas also contain some of the largest trees, which make up a significant portion of the very high biomass; trees > 70 cm dbh equate to 22 % of all measured AGB in unlogged plots. When these giants fall, they can cause massive damage to the surrounding area. Natural treefall events can create canopy gaps of up to 360 m² (Ohkubo et al., 2007), approximately half the size of our 25 x 25 m study plots. On steep slopes like those found in Maliau Basin where our control plots are located, many trees can fall at once, compounding this effect. Therefore, large-scale natural mortality events such as windsnap or landslides can decimate the surrounding biomass, bringing it to a level similar to that of logged forest. Despite this, our lowest recorded 2011 biomass for a Never-logged plot (90 Mg ha⁻¹) is still higher than the mean AGB across all salvage-logged plots (85 Mg ha⁻¹). It is also important to note that some of these landslide events have likely been more recent than the final rounds of logging that the Salvage and Twice-logged plots experienced, and therefore, the vegetation has not had as much time to recover.

Extreme variability in biomass also exists at the other end of the scale. In some plots Never-logged, biomass is predicted to increase to around 2,000 Mg ha⁻¹, double that of the highest biomass plot measured in 2011. While these extreme values are most likely an artefact of model parameterisation, discussed in detail below, we first present a couple of alternative theories.

Firstly, we postulate that assuming primary forests currently exist in a state of equilibrium is overly simplistic (Blanc et al., 2009b; McMahon, Parker & Miller, 2010; Fauset et al., 2019; Riutta et al., 2021). These ecosystems are millions of years old (Wilf et al., 2022) and, therefore, may be reacting to the direct and indirect effects of the Anthropocene (McDowell et al., 2020; Flores & Staal, 2022). A pantropical study of forest biomass dynamics (Chave et al., 2008) previously found that nine of their ten ‘undisturbed’ forest plots were exhibiting growth patterns consistent with recovery from past disturbance. Direct human pressures are unlikely to be significant in the Never-logged plots at Maliau Basin, as it was only officially discovered in 1947. Prior to this, the only human disturbance was occasional hunting trips by the local Murut tribe, and this was restricted to the lower slopes in the North (Eco-Business, 2011). Indirect effects of human pressures such as climate change are a more likely candidate for disturbing any equilibrium that may have existed (McMahon, Parker & Miller, 2010; McDowell et al., 2020). As well as differences in average annual temperature and rainfall (Bugmann & Bigler, 2011; Qie et al., 2017; McAlpine et al., 2018; McDowell et al., 2020), more extreme ENSO events (Thirumalai et al., 2017; Rifai, Li & Malhi, 2019) and biodiversity loss can affect forest dynamics (Granados et al., 2017), which can be compounded by more localised direct drivers such as fragmentation and the associated edge effects (Banks-Leite et al., 2020; Nunes et al., 2021). There is also the possibility of carbon fertilisation to be considered (McMahon, Parker & Miller, 2010; Bugmann & Bigler, 2011; Brien et al., 2015; Sterck et al., 2016; McDowell et al., 2020); it remains to be seen whether higher carbon dioxide availability will have a net positive, negative, or neutral effect on forest growth.

The close fit between the plot biomass numbers predicted for 2019 using the average growth model and the observed values for those plots that were censused in 2019 shows that the method is effective in capturing plot dynamics under the present environmental conditions, but modelling beyond 2050 would require the addition of climatic parameters. The most likely explanation for the persistent, extreme growth in the unlogged plots is that the mortality rates are too low. Previous attempts at using individual-based forest models to estimate the rate of absolute biomass loss through mortality

have also failed to find a correlation with plot attributes such as live AGB and productivity (Johnson et al., 2016; Hiltner, Huth & Fischer, 2022).

However, several studies have found a relationship between ecosystem age and mortality (Yu et al., 2022). In early successional systems dominated by pioneers with fast growth and short lifespans, mortality rate (n. per population) is easier to predict as it is driven by biotic factors such as pathogens, competition or herbivory (Esquivel-Muelbert et al., 2020). This could explain the relationship we found between mortality and plot AGB in the Salvage-logged plots. When pioneers are outcompeted, and species composition is mainly hardwoods, the mortality rate (n. individuals per population) falls, and mortality becomes more stochastic and harder to predict (Esquivel-Muelbert et al., 2020). These late-successional trees are more likely to die from abiotic drivers such as lightning strikes and windsnap or windthrow, which are difficult to model (Gora & Esquivel-Muelbert, 2021), hence our inability to define a relationship between AGB and mortality in non-Salvage plots. The late-successional deaths can have the highest influence on total biomass loss due to the sheer size of the trees involved (Blanc et al., 2009b; San-José et al., 2021). Because of the rarity, irregularity and stochasticity of these drivers (Eid & Tuhus, 2001), mortality causes greater variation in biomass flux than differences in growth rates (Blanc et al., 2009b). The eight-year census period used in our study is too short to capture the full extent of rare but catastrophic mortality events that operate on decadal timescales (Knapp, Attinger & Huth, 2022); we recorded just one such event within the census, where approximately 4,000 Mg of trees died between 2011 and 2014 in one of the Low-logging intensity plots due to slope destabilisation. Strong El Niño events increase the likelihood of landslides more likely, and with climate change increasing the frequency and intensity of the ENSO phenomenon, widespread slope destabilisations may become even more frequent in the future (Ohkubo et al., 2007; Douglas, 2022). The growth and mortality models are based on observations from 2011-2019, a climate resembling which is unlikely to persist until 2050. Under all RCP scenarios, Southeast Asia is forecast to suffer an increase in temperature and a decrease in precipitation from a 2013 baseline. Under RCP 8.5, a temperature anomaly of up to 2.45°C is forecast by 2100, exceeding the 2°C level beyond which tree mortality is predicted to be significantly affected (Sterck et al. 2016).

Branchfall is another phenomenon that is difficult to measure in the field due to the density of vegetation cover on the forest floor, high spatial variance, and episodic nature (Wessman, 1992; Clark *et al.*, 2001). Animals can also confuse the measurements, with bearded pigs collecting branches to make nests (Heydon, 1995; Luskin & Ke, 2017). It has been purported that damage to living trees

may contribute half of all biomass loss in tropical forests (Zuleta et al., 2023), while others consider it the largest route of forest biomass loss (Clark et al., 2001a). Our annual branchfall rate of 1.45 Mg ha^{-1} is comparable to that found in Amazonia (1.38 Mg ha^{-1} , Marvin & Asner, 2016), though the overall deadwood production rate was far lower in that study system, (1.53 Mg ha^{-1}) and therefore our branchfall estimates do not make up such a significant proportion (27%) of total deadwood production. Mortality-based approaches frequently underestimate deadwood production (Palace et al., 2012; Rice et al., 2004) but the alternative method of collection of woody debris from the forest floor has also been criticised for providing low estimates of deadwood production (Saner et al., 2012). Again, a long census campaign is required to overcome this temporal variability, with regular survey intervals to capture the deadwood volume before it decomposes.

The 0.25 annual proportional loss of deadwood mass that we found also did not vary with logging intensity, implying that the decay processes in our forest plots are controlled by intrinsic biological factors rather than environmental variables (H  rault et al., 2010). The decay constant of $k = 0.288$ is within the range of values published for tropical forests globally (Palace 2012), but slightly lower than those found in West Malaysia (mean = 0.31, (Yondea, Yoda & Kira, 1977; Kira, 1978). Even considering that the deadwood stocks and production may be an underestimation, it is clear that deadwood is a significant sink of forest carbon, and its decomposition represents a significant source of emissions (Pfeifer et al., 2015). Therefore, it should always be factored into management decisions.

Another limitation of our simulation, possibly contributing to the issues already discussed, is the lack of a mechanism for a plot to switch between growth or mortality models as they progress through the stages of succession. Theoretically, there should be a point at which the Salvage-logged plots reach a certain level of biomass and forest structure that they begin to behave like the Twice-logged plots, and so on. In the same manner, Never-logged control plots that have experienced catastrophic mortality should behave more like logged plots, with fast recruitment and growth, for a time before shifting back to the slower growth trajectory. Limiting the number of years over which we run the simulation reduces the impact of this effect but does not negate it. To investigate regrowth beyond 2050, we would need to define points, perhaps AGB thresholds, at which forest plots switch from one model to another.

Despite these limitations, the overall trend in predicted recovery rates for logged forests is in line with previous estimates from other locations. From studies in South American and African rainforests, it has been hypothesised that it may take 120 years or more for AGB to recover after low-to-moderate

intensity land use (Poorter *et al.*, 2021). That less than half (42 %) of our logged plots that succeed in regenerating after 70 years post-logging would support this long road to recovery for twice-logged plots; for the Salvage-logged plots, it may be even longer, especially when future climatic impacts and switching trajectories are accounted for.

Multiple rounds of logging with cumulative extraction rates of $> 100 \text{ m}^3 \text{ ha}^{-1}$ significantly affect a forest's ability to regenerate within a 60-year timescale. We therefore conclude that degraded forests that have not exceeded a woody AGB of 160 Mg ha^{-1} 20-30 years post-logging are unlikely to regenerate under passive restoration strategies, so alternatives should be considered for these regions. Further growth in these degraded forests is likely to remain very slow, especially where the landscape is highly fragmented and susceptible to climate and disturbance-related mortality. More research is required into the impacts of climate change and carbon fertilisation on mortality and growth to determine whether the trends we have outlined here will persist under changing temperature and rainfall patterns. We also wish to highlight the ability of intact primary forests to continue gaining large amounts of biomass, reinforcing their importance as a carbon sink requiring ongoing protection.

Supplementary Information

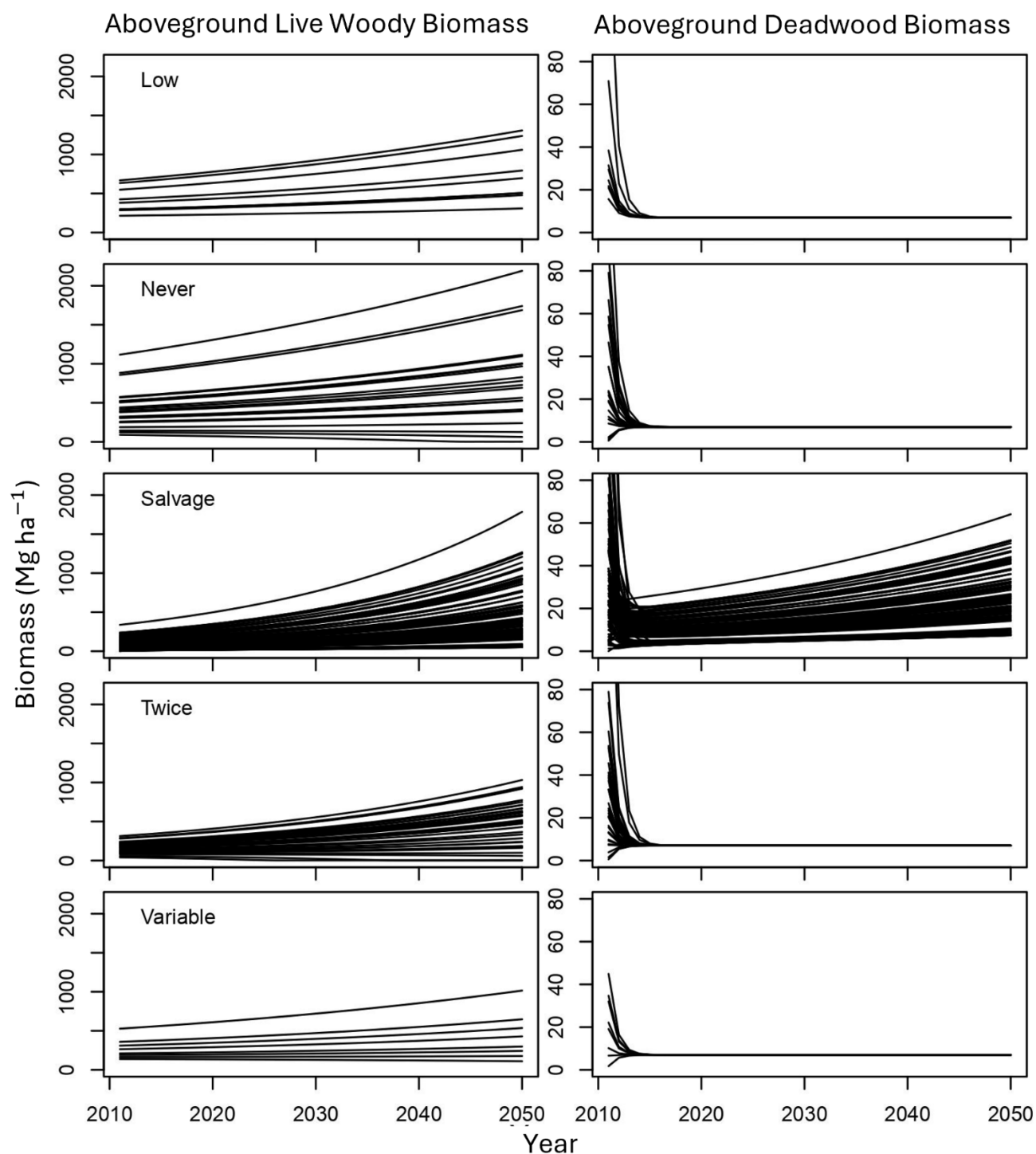


Table S1) Simulated aboveground biomass (left) and deadwood (right) stocks from 2011 to 2050 (in Mg ha⁻¹) of 172 forest plots across a degradation gradient in Sabah. The live AGB simulation accounts for the annual growth of live trees, recruitment, whole-tree mortality, and branchfall. Deadwood includes annual whole-tree mortality and branchfall, decaying at a constant rate (aboveground $K = 0.288$, belowground $K = 0.55$).

Chapter 5) Discussion

The overarching aim of this research was to understand how the above and belowground biomass of logged forests differs from their primary counterparts and how long it takes for them to recover. In Chapter 1, I defined three research objectives.

A) Determine whether the inbuilt LiDAR scanner in iPhone 12 Pro, when used in conjunction with Polycam's LiDAR and Photogrammetry features, can achieve a similar level of resolution as those boasted by more expensive, purpose-built LiDAR technology when capturing tree branching structures.

B) Use a combination of low-cost manual and digital methods to investigate the structure of root systems of seven pioneer *Macaranga* sp. trees in a regenerating logged forest in Malaysian Borneo.

C) Build a simulation to determine the regeneration trajectory for the SAFE project area in Sabah.

In the following paragraphs, I summarise how each chapter has met these objectives.

Key Findings

In Chapter 2, I explored the effectiveness of using an iPhone 12 Pro in conjunction with the Polycam app to capture high-resolution 3D imagery of a leafless tree crown and an excavated root system. I demonstrate that these simple, low-cost methods can produce high-quality point clouds of the branching networks in trees that exist both above and belowground. The Polycam DTP proved more effective than the Polycam LiDAR in producing reconstructions to higher branching orders and showed that the minimum size of branches reconstructed using this method improve upon those previously produced by expensive, cumbersome, purpose-built LiDAR scanners. I trialled TreeQSM as a method to calculate the volume of these 3D reconstructions, however this proved inaccurate when compared to the volume calculated through water displacement methods on the excavated roots. While the methods for calculating volume require further research and development, I show that it is possible to use relatively affordable, common smartphone technology to produce 3D models of tree root systems that can be retained and studied in perpetuity.

In Chapter 3, I used the methods that I trialled in Chapter 2 to create 3D images of the root systems of seven *Macaranga* sp. specimens I excavated from a regenerating logged forest in Borneo. I found that the RSR of these pioneer species is significantly different from that found previously in a large-scale, multi-species experiment in a primary forest in West Malaysia. I show that the partitioning of

this biomass does not vary with tree size within the range covered by our samples, but that maximum rooting depth does significantly increase with diameter at breast height. I found no evidence that branching complexity increased with tree size, surrounding plot AGB, or the steepness of the slope on which the tree grew. I show that the number of roots growing cross-wise to the slope gradient increased with the steepness of the slope, but there was no correlation between the up-and downslope rooting preference with any of the explanatory variables tested. I present the first quantitative evidence of prolific grafting of *Macaranga* tree roots, between roots of the same tree and roots of neighbouring trees. These grafts ranged from superficial to complete inosculation and appeared to be between trees of different species within the same genus.

In Chapter 4, I created a simulation to predict the regeneration of woody biomass in forest plots from c. 30 to 70 years post-logging disturbance. I parameterised the simulation by modelling tree growth, recruitment, mortality, and decomposition using census data for almost 19,000 trees across 172 forest plots spanning a degradation gradient from highly damaged Salvage-logged areas through Twice-logged and Variably logged forests to Lightly logged and Never-logged primary forests. I compared the plot biomass in 2011 across the degradation gradient and projected each plot forward to 2050. I found that in 2011, ‘Salvage logged’ and ‘Twice Logged’ forests contained a significantly lower biomass than their primary counterparts. My simulation predicted that by 2050, less than half of the Salvage-logged plots would recover to a level of biomass comparable with primary forest, and just over half of Twice-logged forests would achieve this level of regeneration. The simulation also predicted significant ongoing biomass gains for most primary forest plots. I used the RSR from Chapter 3 to include belowground biomass in this simulation. These projections provide important insights into forest regeneration which can be used in restoration initiatives to allocate funds in the most time- and cost-effective manner.

Findings in context and suggested future research

Advancing knowledge of root system architecture

In Chapter 2, we showed that it is possible to produce high-resolution, accurate 3D scans of tree root systems using affordable, handheld equipment that is simple to use. The low cost, portability, and lack of specialist training required to use the iPhone 12 Pro and later models in conjunction with the Polycam app make creating 3D scans of root systems far more accessible than using dedicated equipment, especially in remote areas and on limited budgets, making it suitable for the fieldwork undertaken for Chapter 3. While the time and labour required for the excavations remain significant,

we consider that the quantity of data that can be generated from these studies will justify these costs. Accurate 3D scans represent a rich data repository that can be studied for years to come. While we were not able to implement any methods to accurately determine the volume of root systems, any future advances in this field can be retroactively applied to existing root scans, an advantage of collecting root data in a high-quality point cloud format. If, for example, a similar study to that we present in Chapter 3 is completed on *Macaranga* species in primary forest, or on Dipterocarps in logged forest, then the root networks can be compared to the specimens collected in this study, despite the biological samples being long since destroyed.

The mean RSR of 0.22 from our seven sample *Macaranga* trees that we calculated by water displacement in Chapter 3 was significantly higher than the RSR of 0.18 found by Niiyama et al., 2010 from their excavation of 54 trees in a primary forest in the Pasoh Reserve. This highlights the importance of using habitat-specific RSRs to calculate belowground biomass. As Southeast Asia has more degraded forest than primary forest, using incorrect allometric equations could result in huge errors when estimating belowground carbon stores on a large spatial scale. As Niiyama et al. did not measure the dbh of all 54 trees used to calculate their RSR, it was not possible to directly compare a subset of their c. 10-20 cm dbh trees with ours. Instead, we could only compare our RSR to the mean multi-species RSR of all trees 2.5 – 67 cm sampled at Pasoh. The only *Macaranga* sp. included in that study had a dbh of 2.8 cm, further limiting our ability to draw direct comparisons.

While we were unable to get TreeQSM to accurately calculate the volume of the root network in Chapter 2, the frustrations with this package led to the collaborative development of the Node-Joining Algorithm in Chapter 3. We consider the NJA a more appropriate method for modelling the architecture of root systems than Quantitative Structural Models such as TreeQSM. Unlike these existing tools, which are founded in network theory tree topology, the NJA can account for cyclical structures, such as the ones formed by grafted branches. The branching factor that we present using the NJA is a metric representing both bushiness and cycling, rather than forcing the assumption that every node can have only direct parent- an assumption violated by nodes where two roots converge and remain so or diverge beyond the point of inosculation. As such the NJA provides a broader and less assumptive method to digitise and analyse root structures that differ from the models established for tree stems and branches. Our choice to study the network from just three viewpoints (above, and perpendicular sides) was the minimum possible number for the purposes of speed and easy handling. This could be improved by using more viewpoints taken at smaller intervals, such as every 10 degrees

or at each degree up to 360, and then averaging the values. This would require an investigation into a way for CloudCompare to automate the turning and capture of the root system imagery. Alternatively, the NJA could be developed further to work directly on 3D imagery in situations where large data transfer is not a constraint. If time and funds were not so limited, I would also have liked to complete the manual measurements of branch topography to higher branching orders in Chapters 2 and 3, so it could be better compared to the outputs of the NJA.

In Chapter 3, I presented the first quantitative evidence of root grafts for *Macaranga* trees, including self-grafts and inter-tree inoscultations, possibly between different species of the same genus. Two of these inter-tree inoscultations had merged down to the cambium and may have shared vascular tissues. Analysis under a microscope would be able to confirm the level of vascular tissue integration. To determine whether these grafts are truly functional, experiments using radioactive tracers could be implemented after the root systems are excavated but before one or both trees are felled. This kind of experiment would also allow us to determine whether these grafts are parasitic, mutualistic, or opportunistic. For the grafts that appeared to be between trees of different species, it would be possible to use genetic analyses to trace cells to the parent tree and confirm the species of that tree (Schröder & Blanc-Jolivet, 2022), and even investigate the possibility of hybridised chimaera roots (Gaut, Miller & Seymour, 2019). If these grafts do indeed result in the conjoined trees forming a superorganism, then it will have implications for community growth and mortality, and would need to be factored into forest growth models such as the one I parameterised in Chapter 4.

The preference of root directional growth in response to slope also warrants further study, with six out of our seven sample trees showing a clear preference for the majority of roots growing either uphill or downhill. Asymmetrical root growth was also observed in the *Acer pseudoplatanus* in Chapter 2. Though we did not find any correlation between the steepness of the slope and the direction of root growth in Chapter 3, we overlooked the possibility of the location along the slope profile (crest, upper, lower, and toe) in determining this preference. Crown and stem asymmetry have previously been shown to respond to slope inclination (Getzin & Wiegand, 2007; Lang et al., 2010), and in the field, we noted that the dbh of trees of the same species planted at the same time also varied with location along the slope; dbh decreased along a gradient from the bottom of the slope to the top. These relationships could be explained by the increased soil depth and more consistent soil moisture profile under drought conditions at the toe end of the slope (Yanagisawa & Fujita, 1999), though more research is needed. Previous studies, primarily of temperate tree species, have reported preference for

both upslope (Henwood, 1973; Di Iorio et al., 2005) and downslope (Montagnoli et al., 2019, 2020), while still others favour cross-slope growth. It is likely there are many factors at play here, including slope, windloading, nutrients, and hydrology (Wang et al., 2023). Understanding root growth and consequently the success of the whole tree in response to position along the slope profile could have management implications and advise on the best place to plant different species where restoration efforts are focussed on hilly areas, maximising success and reducing landslide risk (Mao et al., 2014; Zhu et al., 2017).

In summary, we encourage more root excavations to further validate root-shoot ratios, specifically for *Macaranga* in gaps of unlogged forests, and the dipterocarps that grow in regenerating forests. We also advise a focussed study on grafting, and the impact of slope on root system architecture.

Growth, recruitment and mortality in Borneo’s forests

In Chapter 4, we showed that approximately 30 years after the latest round of logging, all Salvage and Twice-logged forest plots remain significantly below the threshold of 577 Mg ha⁻¹ indicating a primary forest in good condition, even with the higher investment into belowground biomass calculated using the site-specific RSR from Chapter 3. Our simulation predicts that even by 2050, which exceeds the original 60-year rotation expected for regeneration, 75% of Salvage-logged plots and 45% of twice-logged plots will remain below the baseline.

Improvements could be made to the simulation mechanics by allowing plots to switch between growth trajectories as they recover and by introducing confidence intervals around the parameters. This could be achieved by bootstrapping the models used to parameterise the simulation, or choosing an alternative to *smatr* that supports the generation of confidence intervals, though *smatr* is the most appropriate choice for allometric relationships. To improve the data used to parameterise these models, further research on mortality rates including whole-tree mortality and branchfall would be of benefit. Now that the census campaigns are over, whole-tree mortality would be impossible to review, but intensive branchfall experiments could be completed in nearby forest plots to validate the rates calculated at SAFE. There is a dearth of branchfall data from the tropics, and what exists is accompanied by caveats as to the quality of the survey (Wessman, 1992; Clark et al., 2001a). In Sabah specifically, the density of trees makes it difficult to accurately measure deadwood production, and branches are subject to disturbance by wildlife, such as bearded pigs, *Sus barbatus*, which collect branches and saplings to make nests (Heydon, 1995; Luskin & Ke, 2017). Possibilities for intensive branchfall surveys could include measuring the branch loss from individual trees not by searching for

the dropped branches but by creating 3D scans of the trees as in Chapter 2 and repeating this after a fixed period. The volume of individual branches that are missing from the second scan could be computed from the first scan, providing a reliable estimate of branchfall rates from individual trees. Alternatively, there is the option of using passive acoustic monitoring to detect the sound of trees falling or large branches breaking and provide alerts, as is used to monitor other forms of environmental disturbance (Wrege et al., 2017; Sethi et al., 2020; Cretois, Rosten & Sethi, 2022).

Implications for restoration and management

The propensity of pioneers to form complex root networks with inter-tree grafts on steep slopes that we discussed in Chapter 3 provides some support for following successional trends during restoration activities. In Chapter 4 we highlighted the devastating impacts of landslides on steep slopes in primary forests; colonisation by cooperative communities of pioneers that form stability-enhancing grafts may serve to re-stabilise these slopes before shallow-rooted, larger, heavier trees grow there in the future (Eis, 1972; Basnet et al., 1993; Goldschmidt, 2014). Species like *Macaranga* also demonstrate non-seasonal and continuous flowering, and so provide habitat and food for many generalist pollinator species including stingless bees during the extended periods between Dipterocarp masting years (Sist et al., 2003). Reduction in pollinators has been linked to dipterocarp regeneration failure (Stride et al., 2018; Hayward et al., 2021). Despite this, early successional species such as *Macaranga* are often excluded from planting mixes in enrichment planting schemes, and existing specimens are commonly girdled prior to planting. Research into the value of these early successional species in stabilising slopes and providing food for pollinators is scarce, yet we believe that our evidence of the complex networks that these species can form is enough for regeneration schemes to carefully consider the value in skipping the early successional stages and moving straight to planting slow-growing hardwoods on degraded slopes.

The projections presented in Chapter 4 of this thesis can provide restoration managers with a good idea of how much annual net growth can be expected from logged forests compared to their primary counterparts and how this is projected to continue until 2050. This is a vital resource for restoration initiatives deciding between passive and active regeneration, and in which areas each of these techniques should be applied.

Overall concluding remarks

The research presented in this thesis improves our understanding of how the above and belowground components of forest woody biomass respond to logging pressures and regenerate thereafter. In

particular, it highlights the importance of studying root systems so that information on belowground biomass and root systems architecture can be incorporated into restoration plans and carbon budget calculations. The methods we present for collecting this valuable data are cost-effective and simple to use, which should encourage other researchers and restoration stakeholders to conduct further research into the root systems of regenerating forest trees. The contribution of early successional pioneer species to carbon storage, with their high RSR and propensity to form large networks through root grafts, should not be overlooked. We also show that while some logged forests can recover when left to regenerate naturally, areas that have suffered extremely severe levels of degradation will likely require active interventions if they are ever to resemble their historical counterparts. With all these considerations in mind, we have a better chance of optimising the recovery of degraded tropical rainforest logging estates.

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