# GROWTH RATES AND FUNCTIONAL TRAITS OF TROPICAL RAINFOREST AND SAVANNA SPECIES

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## Summary

Plant growth rates play a crucial role in vegetation dynamics, for example by influencing competitive ability, or the rate of vegetation recovery post disturbance. Plant traits are assumed to underpin variation in growth rates consistently, but most evidence comes from seedlings or closed forest vegetation. Here I aimed to test whether: (1) Trait-growth relationships are the same in adult plants as is known from seedlings; and (2) Trait-growth relationships are consistent across savannas and closed forests.

I used adult growth rate and trait measurements from species in a tropical rainforest in Australia, and three tropical savanna regions (one in Australia, Brazil and South Africa). In all sites I tested clear hypotheses relating to four traits related to carbon gains and losses, namely photosynthetic rate, specific leaf area (SLA), wood density, and the ratio of leaf mass to wood mass on canopy branches. In savannas I also considered bark thickness, which is important for insulation against fire in these fire-prone systems, but assumed to be costly to growth. In tropical forests I further considered whether traits were linked to a species trajectory of growth across its lifetime.

I found evidence that traits were related to adult growth rates in a predictable way in tropical forests, and that variation in trait values was linked to three distinct strategies regarding lifetime growth trajectories. Savannas showed some consistency with forests regarding trait-growth relationships, though the relative importance of traits in each site varied. I attributed differences in trait-growth patterns largely to differences in the prevailing disturbance regime in each savanna. My thesis provides strong evidence that traits have a predictable effect on the growth rates of adult plants, but that generalisations are difficult without an understanding of regional differences in ecology, evolutionary history, and disturbance regimes. These regional differences will have consequences for vegetation response to future changes in climate.

# Candidate declaration

I certify that this thesis entitled ‘Growth rates and functional traits of tropical rainforest and savanna species’ is an original piece of research and has been written by me. The contributions of others have been noted either in the statement of contribution, or in the acknowledgements section. All sources of information and literature used are indicated in the thesis. This thesis has not been previously submitted in any form for a higher degree at any other university or institution.

Emma Fiona Gray

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# Statement of Contribution

I, Emma Fiona Gray, declare that the research contained in this thesis entitled 'Growth rates and functional traits of tropical rainforest and savanna species' is my own work. The contribution of co-authors and data are listed below.

**Chapter 2.** *'Branch-scale leaf:wood mass ratios and tissue traits explain significant variation in stem diameter growth rates of adult trees in a tropical rainforest'*

Ian Wright (Macquarie University) and Daniel Falster (then Macquarie University now University of New South Wales) contributed to the concept development and manuscript preparation. Caroline Lehmann (University of Edinburgh) and Lucas Cernusak (James Cook University) contributed to manuscript preparation. Long term tree measurement data used to calculate growth rates were obtained from Matt Bradford (CSIRO, Atherton) and cleaned by Stuart Allen (Macquarie University). Allyson Eller (Macquarie University) contributed to the collection of leaf photosynthesis data and Daniel Falster collected biomass trait data for 17 species.

Co-authors: Ian Wright, Lucas Cernusak, Caroline Lehmann, Daniel Falster, Matt Bradford and Allyson Eller

**Chapter 3.** *'Do all trees grow similarly? Describing and categorising species growth trajectories and their links to functional traits within a tropical rainforest'*

Ian Wright and Daniel Falster contributed to the concept development and manuscript preparation. Long term tree measurement and trait data were the same as for Chapter 2. Daniel Falster helped to build growth trajectory models.

Co-authors: Ian Wright, Daniel Falster

**Chapter 4.** *'Testing the consistency of links between functional traits and adult stem diameter and height growth rates across three savanna regions'*

Ian Wright, Daniel Falster and Caroline Lehmann contributed to the concept development and manuscript preparation. Tree measurement data used to calculate growth rates in Australian savanna species were obtained from Richard Williams (CSIRO, Darwin) and Brett Murphy (Charles Darwin University). Tree measurement data used to calculate growth rates in Brazilian savanna species were obtained from Giselda Durigan (Assis State

Forest, Forestry Institute of Sao Paulo State, Brazil). Tree measurement data used to calculate growth rates in South African savanna species were obtained from Anthony Swemmer (SAEON Ndlovu Node, Phalaborwa, South Africa). Functional traits of Australian species were measured by Ian Wright and lab members, and Caroline Lehmann.

Co-authors: Ian Wright, Daniel Falster, Caroline Lehmann, Marina Scalon, Giselda Durigan and Anthony Swemmer

**Chapter 5.** *'Relative bark thickness is negatively related to tree growth rates across three biogeographically distinct savannas'*

Ian Wright and Caroline Lehmann contributed to the concept development and manuscript preparation. Tree measurement data were obtained from the same sources as Chapter 4. Bark thickness of Australian species was measured by Wright Lab members including Julia Cooke and Marina Scalon.

Co-authors: Ian Wright, Daniel Falster, Caroline Lehmann, Julia Cooke, Marina Scalon, Giselda Durigan and Anthony Swemmer

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# Chapter 1

General Introduction

# General Introduction

Plant growth rates vary strongly among species, and are crucial in determining their competitive ability (Grime 1977; Westoby et al. 2002). As a result they play a major role in determining vegetation dynamics across landscapes. Morphological and physiological attributes of species (that is, their functional traits) are assumed to underpin variation in their growth rates (Poorter & Remkes 1990; Shipley 2006; Gibert et al. 2016), however empirical evidence of this has been most consistent in experimental studies on seedlings (Poorter & Remkes 1990; Shipley 2006; Gibert et al. 2016). Studies concerning field-grown saplings and adults have found less consistent results (Poorter et al. 2008; Paine et al. 2015; Visser et al. 2016). There are multiple potential reasons for this. Firstly, with respect to traits, as a plant gets larger, the relative proportion of different tissues (such as leaves and wood) changes. As such, the relative cost, as well as the relative benefit, of traits may shift with plant size (Falster et al. 2011; Gibert et al. 2016). In addition, some traits do not remain constant throughout ontogeny (Cornelissen et al. 2003), and growth rates are also rarely constant throughout ontogeny (Lieberman et al. 1985; Clark & Clark 1999). Variability in environmental factors such as rainfall, nutrient availability and disturbance regimes further adds to growth rate variability in different vegetation types (Grime & Hunt 1975; Lambers & Poorter 1992; Prior et al. 2006; Rossatto et al. 2009; Martínez-Vilalta et al. 2010; Murphy et al. 2010). In this thesis I take an inter-species comparative approach, with the aim of understanding the role of functional traits in driving variability in plant growth rates, focusing particularly on adult plants in both tropical forests and savannas.

Plant traits are morphological and physiological attributes of a species which are most often measurable. To be "functional" they should relate to plant ecological strategies and influence a species performance (Grime 1977; Bond 1989; Lambers & Poorter 1992; Reich et al. 1992; Westoby 1998; Lavorel & Garnier 2002; Violle et al. 2007; Reich 2014; Garnier et al. 2016). Species performance could be any aspect of fitness, such as establishment, survival, reproduction, or growth rate (Calow 1987; Ackerly et al. 2000; Reich et al. 2003). In this thesis I focus on growth rates, because they drive landscape productivity and carbon sequestration, and thus an understanding of what drives them is essential in determining how vegetation will respond to, and perhaps mitigate, climate change. Plant growth rates have been considered a key aspect of plant fitness at least since the 1970s, when Grime proposed the existence of three primary growth strategies (Grime 1977). Trade-offs and constraints allow us to understand links between traits and growth rates: what resource investment does a trait represent, and what is the growth benefit of that

investment? Once we know this, we can predict a growth outcome. For example, specific leaf area (SLA) represents the amount of leaf area available per unit mass investment, and so high SLA leaves have a low construction cost per leaf area. As such we might expect high SLA leaves to have fast growth rates, because they cost less to build. On the other hand, while low SLA leaves cost more to construct per area and have a reduced photosynthetic capacity per unit mass, they are (on average) stronger and denser, and live longer, requiring replacement less regularly (Reich 1998; Wright et al. 2004). As such, we might expect that in long-lived species, low SLA leaves might promote fast growth, if resources were scarce. Similar trade-offs exist with respect to all plant organs (Freschet et al. 2010), but in this thesis I focus on leaf and wood traits (Wright et al. 2004; Chave et al. 2009; Baraloto et al. 2010).

This thesis began with one very simple question: 'can functional traits explain significant variation in the growth rates of adult plant species?' This evolved over time to encompass further questions of how observed trait-growth relationships might vary in contrasting vegetation types, or with plant size. Here I introduce each chapter in a chronological sequence, highlighting the thought process underlying the development of each chapter.

**Growth rates and traits of adult tropical forest species**

Evidence suggests that globally, species fall along a continuum of fast – slow resource acquisition and use (Reich 2014). This first became apparent with respect to leaves (Reich et al. 1992; Wright et al. 2004), and was extended to wood (Chave et al. 2009). More recently there has been a suggestion that selection towards a fast or slow trait strategy extends to all organs of a plant (Freschet et al. 2010; Reich 2014), and that all organs converge towards similar strategies (in other words, if a species has 'fast' functioning leaves it should have similarly 'fast' wood, stems and roots). Because a 'fast' trait represents rapid resource acquisition and use, there has been an expectation that a species falling on the fast end of the trait spectrum will have a fast growth rate. As described, this makes intuitive sense when considering SLA: a high SLA species maximises leaf area per unit resource investment in mass, and so should reap the most benefits with regards to carbon gain. Indeed, this has been observed in numerous studies on seedlings (Poorter & Remkes 1990; Lambers & Poorter 1992; Wright & Westoby 1999; Shipley 2006; Gibert et al. 2016). But this prediction fails to consider that as plants get older, they suffer tissue turnover costs, and the leaves of species with traits at the fast end of the spectrum turnover more rapidly. As such, the cost of possessing traits towards the fast end of the spectrum increases, and may result in reduced carbon gain, effectively removing the growth benefit

of fast traits. As a result the fast traits which drive growth in seedlings, may not always continue to do so in adults, which could lead to inconsistent correlations between traits and growth in older plants. The vast majority of studies on plant functional traits and growth rates have only considered seedlings (Poorter & Remkes 1990; Poorter & Lambers 1991; Lambers & Poorter 1992; Walters et al. 1993; Wright & Westoby 1999; Shipley 2006), and indeed, the few that have considered larger plants have found inconsistent results (Gibert et al. 2016). Chapter Two of my thesis is entitled 'Branch-scale leaf:wood mass ratios and tissue traits explain significant variation in stem diameter growth rates of adult trees in a tropical rainforest', and considers trait-growth relationships of adult plant in a tropical forest in Queensland, Australia. I ask whether the trait-growth relationships that are widely observed in seedlings, also hold for adult plants, and test mechanistic predictions for how leaf, wood and biomass traits are related to growth rates of adult plants, based on theory from Pickup et al. (2005) and Gibert et al. (2016).

Throughout this thesis I focus on four functional traits considered to have important consequences for carbon gains and losses in plants. The first, introduced above, is SLA. I also consider light-saturated photosynthetic rate ($A_{area}$), wood density, and leaf mass to wood mass ratios on canopy branches. The decision to focus on these four traits was pragmatic, as well as hypothesis driven. While an ideal study would include all measurable traits, it is time consuming and expensive to sample traits for large numbers of species. Rather than sampling a large number of traits, I chose to focus on sampling key traits from a large number of species across a broad range of environments (as becomes evident in my subsequent chapters).

I chose SLA and $A_{area}$ because they are well understood traits that have been extensively investigated in the seedling literature (Gibert et al. 2016). In addition, I had clear hypotheses for how they should be related to growth rates in adult plants. Rather than expecting a positive relationship between SLA and growth rates, as has often been found for seedlings, I expected no relationship. This was based on theory from Gibert et al. (2016) who suggest that when a tree is large a significant fraction of its total biomass is made up of sapwood. As a result, the marginal cost of building new leaf material may be relatively higher than retaining leaf material with a longer lifespan (low SLA leaves), and as such the perceived growth benefit of high SLA leaves is counteracted (Gibert et al. 2016). In contrast, high $A_{area}$ should always drive faster growth rates, regardless of plants size, because (all else equal) faster photosynthesis increases the rate of biomass production (Gibert et al. 2016). Wood density is one of the few traits that has been widely investigated

in relation to adult growth rates. It has generally been found to be negatively related to growth rates, and I include it here with the same expectation, in order to compare my results to past studies (King et al. 2005; Roque & Fo 2007; Poorter et al. 2010; Wright et al. 2010; Ruger et al. 2012). The fourth trait that I focus on in this thesis is the ratio of leaf to wood on canopy branches. This is a relatively understudied, and potentially very useful, trait. At the whole plant scale more leaf material relative to wood is expected to result in faster growth (Poorter et al. 2012). However, biomass allocation in relation to growth has most often only been considered in seedlings (Shipley 2006), because of the impracticality and destructiveness of its measurement in adults. I test the hypothesis, first proposed by Pickup et al. (2005), that relatively more leaf, sampled only at the branch scale, should result in faster whole plant growth. This thesis represents one of the first tests of the 'branch biomass' hypothesis.

**Species growth rates and traits in savanna vegetation**

Although functional traits are increasingly recognised as important drivers of variation in species growth rates, most of the studies supporting this (including Chapter Two of this thesis) have been restricted to closed tropical forests (Gibert et al. 2016). Chapter Three of this thesis is entitled 'Testing the consistency of links between functional traits and adult stem diameter and height growth rates across three savanna regions'. In this chapter I investigate whether the trait-growth patterns observed in the tropical forest species in Chapter Two are also observed in tropical savanna species. Vegetation dynamics of closed tropical forests have, in general, been far more extensively studied than more open tropical systems such as savannas (Bond & Parr 2010; Parr et al. 2014). This is in large part because savannas were long thought to be anthropogenically 'degraded' versions of tropical forests (Banerjee 1995), and therefore not worthy of extensive study. Savannas are now recognised as alternative stable states to forests in the tropics, with biome boundaries (particularly in mesic regions) maintained by disturbance (Sternberg 2001; Staver et al. 2011). They cover 20% of the earth's land surface, and contribute significantly to the global carbon cycle (Grace et al. 2006). They are also some of the most human-transformed systems, and vulnerable to environmental change (Hoekstra et al. 2005; Sano et al. 2010; Parr et al. 2014; Moncrieff et al. 2016).

Savannas are subject to frequent fires, as well as other forms of disturbance such as herbivory, and thus growth rates are highly variable and unpredictable (Prior et al. 2006; Rossatto et al. 2009; Midgley et al. 2010; Murphy et al. 2010). Growth rates are also likely to vary across biomes as a result of environmental variability in climate and nutrients.

Species from fertile, productive regions tend to have inherently faster growth rates than species from less productive environments, at least in lab-grown seedlings (Grime & Hunt 1975; Lambers & Poorter 1992), and growth rates have been shown to be higher in species from higher rainfall environments (Martínez-Vilalta et al. 2010). Perhaps largely because of the relatively recent ecological interest in savannas, or because of the numerous sources of variability within them, few studies have investigated the nature of trait-growth relationships in savannas (but see Prior et al. 2004; Rossatto et al. 2009; Tomlinson et al. 2014), and none to our knowledge have considered whether they are consistent between field-grown species in different savanna regions, or with those observed in tropical forests. In this chapter I consider growth rates and the previously outlined four functional traits of species in three savanna regions spanning an extensive geographic range; one in Australia, one in Brazil and one in South Africa. These three savannas differ in their prevailing disturbance regimes, and also form a gradient of tree cover, from very open to semi-closed. I ask two primary questions; 1) Are the trait-growth relationships that I observed in forests also observed in savanna systems; and 2) Do the three savanna sites show consistent patterns with respect to growth rates and traits?

**Bark thickness as a crucial functional trait in savanna systems**

In frequently burnt savanna systems, tree species must also invest in thick bark to insulate against fire damage (Hoffmann & Franco 2003; Hoffmann et al. 2009; Keeley et al. 2011; Brando et al. 2012; Dantas & Pausas 2013; Dantas, Batalha, et al. 2013; Pausas 2015). Increased investment in bark is expected to be resource costly and past literature has predicted that investment in thick bark should come at a cost to tree growth rates (Lawes, Adie, et al. 2011; Lawes et al. 2013; Pausas 2015). Despite being widely predicted, this prediction has not been widely tested (indeed, I know of only one study concerning two species that has explicitly tested it: Gignoux et al. 1997). In Chapter Four of this thesis, entitled 'Relative bark thickness is negatively related to tree growth rates across three biogeographically distinct savannas', I consider how growth rates and bark thickness are related across species in three savannas. I also consider tree architecture, which is profoundly influenced by the extent and nature of disturbance within a savanna. Some disturbances (such as frequent fires) favour height growth while other disturbances (such as herbivory) favour investment in diameter growth (Archibald & Bond 2003; Dantas & Pausas 2013; Moncrieff et al. 2014). Bark thickness is tightly linked to tree size, which is tightly linked to growth rates (Falster & Westoby 2005; Wright et al. 2010; Lawes et al. 2013; Hempson et al. 2014). Here I develop a conceptual model to predict how bark thickness will drive growth rates under variable fire regimes, and consider both height and

diameter growth rates, tree architecture, as well as both trunk and canopy bark thickness. This study represents the first empirical evidence of the relationship between bark thickness and growth rates across three distinct savanna regions and multiple species.

**Methods of species growth rate estimation**

So far I have repeatedly referred to 'species growth rates', by which I have meant a single parameter, namely either the annual stem diameter or height increment, of a species. This parameter is based on measures from multiple individual plants within that species. In Chapter Two, which considers tropical forest species, I use the 95$^{th}$ percentile diameter growth rate of individuals within a species. I use this as an estimate of a species 'potential' growth rate, as many expectations of trait-growth relationships are based on growth at optimal conditions (Wright et al. 2010). I am advantaged because the nature of a tropical forest (namely, that tree densities are extremely high) means that the dataset contains thousands of individual trees, and thus significant replication such that a 95$^{th}$ percentile is a sufficiently robust measure. In contrast, in the savanna-focused chapters, I use the mean rather than upper percentiles of species growth rates. This is because the savanna tree measurement dataset is much less replicated than the tropical forest dataset, largely as a result of tree densities in savannas being much lower than in forests. Because the dataset contains very few replicate individuals per species, the mean is a far more robust estimate of a species growth rate.

The low level of replication in growth rate datasets is a recurring theme in this thesis. One of the major results of having such low replication is that species selection is driven largely by replication, because growth rates can only be calculated for species with sufficient individual measurements. This was particularly relevant in the savanna dataset. However, despite the low level of replication in the savanna dataset, it has one important advantage over the forest dataset. The smaller stature of trees in savannas, and the lack of canopy overlap, mean that height is easier to measure than in tropical forests, and it is more accurately done. As such, in the two savanna chapters I am able to consider both height and diameter growth rates, as well as tree architecture, which is expected to be tightly linked to growth rates (Archibald & Bond 2003; Dantas & Pausas 2013; Moncrieff et al. 2014).

**Ontogenetic variation in species growth rates**

While a single estimate of a species growth rate allows us to test simple predictions surrounding relationships between traits and growth rates, this is perhaps an oversimplification, because a plant's growth rate is not constant throughout ontogeny

(Clark & Clark 1999; Hérault et al. 2011). I attempt to address this issue in Chapter Five of this thesis, which is entitled 'Do all trees grow similarly? Describing and categorising species growth trajectories and their links to functional traits within a tropical rainforest'. Ecologists in the past have dealt with issues of ontogenetic variation in growth rates in various ways. Many consider growth rates as a function of size, in other words relative growth rates (Hoffmann & Franco 2003; Muller-Landau 2004; Mencuccini et al. 2005; Poorter et al. 2008; Iida, Kohyama, et al. 2014). Some have separated trees into size classes and estimated growth rates only within these size classes (Clark & Clark 1999; Wright et al. 2010; Lasky et al. 2015). Foresters have long grappled with this problem, with a need to identify large species likely to achieve maximum size quickly (Oldeman & Van Dijk 1991), as well as model sustainable harvesting levels (Vanclay 1989). This requires a predictive understanding of species growth rates at all ages, or more simply, an understanding of the shape of their growth trajectories (Vanclay 1989; Jogiste 2000; Rozendaal et al. 2010). Foresters and ecologists alike have established that different species exhibit different shaped trajectories of size over time (Lieberman et al. 1985; Vanclay 1989), and as a result have aimed to describe growth throughout ontogeny using more than one parameter (Lieberman & Lieberman 1985; Vanclay 1994; Rozendaal et al. 2010; Falster et al. 2011; Hérault et al. 2011). While foresters have traditionally focused on a few economically important species, ecologists have further developed their methods with the goal of understanding the dynamics of highly-speciose systems such as tropical rainforests. What drives species to exhibit different growth trajectory shapes? For example, some species might invest in fast growth when they are small, but then reduce their growth rate as adult plants (Species A in Figure 1). Another species might exhibit a similar shaped trajectory, but reach a higher maximum growth rate, and be a larger tree overall (Species B). Other species might be slow growing as seedlings but increase their growth rate as adults (Species C), while yet another species might maintain a constant growth rate throughout its life (Species D).

What becomes apparent when considering the possible trajectories in Figure 1 is that a species' growth rate is likely to vary significantly depending on the size or age at which it is estimated, and that the ranking of different species with respect to growth rates might not remain constant throughout ontogeny either. As such, a study considering trait-growth relationships of larger plants might find considerably different results depending on the size at which trees are sampled, or the method used to estimate growth rates. While my earlier chapters consider how traits influence a static measure of growth rate, this final data chapter considers that a species' growth trajectory, as well as its ability to modulate its growth over

its lifetime, should be linked to functional traits. In this chapter I model the growth trajectories of tropical forest tree species using three parameters: maximum growth rate, diameter at maximum growth rate, and ontogenetic variability in growth rate. I ask whether species can be clustered according to these parameter values, and if so, whether these clusters are patterned with respect to plant functional traits.

**Conclusion**

My thesis represents a chronological development of my thought process as I set out to address two clear gaps in the literature surrounding species growth rates. Firstly, it considers the issue of whether trait-growth relationships are consistent in adults and seedlings. Secondly, it considers species growth rates in savanna vegetation, whether they vary across different savanna systems, and whether trait-growth relationships in these environments are consistent with those expected in tropical forests. The fourth and fifth chapters of this thesis represent lines of thought that evolved naturally from these two main themes. Firstly, because of their high levels of disturbance, are there other, more important, traits driving growth rates in savannas, and secondly, can we describe species growth rates using one parameter, or must we consider the entire growth trajectory? My thesis is presented as an introduction, followed by four data chapters with a short discussion chapter at the end. As described, each chapter, apart from the general discussion, follows the format of a stand-alone manuscript, and focuses on one or more of the above-mentioned aspects of species growth rates and traits. In the final Chapter Six (General Discussion) I integrate the main findings of all data chapters, discuss these findings in relation to the relevant literature, and point to future areas of research which could usefully contribute to our understanding of species growth rates and their relation to functional traits.

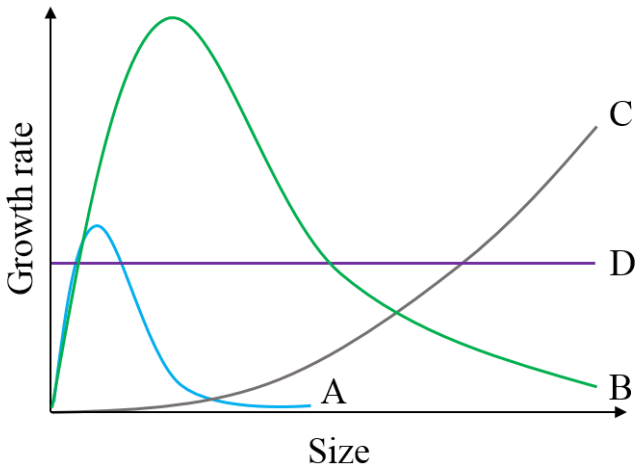


**Figure 1** Examples of growth trajectories of hypothetical species A, B, C, and D

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# Chapter 2

## Branch-scale leaf:wood mass ratios and tissue traits explain significant variation in stem diameter growth rates of adult trees in a tropical rainforest

# Abstract

Woody plant growth rates affect ecosystem productivity, yet what determines interspecific variation in growth rates remains a pivotal and unresolved question in ecology. Functional traits are considered to underpin growth rate variation but most consistent evidence for this has been observed in seedlings. Here we consider how trait-growth rate relationships in adult plants should be expected to differ from those commonly observed in seedlings.

We quantified relationships between stem diameter growth rates and functional traits of adult woody plants for 41 species in an Australian tropical rainforest. Key predictions included that: 1) Photosynthetic rate would be positively related to stem diameter growth rate; 2) Specific leaf area (SLA) would be unrelated to stem diameter growth rate (unlike in seedlings); 3) Wood density would be negatively related to stem diameter growth rate; and, 4) Leaf mass:sapwood mass ratios (LM:SM) in branches would be positively related to stem diameter growth rate.

All our predictions found support, particularly those for photosynthetic rate, wood density and LM:SM. SLA was in fact negatively related to stem diameter growth rates – a greater departure from the typical relationship observed in seedlings than was predicted. Branch LM:SM was most strongly related to stem diameter growth rates. Bivariate and multivariate analyses revealed strong correlation structure among most measured traits, but SLA, wood density and branch LM:SM each explained independent variation in stem diameter growth rates (together accounting for 52 % variation).

Our findings illustrate that in in adult plants, low SLA species can achieve faster diameter growth rates than high SLA species. We showed for the first time that branch-scale LM:SM ratios are strongly related to stem diameter growth rates. A linear combination of a leaf trait (SLA), a wood trait (wood density), and branch-scale LM:SM explain most variation in growth rates, and appear to act independently of each other. Our results provide strong evidence that trait variation influences adult plant growth rates, but highlight the importance of covariance between traits, which can influence both the direction and extent to which traits drive growth.

# Introduction

Terrestrial primary productivity is a key factor controlling rates of land-atmosphere $CO_2$ exchange (Beer et al. 2010). Tropical forests account for 34% of global terrestrial primary productivity, a disproportionate percentage considering they cover 7-10% of the global land surface (Lewis et al. 2009; Beer et al. 2010). Plant growth rates influence ecosystem productivity, yet the most important drivers of interspecific variation in plant growth rates remain contested (Poorter et al. 2008; Wright et al. 2010; Hérault et al. 2011; van der Sande et al. 2015).

Functional traits are morphological and physiological properties of plants that underpin variation in plant function and influence plant performance (Westoby et al. 2002; Adler et al. 2014). Two spectra of variation in leaf and wood functional traits organise species along a continuum of low to high tissue construction costs (Wright et al. 2004; Chave et al. 2009). In the case of leaves, the benefit of high specific leaf area (SLA, mass construction costs per unit leaf area) trades off against high tissue turnover rates (shorter leaf lifespans) (Reich 1998; Wright et al. 2004). For wood, the benefit of low tissue construction costs (low wood density) trades off against high whole-plant mortality rates (Chave et al. 2009; Wright et al. 2010). In general there is an expectation that low tissue construction costs should promote fast growth rates (for example Grime & Hunt 1975; Poorter & Remkes 1990; Garnier 1992; Lambers & Poorter 1992; Wright & Westoby 2001).

In seedlings this idea has found strong empirical support, particularly when considering leaf traits. Species with high SLA, high leaf nitrogen and phosphorus content, or fast photosynthetic rates, generally have faster seedling relative growth rates, at least when grown under high-resource conditions (i.e. ample light, water and nutrients; Lambers & Poorter 1992; Poorter & van der Werf 1998; Shipley 2006). However, studies examining saplings and adult plants have generally not found strong relationships between field-measured growth rates and traits, and especially not with SLA (Coomes & Grubb 1998; Poorter et al. 2008; Aiba & Nakashizuka 2009; Wright et al. 2010; Hérault et al. 2011; Ruger et al. 2012; Paine et al. 2015). These inconsistencies have led an increasing number of researchers to conclude that those leaf traits considered to be important drivers of seedling growth rates may not be important drivers of adult growth rates (Wright et al. 2010; Paine et al. 2015). Recent studies have suggested that these inconsistencies emerge because for certain traits the strength and direction of the correlation with growth rate can change systematically as plants increase in size (Falster et al. 2011; Ruger et al. 2012; Iida,

Kohyama, et al. 2014).

Leaf and wood tissue traits are unlikely to operate independently, and a means of relating these spectra is through consideration of the costs and benefits associated with the allocation of tissues to leaf or wood. In large plants, the relative amount of different tissues, rather than the tissue traits themselves, may have a decisive influence on growth rates. However, measuring total biomass allocation in large plants is generally impractical. Pickup et al. (2005) suggest that the relative costs of deploying new leaf area will be evident even at the branch scale. They predicted that, all else being equal, species with relatively more leaf mass per unit wood mass sampled at the branch scale should achieve faster whole-plant growth rates.

The majority of studies on seedling trait-growth relationships consider the linear relationship between a species mean trait value, and a maximum potential growth rate (Shipley 2006; Gibert et al. 2016). Here we adopt a similar approach, but consider only adult plants, and test predictions for how commonly studied leaf and wood tissue traits, as well as branch scale leaf:wood ratios, should influence adult stem diameter growth rates. Our expectations are outlined below, and summarised in Table 1. Traits were selected either for their comparability with seedling literature, or because we had clear hypotheses for how they should drive growth rates.

*Leaf tissue traits*

We investigate three hypotheses related to leaf tissue traits. Firstly, regardless of plant size, higher light-saturated photosynthetic rate ($A_{area}$) should (all else being equal) drive faster growth rates, because faster photosynthesis increases the rate of biomass production (Gibert et al. 2016). Secondly, higher leaf N and leaf P contents should be associated with faster growth rates. This prediction is based on the premise that higher leaf N and P should lead to higher photosynthetic rates (Domingues et al. 2010) and are generally indicative of a 'faster' metabolic strategy (Reich 2014). Thirdly, because of the large stature of our study plants we expect that SLA and stem diameter growth rate should be unrelated, or perhaps negatively related (Gibert et al. 2016). In seedlings, where leaves make up a large fraction of total biomass, and leaf turnover is minimal, higher SLA should lead directly to higher plant growth rate because higher SLA connotes low per-area leaf construction costs. However, at increasingly larger plant sizes two effects are capable of counteracting the positive effect of high SLA and even generating an opposite trend: (i) Higher SLA leaves need to be replaced more frequently (they have shorter leaf lifespans) than lower SLA

leaves, and so could ultimately be more costly across a plants entire lifetime; (ii) Whole plant sapwood mass becomes a sufficiently large fraction of total biomass that the marginal cost of building sapwood to support new leaf area negates any potential growth benefits from higher SLA. That is, as plant size increases, the effect of SLA on growth rates (whether considered in terms of height, diameter or mass) diminishes and should shift from positive to unrelated, and possibly even to negative when trees are very large, or contain a very large amount of sapwood relative to leaf area (Falster et al. 2011; Gibert et al. 2016). We note that a similar prediction was made in much earlier work, based on the idea that species with longer leaf lifespans can over time generate more massive canopies than short leaf lifespan species, and thus achieve similar above-ground net productivity (Matyssek 1986; Bond 1989; Gower et al. 1993).

**Table 1** Predicted relationships between adult stem diameter growth rates and key leaf and wood traits, as well as branch scale leaf:wood ratios

| Trait | Units | Definition | Expected relationship |
|---|---|---|---|
| **Leaf Traits** | | | |
| SLA | $cm^2\ g^{-1}$ | Specific Leaf Area, one-sided leaf area per unit dry mass | Unrelated |
| $A_{area}$ | $\mu mol\ m^{-2}\ s^{-1}$ | Light-saturated photosynthetic rate, area basis | Positive |
| $N_{area}$ and $P_{area}$ | $g\ cm^{-2}$ | Leaf nitrogen and phosphoros content, area basis | Positive |
| **Wood traits** | | | |
| Branch WD | $g\ cm^{-3}$ | Wood density of the sapwood in a terminal branch | Negative |
| Trunk WD | $g\ cm^{-3}$ | Wood density of the main stem | Negative |
| **Branch leaf:wood ratios** | | | |
| LM:SM | $g\ g^{-1}$ | Ratio of leaf mass to sapwood mass on a terminal branch | Positive |
| LA:SM | $cm^2\ g^{-1}$ | Ratio of leaf area to sapwood mass on a terminal branch | Positive |

*Wood tissue traits*

Wood density should be negatively related to stem diameter growth rates (Enquist et al. 1999; Roque & Fo 2007; Poorter et al. 2008; Poorter et al. 2010; Wright et al. 2010; Hérault et al. 2011; Gibert et al. 2016), because high wood density has a high construction cost (Hacke et al. 2000; Chave et al. 2009). Gibert et al. (2016) predicted that the strength of this negative correlation should be greatest in adults, because they typically have more sapwood mass (on a whole-plant basis) per unit of leaf area.

*Branch-scale leaf:wood ratios*

As outlined above, we expect the relative costs of deploying new leaf area to be evident at the branch scale. All else being equal, species with relatively more leaf material on outer canopy branches should have faster growth rates, and those with relatively more wood should have slower growth rates (Pickup et al. 2005).

In addition to testing the individual trait-growth predictions outlined above we investigate how traits vary in relation to each other, and how traits influence growth rates in combination.

# Methods

### Growth data

Stem diameter increment data were obtained from twenty 0.5 ha permanent plots in tropical rainforest in northern Queensland, Australia, located between 145° 04' E to 145° 50' E and 16° 08' S to 18° 30' S. Plots were established between 1971 and 1980 to provide long-term ecological and growth data (Bradford et al. 2014). The plots range in mean annual rainfall from 1200 to 3500 mm, and in elevation from 15 to 1200 m above sea level. Besides minor selective logging on two plots, all plots have been protected since their establishment. The dataset comprises over 10 700 individual trees, with 481 species. To estimate growth rates reliably, it is necessary to have a sufficient number of individuals measured within a species. For this reason, we focused on 41 species based on their abundance in the dataset. Of these 24 were chosen because they were the most abundant in the dataset (diameter increments were measured on at least 100 individuals); the remaining 17 species were selected because their traits had been measured previously by Falster & Westoby (2005). These 17 species had associated diameter increment data from a minimum of 57 individuals per species, and so were also relatively abundant. The vast spatial extent covered by the measurement plots makes it likely that the species that we observed to be most abundant in the dataset are representative of the most abundant species in the wider landscape.

For all species, individuals greater than or equal to 10 cm diameter at breast height (dbh) were measured every two years for a minimum of ten years after establishment (until 1990). After 1990, re-measurements were generally carried out every five years. We used all of these measurements to calculate the annual diameter growth increment of each individual using the formula $GR = (dbh_{final} - dbh_{init})/ (y_{final} - y_{init})$ where GR is annual absolute diameter growth increment, $dbh_{init}$ and $dbh_{final}$ are diameter at breast height of individuals at

the initial and final measurement dates respectively, and $y_{init}$ and $y_{final}$ are the initial and final years of measurement respectively. Before calculating annual diameter increments we removed unreasonable measurements. We considered unreasonable measurements to be those where dbh seemingly decreased > 5% over the census period, a common practise when cleaning permanent plot growth datasets (Condit et al. 1993). This resulted in deletion of just 91 records from a total of 24 521.

So as to make our study comparable to seedling trait-growth studies, we used these annual diameter increments for each individual to estimate a single parameter species level growth rate. Tropical rainforests are characterised by low understory light levels, with many individuals suppressed beneath the canopy. Because most growth-trait trade-off predictions concern growth rates when resource availability is high (Wright et al. 2010), we chose to estimate species-level potential diameter growth rates at a standard higher percentile of realised values (i.e. potential near-maximum diameter growth rate). Specifically, we used the 95$^{th}$ percentile of the annual diameter increment across all individuals of each species (hereafter referred to as $GR_{95}$), as it can be considered as being close to the maximum attainable growth rate for that species (following Wright et al. 2010). For comparison, we also ran analyses using mean diameter growth rates ($GR_{mean}$) as well as 95$^{th}$ percentiles of diameter increments across individuals within a restricted size class (10-30 cm dbh), hereafter referred to as $GR_{10\text{-}30}$.

## Trait Data

*Leaf traits*

Leaf trait data for all 41 species were collected in and around Danbulla State Forest in far northern Queensland (situated at approximately 17°07’30”S and 145°37’30”E, within the area encompassed by the permanent plots) in October 2013 and May 2014. All leaf trait measurements were made on outer canopy leaves to reduce any variation due to light environment. For three to eight adult individuals of each species (Table S2) we measured $A_{area}$, individual leaf mass, individual leaf area and leaf nutrient concentrations. Photosynthesis measurements were made under ambient $CO_2$ concentrations (approx. 400 mg $l^{-1}$) and temperature (25–27°C), and high light (2000 µmol $m^{-2}$ $s^{-1}$), using a Li-Cor 6400XT portable infrared gas analyser (LICOR Inc., Lincoln, NE, USA). VPD ranged between 0.61 kPa and 1.94 kPa for our measurements. Three leaves from each individual were scanned and leaf area calculated using ImageJ software (U. S. National Institutes of Health, Bethesda, Maryland, USA). Leaves were oven dried at 60-70°C for at least five days and reweighed to determine dry mass. SLA was calculated by dividing leaf area by

dry mass. Leaf nutrient analyses were performed at the Appleton Laboratory (University of Queensland). Leaf nitrogen concentration was determined by combustion using a LECO TruSpec CHN analyser. Leaf samples were digested in acid and total P concentration was determined by inductively coupled plasma optical emission spectrometry (ICP-OES). Leaf $N_{area}$ and $P_{area}$ were calculated from these data and SLA.

*Trunk wood density*

Trunk wood density (hereafter referred to as trunk WD) for all species was sourced from published (Cause et al. 1989; Hyland 1989) and from unpublished data (M. Bradford), collected previously within the study area.

*Leaf:wood ratios and branch sapwood density*

We measured leaf:wood ratios on terminal, outer-canopy branches. For the 24 species sampled during the 2013-2014 field campaigns, leaf:wood ratios were measured for at least five individuals from each species. Total leaf mass and wood mass were measured for stem segments at 0-5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-80 cm and 80-100 cm from the tip, including biomass on any side branches extending from a segment. Fruit and flowers were generally absent, but when present they were discarded to allow direct comparison of leaf and wood material. Branch diameter was measured at each of the separation points. Leaf:wood ratios for the remaining 17 species were sampled by Falster & Westoby (2005). In that study they measured the mass of leaves and wood between the tip of the branch and the first node, and between this node and 100 cm, including all side branches. Branch diameter was measured at the node, and at 100 cm. For further information see Falster & Westoby (2005).

For samples of branch materials, we measured or calculated the following metrics: 1) leaf mass (LM), 2) leaf area (LA), 3) wood mass (WM), 4) sapwood mass (SM), 5) Leaf mass to wood mass ratio (LM:WM), 6) Leaf area to wood mass ratio (LA:WM), 7) Leaf mass to sapwood mass ratio (LM:SM), and 8) Leaf area to sapwood mass ratio (LA:SM). Leaf area was determined by multiplying the total leaf mass by SLA. We sampled leaves and wood only on the terminal 100 cm of branches, as these showed little evidence of leaf turnover. Nevertheless, the leaves present at the time of measurement could potentially result from leaf accumulation minus leaf turnover. As such, we refer to these metrics as leaf:wood ratios rather than leaf:wood allocation.

There is no established standard way to sample branch-scale leaf:wood ratios across a range of species, with support for sampling at a common distance (e.g. Falster et al. 2005), a

common cross sectional area (e.g. Pickup et al 2005), and at the first node along a terminal branch (eg. Westoby & Wright 2003). We chose not to sample ratios at the first node because variance components analysis using the *ape* and *nlme* packages in R showed that most of the variance in LM:WM when sampled at the first node was within species (68%) rather than between species. At a common distance of 100 cm along the branch most of the variance in LM:WM was observed between species (67%). This suggests leaf:wood ratios at a common distance are a more stable species-level trait than ratios at the first node. Because our data came from two separate field campaigns (and branches were sampled slightly differently), we were unable to use raw data at each sampling point. Instead, we estimated leaf:wood ratios at a common distance of 100 cm, as well as a common cross-sectional area of 100 $mm^2$ by interpolating between adjacent sampled points. For each species the branch cross-sectional area of each individual at each separation point was plotted against leaf and wood metrics (both axes were log-transformed), and leaf:wood ratios were estimated at 100 $mm^2$ using the resultant regression equations. Similarly, ratios were estimated at a common distance of 100 cm. Species were discarded if the branch cross-sectional area of 100 $mm^2$ fell outside the range of sampled cross sectional areas.

Branch sapwood density for all species was measured by removing a small section of branch approximately 10 mm in diameter and 40 mm in length, and measuring fresh volumes of the bark and sapwood by water displacement. Pith and bark were removed and branch sapwood density (hereafter referred to as branch WD) was determined by dividing dry sapwood mass by fresh sapwood volume. In addition the relative proportions of sapwood, bark and pith were calculated. This proportion was assumed to be approximately constant along the entirety of the branch section for subsequent analyses, and sapwood mass (SM) was estimated by multiplying wood mass by this proportion.

**Data analysis**

All statistical analyses were performed in R (R Development Core Team 2015). Any strongly right-skewed traits were log transformed; this was the case for growth data, SLA, $N_{area}$, $P_{area}$, and all branch leaf:wood ratios. Normality of variables was confirmed using Shapiro-Wilk test for normality. For those variables that still appeared non-normal, we plotted the residuals of the linear regressions to ensure there were no major deviances from normality or homoscedasticity. Variance components analysis using the *ape* and *nlme* packages in R showed that more of the variance in SLA, $N_{area}$, $P_{area}$, LM:WM (at 100 cm) and branch WD was found between rather than within species. For $A_{area}$, variance was split equally within- and between species.

Analysis of the data was a two-part process. Firstly, we aimed to test the clear hypotheses laid out in Table 1 in a manner comparable to studies undertaken on seedlings. For this purpose, we used linear regressions to quantify the explanatory power of individual traits for growth rates, as well as the slope of the relationship. Secondly, also of interest is which traits (singularly or in combination) can be used to capture the most variation in growth rates. To determine this, it was first necessary to understand the covariance structure in trait data. To this end, we used pearson correlation and principal components analysis (PCA). PCA was run in the 'prcomp' function from the *stats* package in R. Throughout, relationships are considered significant at $p < 0.05$, but marginal significance is also noted, when $0.05 < p < 0.1$. From our trait correlations and PCA we selected those traits explaining the major axes of trait variation, and used forward stepwise regression using the *leaps* package ('regsubsets' function) to construct models to explain growth rate variation. Here we used the Bayesian Information Criterion to select the most parsimonious model. The Bayesian Information Criterion estimates goodness of fit using maximum log-likelihood, and penalises a model for increased number of parameters (Hooten & Hobbs 2015).

# Results

Species-level growth rate estimates are reported in Table S1, species mean tissue traits are reported in Table S2, and leaf:wood ratios in Table S3 and Table S4. $GR_{95}$ varied 9-fold between species, from 0.2 to 1.85 cm $yr^{-1}$ (Table S1). Here we report only results relating to $GR_{95}$, as species measures of the three different growth estimates were strongly correlated (all $r > 0.90$, $p < 0.0001$, Fig. S1). SLA varied *ca.* five-fold among species, from 40.2 to 196.2 $cm^2\ g^{-1}$ (Table S2). Branch WD varied the least among species (less than 3-fold, from 0.28 to 0.74 g $cm^{-3}$). Branch scale leaf and wood distribution traits showed the most variation among species, and of these total wood (including bark) mass estimated at 100 $mm^2$ cross sectional area was the most variable, ranging nearly 40-fold from 1.9 g to 74.3 g (Table S4).

All predictions regarding the direction in which traits should be related to growth rates found some support (Table S5). As expected, $A_{area}$ was positively related to $GR_{95}$, albeit only weakly ($R^2 = 0.095$, $p = 0.05$; Fig. 1a). Both $P_{area}$ ($R^2 = 0.22$, $p = 0.002$) and $N_{area}$ ($R^2 = 0.19$, $p = 0.004$) were more strongly and positively related to $GR_{95}$ (Figs 1b,c). SLA was negatively related to $GR_{95}$ ($R^2 = 0.21$, $p = 0.002$; Fig. 1d). Although removing the apparent outlier with very high $P_{area}$ in Fig. 1b (*Acronychia acidula*) increased the $R^2$ of that

relationship from 0.22 to 0.33, we retained that data point in our analyses because we were confident that it was not erroneous (it was the mean of five similar replicate values, Table S2).

We observed the expected negative relationship between trunk WD and $GR_{95}$ ($R^2 = 0.17$, $p = 0.007$; Fig. 2a). Branch WD showed a similar trend, though it was weaker and only marginally significant ($R^2 = 0.09$, $p = 0.054$; Table S5). Branch WD was positively related to trunk WD ($R^2 = 0.43$; Fig. 2b).

The ratio of branch leaf mass to branch sapwood mass (LM:SM, analogous to a benefit:cost ratio) explained the most variation in $GR_{95}$ of all biomass traits, and was positively related to $GR_{95}$ both at a standard distance ($R^2 = 0.27$, $p < 0.001$; Fig. 3a) and at a standard branch cross sectional area ($R^2 = 0.34$, $p < 0.0001$; Fig. 3c). That is, a relatively higher biomass allocation to leaf mass was consistently correlated with faster growth rate.

When branch-scale leaf mass was converted to total leaf area (via SLA), branch-scale leaf area:wood mass ratios explained markedly less variation in $GR_{95}$. The difference was more pronounced when data were expressed at a common distance (Fig. 3b) than at a common cross-sectional area (Fig. 3d). In either case, the lower explanatory power presumably resulted from multiplying through by SLA, since $GR_{95}$ and SLA were negatively correlated; or, equally, from other trait-trait relationships.

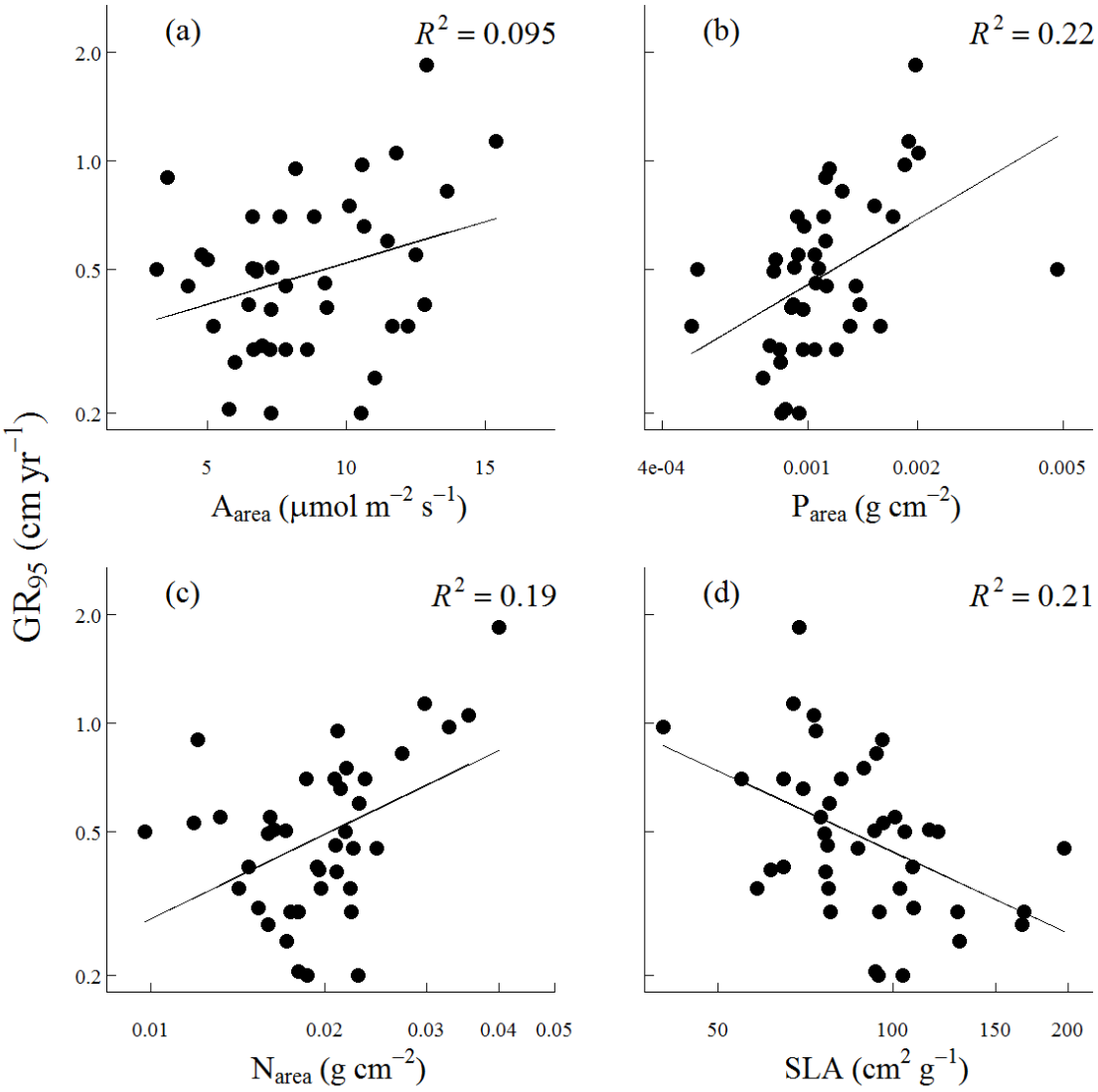


**Figure 1** Linear regression relationships between $GR_{95}$ and a) $A_{area}$; b) $P_{area}$; c) $N_{area}$; and d) SLA. All variables except for $A_{area}$ were log transformed. All relationships were statistically significant, $p \leq 0.05$ (Table S5). Relationships are for 41 tropical rainforest species (species details provided in supplementary information).

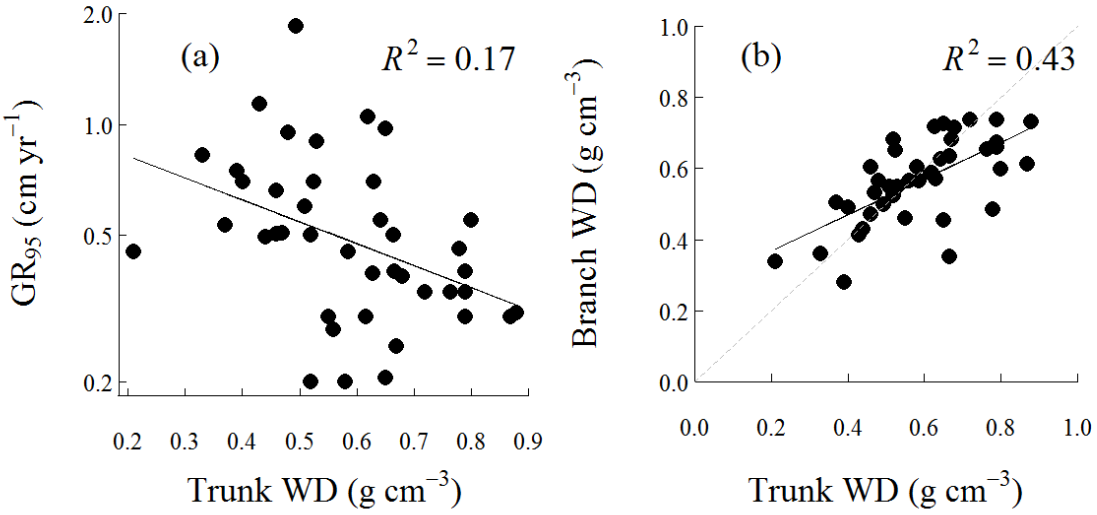


**Figure 2** Linear regression relationships between (a) $GR_{95}$ and trunk wood density; and (b) branch and trunk wood density (for comparison the 1:1 line is also shown). Only $GR_{95}$ was log transformed. Relationships are for 41 tropical rainforest species (species details provided in supplementary information).

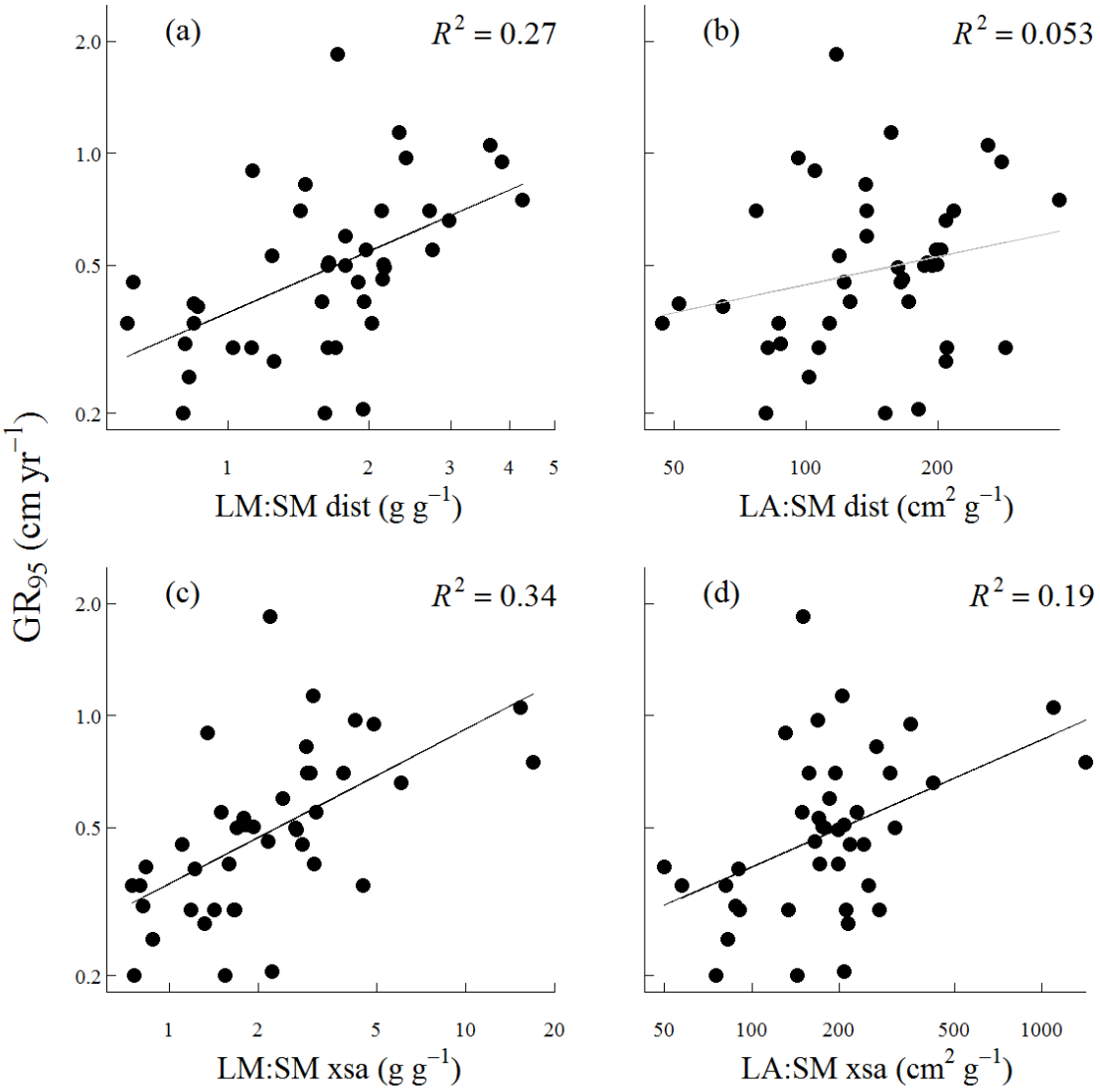


**Figure 3** Linear regression relationships between $GR_{95}$ and leaf:sapwood ratios expressed at a standard distance of 100 cm from the branch tip (a-b) and a standard cross-sectional area (xsa) of 100 $mm^2$ (c-d). Biomass ratios are leaf mass per sapwood mass at (a) 100 $mm^2$ branch cross-sectional area (LM:SM xsa); and (c) a distance of 100 cm from branch tip (LM:SM dist); and leaf area per sapwood mass at (b) 100 cm from branch tip (LA:SM dist); and 100 $mm^2$ branch cross-sectional area (LA:SM xsa). All variables were $log_{10}$ transformed. Black trend lines indicate significant regression relationships, grey lines show non-significant relationships (p-values reported in Table S5). Relationships are for 41 tropical rainforest species (species details provided in supplementary information).

The second part of our analysis aimed to estimate trait covariation, and determine whether multi-trait models could better explain variation in growth rates. As such we aimed to identify traits which were uncorrelated, and thus captured the major axes of trait variation. Table S6 reports correlation coefficients between traits. All leaf tissue traits were significantly correlated with each other (except SLA and $P_{area}$, which were only marginally significantly correlated), while wood density was not significantly correlated with any traits (Table S6).

We then explored the multivariate correlation structure among traits with a PCA fitted to species-mean data for SLA, $A_{area}$, $N_{area}$ , $P_{area}$ , LM:SM (at a standard cross-sectional area) and trunk WD. The first principal axis (PC 1; 47.3 % of variation; Fig. 4, Table S7) represented correlated variation in leaf physiology ($A_{area}$, $N_{area}$ and $P_{area}$ ) and LM:SM (all negatively), and also SLA (positively, and somewhat more weakly than the other traits). The position of species along PC 1 was negatively correlated to $GR_{95}$, and more strongly than any individual trait ($R^2 = 0.39$, Fig. S2a). The second principal component (19.5% of variation; Fig. 4) represented variation in trunk WD (positively) and SLA (negatively) and was not significantly related to $GR_{95}$ (Fig. S2b). The third axis (13.2% variation) represented residual variation in all traits and explained 10% of variation in $GR_{95}$ (Fig. S2c). Considering both the axis loadings of the PCA (Table S7), as well as the trait-trait correlations (Table S6) in combination, we observe that SLA, trunk WD and LM:SM all explained independent trait variation. On the other hand $A_{area}$, $N_{area}$ and $P_{area}$ were all highly correlated, and did not differentiate along any of the PC axes, except for a slight positive loading by $A_{area}$ on PC 2. As such, we retained only $A_{area}$ from these three traits for the stepwise regression.

Stepwise regression of SLA, $A_{area}$, trunk WD, and LM:SM against $GR_{95}$ indicated that a model including SLA, trunk WD and LM:SM was the most parsimonious (lowest Bayesian Information Criterion; Table 2). This model explained 51% of variation in $GR_{95}$ ($p < 0.0001$). Consistent with the bivariate results the coefficients in this model were positive for LM:SM and negative for SLA and WD. Each trait contributed approximately similar explanatory power to the model (as judged by their *t*-values having similar magnitude; Table 2).

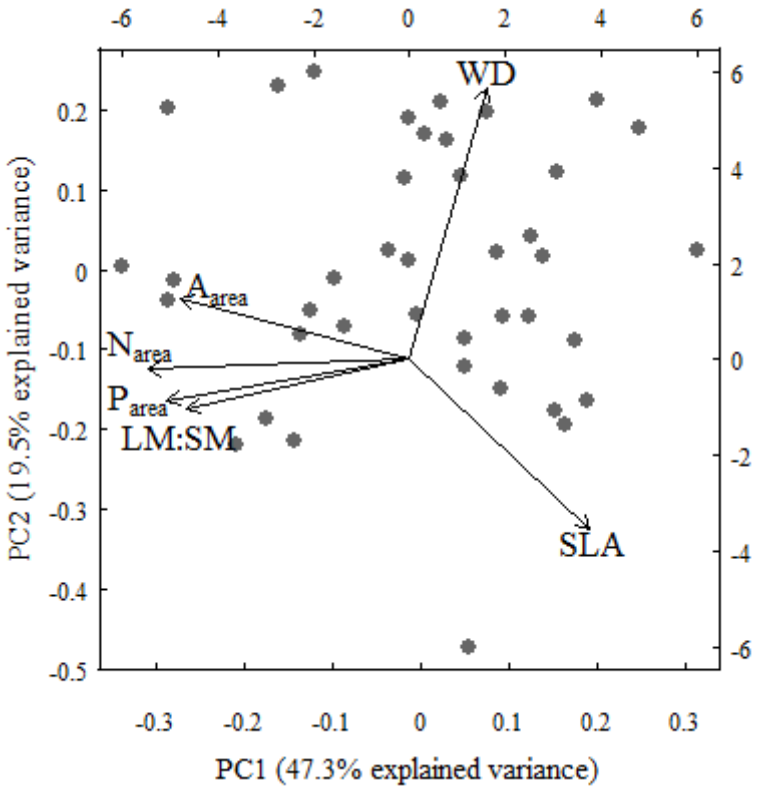


**Figure 4** A principal components analysis (PCA) showing the two main axes of variability in traits amongst 41 rainforest species. Traits are log-transformed specific leaf area (SLA), log-transformed light-saturated photosynthetic rate ($A_{area}$), log-transformed leaf nitrogen ($N_{area}$), log-transformed leaf phosphorus ($P_{area}$), trunk wood density (WD) and log-transformed branch-scale ratio of leaf mass:sapwood mass estimated at a standard branch cross sectional area of 100mm$^2$ (LM:SM). Each data point represents a species mean. PCA axis 1 and 2 account for 66.7% of the variation in the data. Length of vectors represent the contribution of a trait to the ordination.

**Table 2** Results of the best multiple regression model to predict $GR_{95}$, identified using forward stepwise regression. Full model included all traits (using LM:SM estimated at a standard cross-sectional area) and had a BIC of -11.9. Stepwise reduced model had a BIC of -20.5 and an $R^2$ of 0.52, and included just SLA, WD and LM:SM

| Model terms | Coefficient | t | p |
|---|---|---|---|
| Intercept | 1.15 | 2.39 | 0.02 |
| log (SLA) | -0.63 | 2.27 | 0.006 |
| WD | -0.55 | -2.89 | 0.004 |
| log (LM:SM) | 0.22 | -3.04 | 0.03 |

We used the 95th percentiles of species growth rates as our preferred growth measure, operating under the assumption that the influence of traits would be strongest in plants which were growing under more favourable conditions (Wright et al. 2010). As it turned out, all growth estimates were highly correlated (Fig. S1), and our key predictions held regardless of the growth measure used (Table S5). In general, the strength of relationships were slightly weaker when $GR_{mean}$ or $GR_{10\text{-}30}$ were used, although notably in the case of SLA the relationship was stronger with both of these alternative growth measures.

# Discussion

To date, the majority of investigations of trait-growth relationships in plants have focused on seedlings, as seen in existing data compilations and meta analyses (Lambers et al. 1990; Poorter & van der Werf 1998; Shipley 2006; Poorter et al. 2009; Gibert et al. 2016). The relatively few studies that have considered sapling or adult plants have found conflicting results, with some finding similar patterns to those observed for seedlings (Wright et al. 2010; Iida, Kohyama, et al. 2014) and others not (Poorter et al. 2008; Gibert et al. 2016; Visser et al. 2016). Presumably, this is partly because stem diameter growth rates are not necessarily constant throughout ontogeny (Clark & Clark 1999; Hérault et al. 2011), and some traits also shift predictably with plant size and age (Cornelissen et al. 2003; Price et al. 2014). Trait-growth relationships may therefore also shift across ontogeny, but whether this is generally the case is unclear. In addition, if predictable shifts do occur, the mechanisms responsible are unclear. Here, based on cost-benefit considerations from Gibert et al (2016) and Pickup et al (2005), we predicted the nature of individual trait-growth relationships in adult plants, finding some support for all of our predictions (Table 1). Stepwise regression further supported these findings, highlighting that SLA, trunk WD and LM:SM each explained independent variation in $GR_{95}$, and together accounted for 52% of its variation. Here we touch on all aspects of our results, but focus on three particularly

striking results: the negative relationship between SLA and $GR_{95}$, the strong positive relationship between branch-scale LM:SM and $GR_{95}$, and the combined effects of traits on $GR_{95}$.

*Specific leaf area*

High SLA generally translates into fast growth in seedlings grown under non-limiting conditions (Lambers & Poorter 1992; Shipley 2006) but a growing body of literature suggests that this pattern rarely holds in adult plants (Poorter et al. 2008; Aiba & Nakashizuka 2009; Wright et al. 2010; Hérault et al. 2011; Iida, Kohyama, et al. 2014; Gibert et al. 2016; Visser et al. 2016). SLA is considered an important trait because while leaf construction costs per gram of dry mass vary relatively little among species (Poorter & De Jong 1999), SLA varies far more widely, and so should generally index variation in construction costs per unit leaf area. However, as pointed out by Reich (Reich et al. 1992; Gower et al. 1993; Reich 1998) and others (Matyssek 1986; Bond 1989) it is also important to consider how leaf lifespan varies with SLA. Specifically, low SLA species with very long leaf lifespans have the potential to, over time, build more massive canopies than high SLA species, and this may lead to total canopy productivity at least as high as that of high SLA species, despite the lower physiological rates per unit leaf mass.

Gibert et al. (2016), and before that Falster et al. (2011), took this line of reasoning further, providing a mathematical formulation for understanding how SLA-growth relationships may change with plant size. The trade-off between SLA and leaf lifespan is crucial to their argument, but importantly it also considers sapwood costs per unit leaf area at a whole-plant scale, which appear to be the decisive cost that varies with plant size. On the basis of their predictions we expected that there would be no relationship between growth rate and SLA, or perhaps – due to the large size of trees in our study area – that we would observe a negative relationship. Indeed, we observed a convincing negative relationship. We know of only one previous study showing a negative relationship between SLA and adult growth rate (Poorter et al. 2008; where growth was expressed as RGR), though in that instance the authors questioned the validity of this negative relationship. Considering that it was also undertaken in rainforest vegetation containing very large trees, with hindsight the negative relationship may well have been valid.

*Leaf:wood ratios*

In general, branch biomass traits were more strongly related to $GR_{95}$ than were tissue traits. In particular, of all traits LM:SM was most strongly related to $GR_{95}$, and this was the case

for ratios expressed at a standard distance from the branch tip (100 cm, Fig. 3a) or at a given cross sectional area (100 $mm^2$; Fig. 3c). This positive relationship between branch-level leaf:wood ratios and growth rate was predicted by Pickup et al. (2005), but to our knowledge this is the first reported test of the proposition. Pickup et al. (2005) arrived at this prediction by analogy with seedling growth equations, which most commonly decompose RGR into the product of SLA, leaf mass fraction (ratio of leaf mass to plant mass) and net assimilation rate (rate of mass increase per unit leaf area). By definition, an increase in any one of these factors must result in a proportional increase in RGR, unless the effect is counteracted by negative covariance between other terms in the equation (Wright & Westoby 2001). Pickup et al. (2005) argued that leaf mass fraction could also be considered at branch-scale, and that species with higher branch-level leaf mass fraction would either show faster RGR at the branch-scale, and/or export more photosynthate to the rest of the plant. Our results here accord with this interpretation, and we suggest that branch-scale leaf:sapwood mass ratios could usefully be considered in future studies on trait-growth relationships.

We were uncertain about how to express biomass ratios, and so used both a distance-based and a cross sectional area-based standardisation. Cross-sectional area-based ratios in general explained more variation in $GR_{95}$ than did the various distance-based ratios (Table S5). Why was this so? One possibility is that, when expressed at a standard cross-sectional area, branch-scale total leaf mass and total sapwood mass contain more independent information from one another: they are not correlated (Fig. S3, $R^2 = 0.014$). By contrast, expressed at a standard distance, branch-scale total leaf mass and total sapwood mass scale closely together ($R^2 = 0.6$; Fig. S3). Further investigation would be needed to verify this interpretation and, indeed, we see both methods of sampling as having their respective merits.

Relationships between growth rates and biomass ratios were weaker when containing a leaf area component than a leaf mass component (Fig. 3). Similarly, Walters et al. (1993) found that leaf mass based parameters were better at explaining growth rate variation than leaf area based parameters. They attributed this to the negative covariance between key traits. We draw a parallel conclusion here: the negative relationship between growth rate and SLA likely reduced the explanatory power of leaf area:sapwood ratios for growth rate, compared to that of leaf mass:sapwood ratios. That said, LM:SM and SLA were themselves negatively correlated (Table S6), which likely promoted the observed negative relationship between SLA and $GR_{95}$ and, equally, the positive relationship between LM:SM and $GR_{95}$.

Clearly, it is not a straightforward matter to disentangle the many cross-correlations between interacting functional traits, and their effects on plant growth rates (Poorter et al. 2015).

*Trait interactions and complementary explanatory power for growth rates*

Despite all of our individual trait – growth predictions finding some support in the data, most of the relationships were fairly weak, most notably the relationship between $GR_{95}$ and $A_{area}$. The relationship between $GR_{95}$ and trunk WD ($R^2 = 0.17$) was weaker than in some studies (King et al. 2006; Roque & Fo 2007; Osunkoya et al. 2007; Poorter et al. 2008; Wright et al. 2010), but stronger than others (Russo et al. 2010; Fan et al. 2012). Fairly low explanatory power for whole-plant growth rates should perhaps not be surprising (Paine et al. 2015). One reason may be that negative covariance between traits weakens their individual relationships to growth rate. For example, $A_{area}$ and SLA were negatively correlated (Table S6) which, because of the negative $GR_{95}$ – SLA relationship, would tend to counteract the otherwise positive effect of higher $A_{area}$ on growth rates. In support of this explanation, the negative covariance between SLA and both of $P_{area}$ and $N_{area}$ was not as strong as that between SLA and $A_{area}$, which might explain why they were more tightly related to $GR_{95}$ than was $A_{area}$.

But what of traits in multivariate space? The stepwise regression results showed that trunk WD, LM:SM and SLA each explained important, independent variation in $GR_{95}$ – and all to about the same extent (similar t values), totalling > 50% explanatory power for $GR_{95}$. Faster growth rates corresponded to higher LM:SM, lower WD and lower SLA. Because of the strong correlation structure among measured traits (bivariate: Table S6; multivariate: Fig. 4), presumably in this regression model the effects of $A_{area}$, $N_{area}$ and $P_{area}$ were tied up in both the LM:SM and SLA effects. That is, each of these three traits was negatively correlated with SLA, and positively correlated with LM:SM. By contrast, both the PCA and bivariate correlation results indicated that the trunk WD effect on growth rate was substantially independent from the effects of other traits.

*Growth rate measures*

Our hypotheses were based around higher percentile growth rates ($GR_{95}$) because much of the theory focuses on growth rates when resource availability is high (Wright et al. 2010). However, we did compare these results with those using mean diameter growth estimates ($GR_{mean}$), as well as diameter growth rates estimated within a restricted size class ($GR_{10\text{-}30}$). One possible reason for discrepancies between seedling and adult studies is that the former

usually consider growth on a whole-plant mass basis, and the latter in terms of stem increments or, more rarely, height increments. Interestingly, in the model of Gibert et al. (2016), for many of the traits they consider (including SLA, WD and $A_{area}$), the same trait-growth predictions are made irrespective of the measure of growth – including whether or not growth is relativised by initial mass (or height, or stem diameter); i.e. as relative growth rate, RGR. We considered diameter-based, absolute growth rates of adult plants. Our patterns were generally consistent regardless of which diameter growth rate measure we considered. In general, $GR_{95}$ was better explained by traits than were the other measures of growth rate ($GR_{mean}$ and $GR_{10\text{-}30}$). However, the slopes of the relationships were similar when considering $GR_{mean}$ as well as $GR_{10\text{-}30}$. The only notable exception was SLA, which explained more variation in both $GR_{mean}$ and $GR_{10\text{-}30}$, than it did in $GR_{95}$. Why this might be remains unclear.

**Conclusion**

An increasing number of studies have concluded that key trait-growth relationships are not always (or not often) the same in adult plants as in seedlings (Wright et al. 2010; Paine et al. 2015; Gibert et al. 2016; Visser et al. 2016). Our study provides strong support for the idea that covariance between traits influences both the direction and extent to which traits drive growth, and also that the relative importance of traits will shift with an increase in total sapwood mass per leaf area (Gibert et al. 2016). Of particular interest in our results was that leaf:sapwood mass ratios measured simply at the branch level explained the most variation in stem diameter growth rates, suggesting that this easy-to-measure property should be included in future studies. We also found a convincing negative relationship between SLA and $GR_{95}$, a result which is well explained by theory (Gibert et al. 2016), despite being opposite to that generally observed in seedlings (Lambers & Poorter 1992; Poorter & van der Werf 1998; Shipley 2006). A multiple regression model including a leaf trait (SLA), a wood trait (trunk WD) and a biomass trait (LM:SM) was the best model of $GR_{95}$. In this study, species were selected based on their dominance within the growth dataset (to ensure adequate replication), and thus we did not consider any effects that phylogeny might have on these relationships. It is uncertain whether phylogenetic relatedness would have any effect on the relationships we found (Felsenstein 1985; Westoby et al. 1995), and this would be a worthy topic of future investigation. Future investigations could also usefully consider how trait-growth relationships might vary among habitats that differ in the maximum size of the canopy trees, to further test the effects of proportional total biomass allocation to sapwood.

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# Supplementary Information

***Table S1*** *Species estimates for the three growth rate measures, namely 95$^{th}$ percentile of all individuals ($GR_{95}$), mean growth rate of all individuals ($GR_{mean}$), and the 95$^{th}$ percentile of of all individuals between 10cm and 30 cm in diameter ($G_{10-30}$).*

| **Species** | **Family** | **$GR_{95}$ (n)** | **$GR_{mean}$ (± SD)** | **$GR_{10-30}$ (n)** |
|---|---|---|---|---|
| | | cm yr$^{-1}$ | cm yr$^{-1}$ | cm yr$^{-1}$ |
| *Alstonia muelleriana* | Apocynaceae | 0.25 (669) | 0.09 (± 0.11) | 0.25 (620) |
| *Alstonia scholaris* | Apocynaceae | 0.82 (111) | 0.31 (± 0.55) | 0.48 (54) |
| *Agathis robusta* | Araucariaceae | 0.70 (296) | 0.31 (± 0.22) | 0.80 (97) |
| *Daphnandra repandula* | Atherospermataceae | 0.28 (474) | 0.07 (± 0.12) | 0.30 (408) |
| *Gillbeea adenopetala* | Cunoniaceae | 0.49 (83) | 0.20 (± 0.61) | 0.50 (72) |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 0.35 (582) | 0.12 (± 0.61) | 0.35 (502) |
| *Pullea stutzeri* | Cunoniaceae | 0.50 (284) | 0.17 (± 0.61) | 0.50 (233) |
| *Aleurites rockinghamensis* | Euphorbiaceae | 0.75 (195) | 0.27 (± 0.37) | 0.42 (72) |
| *Cleistanthus myrianthus* | Euphorbiaceae | 0.30 (159) | 0.10 (± 0.12) | 0.30 (158) |
| *Cleistanthus semiopacus* | Euphorbiaceae | 0.31 (1313) | 0.12 (± 0.11) | 0.33 (1075) |
| *Croton insularis* | Euphorbiaceae | 0.35 (407) | 0.14 (± 0.11) | 0.35 (399) |
| *Rockinghamia angustifolia* | Euphorbiaceae | 0.21 (672) | 0.06 (± 0.61) | 0.21 (661) |
| *Acacia celsa* | Fabaceae | 1.85 (703) | 0.65 (± 0.61) | 1.80 (340) |
| *Castanospora alphandii* | Fabaceae | 0.45 (214) | 0.15 (± 0.18) | 0.35 (150) |
| *Homalium circumpinnatum* | Flacourtiaceae | 0.39 (294) | 0.15 (± 0.61) | 0.31 (248) |
| *Cinnamomum laubatii* | Lauraceae | 0.51 (254) | 0.16 (± 0.21) | 0.32 (154) |
| *Cryptocarya mackinnoniana* | Lauraceae | 0.35 (906) | 0.12 (± 0.13) | 0.35 (779) |
| *Cryptocarya murrayi* | Lauraceae | 0.40 (189) | 0.14 (± 0.15) | 0.40 (168) |
| *Endiandra leptodendron* | Lauraceae | 0.30 (208) | 0.10 (± 0.12) | 0.30 (200) |
| *Endiandra monothyra* | Lauraceae | 0.55 (323) | 0.12 (± 0.20) | 0.50 (270) |
| *Litsea leefeana* | Lauraceae | 0.60 (571) | 0.20 (± 0.61) | 0.65 (332) |
| *Neolitsea dealbata* | Lauraceae | 0.40 (68) | 0.15 (± 0.61) | 0.41 (57) |
| *Argyrodendron peralatum* | Malvaceae | 0.98 (121) | 0.40 (± 0.37) | 0.83 (38) |
| *Franciscodendron laurifolium* | Malvaceae | 0.53 (3325) | 0.19 (± 0.61) | 0.45 (2257) |
| *Tetrasynandra laxiflora* | Monimiaceae | 0.30 (518) | 0.07 (± 0.61) | 0.25 (255) |
| *Myristica insipida* | Myristicaceae | 0.50 (975) | 0.16 (± 0.61) | 0.55 (774) |
| *Gossia hillii* | Myrtaceae | 0.39 (365) | 0.18 (± 0.61) | 0.39 (365) |
| *Syzygium sayeri* | Myrtaceae | 0.46 (57) | 0.21 (± 0.61) | 0.19 (25) |
| *Cardwellia sublimis* | Proteaceae | 0.66 (613) | 0.22 (± 0.21) | 0.70 (372) |
| *Darlingia darlingiana* | Proteaceae | 0.55 (565) | 0.14 (± 0.17) | 0.55 (402) |
| *Alphitonia petriei* | Rhamnaceae | 1.14 (87) | 0.40 (± 0.33) | 1.35 (31) |
| *Alphitonia whitei* | Rhamnaceae | 0.70 (666) | 0.23 (± 0.22) | 0.70 (466) |
| *Acronychia acidula* | Rutaceae | 0.50 (310) | 0.19 (± 0.18) | 0.48 (282) |
| *Acronychia laevis* | Rutaceae | 0.20 (934) | 0.06 (± 0.09) | 0.20 (934) |
| *Brombya platynema* | Rutaceae | 0.20 (2087) | 0.06 (± 0.08) | 0.20 (2087) |
| *Dinosperma erythrococcum* | Rutaceae | 0.30 (686) | 0.14 (± 0.09) | 0.30 (628) |
| *Flindersia bourjotiana* | Rutaceae | 0.70 (1577) | 0.26 (± 0.61) | 0.60 (880) |
| *Flindersia brayleyana* | Rutaceae | 0.95 (520) | 0.32 (± 0.61) | 0.59 (183) |
| *Flindersia pimenteliana* | Rutaceae | 0.90 (743) | 0.37 (± 0.61) | 0.86 (356) |
| *Castanospermum australe* | Sapindaceae | 1.05 (300) | 0.31 (± 0.48) | 1.06 (158) |
| *Dendrocnide photinophylla* | Urticaceae | 0.45 (803) | 0.10 (± 0.17) | 0.37 (566) |
| **Mean** | | **0.55** | **0.19** | **0.49** |
| **Minimum** | | **0.20** | **0.06** | **0.2** |
| **Maximum** | | **1.85** | **0.65** | **1.8** |

***Table S2*** *Species estimates for mean tissue trait values (with standard deviation, and number of replicates, in brackets). Mean trunk diameter of individuals sampled for traits is also indicated. Trunk wood density (Trunk WD) does not have an associated standard deviation and samples size as these values are taken from the literature.*

| **Species** | **Family** | **$A_{area}$ (SD, n)** µmol $m^{-2}$ $s^{-1}$ | **$N_{area}$ (SD, n)** g $cm^{-2}$ | **$P_{area}$ (SD, n)** g $cm^{-2}$ | **SLA (SD, n)** $cm^2$ $g^{-1}$ | **Branch WD (SD, n)** g $cm^{-3}$ | **Trunk WD** g $cm^{-3}$ | **Trunk Diameter (SD, n)** cm |
|---|---|---|---|---|---|---|---|---|
| *Alstonia muelleriana* | Apocynaceae | 11.04 (2.74, 7) | 0.017 (0.0009, 5) | 0.0008 (0.00009, 5) | 129.95 (46.23, 7) | 0.68 (0.047, 5) | 0.67 | 13.0 (1.94, 6) |
| *Alstonia scholaris* | Apocynaceae | 13.64 (1.28, 4) | 0.027 (0.0012, 5) | 0.0012 (0.00012, 5) | 93.34 (3.97, 3) | 0.36 (0.026, 3) | 0.33 | NA |
| *Agathis robusta* | Araucariaceae | 6.63 (3.49, 13) | 0.023 (0.0021, 5) | 0.0017 (0.00030, 5) | 54.69 (9.18, 7) | 0.49 (0.054, 7) | 0.40 | 30.5 (4.47, 9) |
| *Daphnandra repandula* | Atherospermataceae | 5.99 (0.85, 6) | 0.016 (0.0005, 5) | 0.0008 (0.00013, 5) | 166.35 (14.11, 6) | 0.56 (0.193, 4) | 0.56 | 16.6 (2.77, 5) |
| *Gillbeea adenopetala* | Cunoniaceae | 6.77 (1.11, 5) | 0.016 (0.0018, 5) | 0.0008 (0.00009, 5) | 75.98 (13.42, 3) | 0.43 (0.049, 3) | 0.44 | NA |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 5.23 (1.65, 6) | 0.014 (0.0009, 5) | 0.0005 (0.00014, 5) | 77.35 (8.78, 6) | 0.74 (0.043, 6) | 0.72 | 16.1 (1.99, 6) |
| *Pullea stutzeri* | Cunoniaceae | 3.17 (1.88, 6) | 0.010 (0.0004, 5) | 0.0005 (0.00008, 5) | 104.76 (12.24, 6) | 0.63 (0.126, 5) | 0.67 | 15.2 (1.75, 6) |
| *Aleurites rockinghamensis* | Euphorbiaceae | 10.11 (3.01, 6) | 0.022 (0.0016, 5) | 0.0015 (0.00016, 5) | 88.93 (6.88, 3) | 0.28 (0.035, 3) | 0.39 | 10.2 (1.69, 3) |
| *Cleistanthus myrianthus* | Euphorbiaceae | 7.81 (2.03, 5) | 0.018 (0.0013, 5) | 0.0010 (0.00010, 5) | 128.88 (13.71, 3) | 0.59 (0.003 3) | 0.62 | NA |
| *Cleistanthus semiopacus* | Euphorbiaceae | 6.99 (1.29, 8) | 0.015 (0.0005, 5) | 0.0008 (0.00007, 5) | 108.13 (6.07, 6) | 0.73 (0.242, 6) | 0.88 | 20.3 (1.95, 9) |
| *Croton insularis* | Euphorbiaceae | 11.67 (1.91, 6) | 0.022 (0.0008, 5) | 0.0013 (0.00009, 5) | 102.64 (9.19, 6) | 0.66 (0.062, 6) | 0.79 | 15.7 (0.96, 9) |
| *Rockinghamia angustifolia* | Euphorbiaceae | 5.78 (3.30, 5) | 0.018 (0.0007, 4) | 0.0009 (0.00016, 4) | 92.99 (8.82, 3) | 0.45 (0.006, 3) | 0.65 | 12.0 (2.04, 5) |
| *Acacia celsa* | Fabaceae | 12.90 (1.34, 5) | 0.040 (0.0032, 5) | 0.0020 (0.00051, 5) | 68.96 (4.13, 3) | 0.50 (0.054, 3) | 0.49 | 26.0 (5.51, 7) |
| *Castanospermum australe* | Fabaceae | 11.81 (5.28, 5) | 0.036 (0.0020, 5) | 0.0020 (0.00026, 5) | 72.88 (11.71, 3) | 0.59 (0.061, 3) | 0.62 | NA |
| *Homalium circumpinnatum* | Flacourtiaceae | 7.29 (2.78, 6) | 0.021 (0.0013, 5) | 0.0010 (0.00010, 5) | 76.51 (15.32, 6) | 0.72 (0.035, 6) | 0.68 | 28.8 (5.85, 6) |
| *Cinnamomum laubatii* | Lauraceae | 7.35 (1.75, 4) | 0.016 (0.0005, 4) | 0.0009 (0.00012, 4) | 115.10 (6.90, 4) | 0.53 (0.045, 4) | 0.47 | 10.1 (1.43, 4) |
| *Cryptocarya mackinnoniana* | Lauraceae | 12.22 (3.30, 6) | 0.020 (0.0018, 5) | 0.0016 (0.00033, 5) | 54.87 (11.54, 4) | 0.65 (0.075, 3) | 0.76 | 19.6 (2.64, 5) |
| *Cryptocarya murrayi* | Lauraceae | 12.82 (2.46, 5) | 0.019 (0.0022, 4) | 0.0014 (0.00024, 4) | 64.74 (1.02, 3) | 0.67 (0.075, 3) | 0.79 | 21.5 (1.75, 2) |
| *Endiandra leptodendron* | Lauraceae | 8.59 (3.02, 5) | 0.022 (0.0009, 5) | 0.0012 (0.00007, 5) | 94.54 (8.87, 3) | 0.61 (0.052, 3) | 0.87 | NA |
| *Endiandra monothyra* | Lauraceae | 4.80 (3.10, 5) | 0.016 (0.0006, 5) | 0.0009 (0.00013, 5) | 100.62 (12.62, 6) | 0.60 (0.027, 5) | 0.80 | 12.9 (2.29, 6) |

| **Species** | **Family** | **$A_{area}$ (SD, n)** µmol $m^{-2}$ $s^{-1}$ | **$N_{area}$ (SD, n)** g $cm^{-2}$ | **$P_{area}$ (SD, n)** g $cm^{-2}$ | **SLA (SD, n)** $cm^2$ $g^{-1}$ | **Branch WD (SD, n)** g $cm^{-3}$ | **Trunk WD** g $cm^{-3}$ | **Trunk Diameter (SD, n)** cm |
|---|---|---|---|---|---|---|---|---|
| *Litsea leefeana* | Lauraceae | 11.48 (1.70, 60 | 0.023 (0.0008, 5) | 0.0011 (0.00022, 5) | 77.54 (7.63, 3) | 0.55 (0.047, 3) | 0.51 | NA |
| *Neolitsea dealbata* | Lauraceae | 6.49 (1.87, 7) | 0.015 (0.0009, 5) | 0.0009 (0.00022, 5) | 107.75 (3.82, 3) | 0.35 (0.025, 3) | 0.67 | 4.5 (0.07, 2) |
| *Argyrodendron peralatum* | Malvaceae | 10.57 (2.69, 5) | 0.033 (0.0019, 5) | 0.0018 (0.00037, 5) | 40.22 (6.22, 3) | 0.73 (0.022, 3) | 0.65 | 9.4 (0, 1) |
| *Franciscodendron laurifolium* | Malvaceae | 5.00 (1.92, 5) | 0.012 (0.0013, 5) | 0.0008 (0.00003, 5) | 96.17 (10.84, 5) | 0.50 (0.041, 5) | 0.37 | 13.9 (1.64, 5) |
| *Tetrasynandra laxiflora* | Monimiaceae | 6.65 (1.72, 6) | 0.017 (0.0006, 5) | 0.0008 (0.00014, 5) | 167.62 (16.43, 6) | 0.46 (0.051, 6) | 0.55 | 13.4 (1.03, 5) |
| *Myristica insipida* | Myristicaceae | 6.62 (2.90, 8) | 0.017 (0.0015, 5) | 0.0011 (0.00012, 5) | 92.80 (11.21, 8) | 0.47 (0.031, 6) | 0.46 | 19.8 (1.78, 7) |
| *Gossia hillii* | Myrtaceae | 9.31 (2.46, 6) | 0.020 (0.0014, 5) | 0.0009 (0.00012, 5) | 61.61 (11.54, 6) | 0.72 (0.010, 6) | 0.63 | 21.5 (1.89, 7) |
| *Syzygium sayeri* | Myrtaceae | 9.25 (3.12, 5) | 0.021 (0.0008, 5) | 0.0010 (0.00008, 5) | 77.03 (7.40, 3) | 0.48 (0.023, 3) | 0.78 | NA |
| *Cardwellia sublimis* | Proteaceae | 10.65 (3.77, 5) | 0.021 (0.0013, 5) | 0.0010 (0.00011, 5) | 69.82 (7.07, 3) | 0.60 (0.046, 3) | 0.46 | 6.0 (0, 1) |
| *Darlingia darlingiana* | Proteaceae | 12.50 (3.90, 6) | 0.013 (0.0014, 5) | 0.0010 (0.00028, 5) | 74.95 (11.79, 6) | 0.63 (0.094, 6) | 0.64 | 13.6 (1.07, 7) |
| *Alphitonia petriei* | Rhamnaceae | 15.38 (3.86, 5) | 0.030 (0.0021, 5) | 0.0019 (0.00032, 5) | 67.29 (4.29, 3) | 0.41 (0.017, 3) | 0.43 | 11.7 (2.11, 4) |
| *Alphitonia whitei* | Rhamnaceae | 7.60 (2.57, 7) | 0.021 (0.0017, 5) | 0.0011 (0.00013, 5) | 81.25 (13.51, 7) | 0.57 (0.051, 6) | 0.63 | 20.7 (2.97, 8) |
| *Acronychia acidula* | Rutaceae | 6.78 (1.75, 6) | 0.022 (0.0010, 5) | 0.0048 (0.00130, 5) | 119.31 (16.86, 3) | 0.52 (0.031, 3) | 0.52 | 16.4 (1.54, 8) |
| *Acronychia laevis* | Rutaceae | 7.28 (1.46, 6) | 0.019 (0.0027, 5) | 0.0009 (0.00017, 5) | 103.77 (28.04, 6) | 0.68 (0.051, 6) | 0.52 | 12.6 (0.58, 8) |
| *Brombya platynema* | Rutaceae | 10.53 (2.38, 5) | 0.023 (0.0008, 5) | 0.0009 (0.00009, 5) | 94.02 (2.99, 3) | 0.60 (0.069, 3) | 0.58 | NA |
| *Dinosperma erythrococcum* | Rutaceae | 7.25 (2.98, 5) | 0.018 (0.0008, 5) | 0.0010 (0.00007, 5) | 77.82 (2.99, 4) | 0.74 (0.044, 6) | 0.79 | 20.7 (3.55, 9) |
| *Flindersia bourjotiana* | Rutaceae | 8.85 (2.96, 7) | 0.019 (0.0025, 5) | 0.0009 (0.00014, 5) | 64.78 (4.80, 6) | 0.65 (0.142, 6) | 0.53 | 26.8 (5.39, 6) |
| *Flindersia brayleyana* | Rutaceae | 8.17 (4.16, 7) | 0.021 (0.0025, 5) | 0.0011 (0.00010, 5) | 73.55 (14.35, 7) | 0.56 (0.154, 6) | 0.48 | 19.3 (3.77, 9) |
| *Flindersia pimenteliana* | Rutaceae | 3.58 (1.33, 5) | 0.012 (0.0014, 5) | 0.0011 (0.00037, 5) | 95.64 (29.47, 5) | 0.55 (0.098, 5) | 0.53 | 14.1 (2.00, 5) |
| *Castanospora alphandii* | Sapindaceae | 4.29 (2.62, 6) | 0.022 (0.0008, 5) | 0.0014 (0.00013, 5) | 86.81 (7.59, 6) | 0.56 (0.055,6) | 0.59 | 19.2 (2.51, 5) |
| *Dendrocnide photinophylla* | Urticaceae | 7.84 (2.70, 7) | 0.025 (0.0034, 5) | 0.0011 (0.00010, 5) | 196.23 (22.71, 7) | 0.34 (0.006, 6) | 0.21 | 21.3 (2.11, 8) |

***Table S3*** *Species level branch biomass metrics estimated at a standard distance of 100 cm from the branch tip (with 95 % confidence interval shown in brackets).*

| Species | Family | $LM_{dist}$ [95% CI] | $LA_{dist}$ [95% CI] | $WM_{dist}$ [95% CI] | $SM_{dist}$ [95% CI] |
|---|---|---|---|---|---|
| *Alstonia muelleriana* | Apocynaceae | 21.6 [14.6; 31.9] | 2663 [1983; 3576] | 36.0 [26.9; 48.2] | 26.2 [19.0; 36.2] |
| *Alstonia scholaris* | Apocynaceae | 94.6 [45.1; 198.3] | 8815 [4303; 18058] | 91.0 [66.3; 124.8] | 64.5 [44.5; 93.6] |
| *Agathis robusta* | Araucariaceae | 130.1 [88.6; 191.1] | 7029 [4680; 10558] | 193.2 [110.3; 338.5] | 91.1 [50.7; 163.6] |
| *Daphnandra repandula* | Atherospermataceae | 33.6 [23.4; 48.1] | 5567 [4010; 7729] | 28.7 [20.9; 39.6] | 26.8 [18.0; 39.7] |
| *Gillbeea adenopetala* | Cunoniaceae | 140.8 [51.8; 382.8] | 10524 [4476; 24746] | 83.1 [29.0; 238.6] | 65.0 [23.8; 178.1] |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 42.3 [29.7; 60.4] | 3264 [2335; 4561] | 106.7 [80.1; 142.2] | 69.4 [51.9; 92.7] |
| *Pullea stutzeri* | Cunoniaceae | 52.8 [36.7; 76.0] | 5502 [3866; 7830] | 38.9 [28.8; 52.5] | 29.6 [21.0; 41.9] |
| *Aleurites rockinghamensis* | Euphorbiaceae | 229.1 [81.7; 642.4] | 20333 [6577; 62862] | 69.9 [25.9; 188.9] | 53.8 [20.7; 140.1] |
| *Cleistanthus myrianthus* | Euphorbiaceae | 57.3 [37.1; 88.5] | 7296 [4618; 11527] | 44.1 [26.5; 73.6] | 34.9 [20.5; 59.5] |
| *Cleistanthus semiopacus* | Euphorbiaceae | 41.5 [33.1; 52.2] | 4486 [3565; 5643] | 69.1 [46.3; 103.2] | 51.3 [34.4; 76.5] |
| *Croton insularis* | Euphorbiaceae | 31.3 [24.0; 41.0] | 3207 [2440; 4214] | 50.3 [38.7; 65.3] | 37.0 [28.8; 47.6] |
| *Rockinghamia angustifolia* | Euphorbiaceae | 68.9 [38.2; 124.3] | 6398 [3167; 12928] | 43.4 [26.1; 72.1] | 35.4 [20.6; 60.9] |
| *Acacia celsa* | Fabaceae | 76.2 [16.5; 352.9] | 5200 [1063; 25431] | 54.6 [14.6; 204.3] | 44.3 [11.7; 167.9] |
| *Castanospermum australe* | Fabaceae | 344.6 [194.5; 610.5] | 24557 [13148; 45865] | 130.2 [79.9; 212.3] | 94.5 [57.8; 154.6] |
| *Homalium circumpinnatum* | Flacourtiaceae | 55.3 [41.1 74.4] | 4151 [3113; 5536] | 107.0 [82.3; 139.1] | 64.2 [49.6; 83.0] |
| *Cinnamomum laubatii* | Lauraceae | 55.6 [39.9; 77.3] | 6386 [4531; 9003] | 43.4 [30.2; 62.5] | 33.8 [23.6; 48.4] |
| *Cryptocarya mackinnoniana* | Lauraceae | 206.0 [108.1; 392.6] | 11469 [5964; 22056] | 88.0 [44.1; 175.6] | 101.4 [21.7; 474.4] |
| *Cryptocarya murrayi* | Lauraceae | 145.4 [72.4; 292.0] | 9384 [4589; 19192] | 92.4 [32.6; 261.8] | 74.4 [26.4; 209.6] |
| *Endiandra leptodendron* | Lauraceae | 81.1 [21.9; 300.5] | 7699 [1968; 30126] | 88.2 [33.2; 234.5] | 72.0 [27.6; 188.2] |
| *Endiandra monothyra* | Lauraceae | 43.3 [31.8; 59.0] | 4326 [3172; 5900] | 32.4 [23.9; 44.1] | 21.9 [15.3; 31.2] |
| *Litsea leefeana* | Lauraceae | 220.5 [127.5; 381.2] | 16993 [8719; 33117] | 162.4 [101.5; 259.9] | 123.5 [84.7; 180.1] |
| *Neolitsea dealbata* | Lauraceae | 49.2 [22.3; 108.8] | 5302 [2324; 12096] | 41.7 [23.6; 73.9] | 30.9 [17.0; 56.4] |
| *Argyrodendron peralatum* | Malvaceae | 294.2 [94.9; 912.1] | 11735 [3722; 37001] | 210.9 [59.4; 748.5] | 122.4 [33.3; 449.8] |

| Species | Family | $LM_{dist}$ [95% CI] | $LA_{dist}$ [95% CI] | $WM_{dist}$ [95% CI] | $SM_{dist}$ [95% CI] |
|---|---|---|---|---|---|
| *Franciscodendron laurifolium* | Malvaceae | 44.9 [30.2; 66.9] | 4298 [2918; 6330] | 54.0 [38.7; 75.4] | 36.1 [25.4; 51.4] |
| *Tetrasynandra laxiflora* | Monimiaceae | 35.7 [27.1; 46.9] | 5956 [4444; 7982] | 26.2 [19.1; 35.9] | 20.9 [15.2; 28.9] |
| *Myristica insipida* | Myristicaceae | 43.1 [35.6; 52.2] | 3973 [3320; 4755] | 33.9 [28.1; 40.8] | 20.0 [16.2; 24.6] |
| *Gossia hillii* | Myrtaceae | 44.3 [32.2; 60.8] | 2687 [2009; 3593] | 73.4 [42.1; 128.0] | 52.3 [30.3; 90.3] |
| *Syzygium sayeri* | Myrtaceae | 141.1 [29.0; 686.1] | 10938 [2458; 48688] | 92.6 [11.1; 773.6] | 65.9 [8; 538.8] |
| *Cardwellia sublimis* | Proteaceae | 337.5 [251.9; 452.2] | 23670 [17510; 31998] | 148.5 [75.6; 291.8] | 113.7 [59.4; 217.5] |
| *Darlingia darlingiana* | Proteaceae | 84.9 [66.7; 107.9] | 6293 [4978; 7955] | 41.3 [34.5; 49.5] | 31.0 [25.9; 37.2] |
| *Alphitonia petriei* | Rhamnaceae | 79.7 [48.1; 132.0] | 5345 [3512; 8135] | 47.5 [31.2; 72.3] | 34.2 [22.0; 53.3] |
| *Alphitonia whitei* | Rhamnaceae | 190.7 [113.8; 319.6] | 15304 [9659; 24248] | 133.4 [74.7; 238.0] | 70.6 [43.9; 113.5] |
| *Acronychia acidula* | Rutaceae | 121.9 [43.0; 345.2] | 14473 [6031; 34734] | 92.6 [30.6; 280.4] | 74.5 [24.5; 226.3] |
| *Acronychia laevis* | Rutaceae | 35.0 [23.1; 53.1] | 3535 [2235; 5592] | 57.6 [37.9; 87.5] | 43.6 [29.3; 65.0] |
| *Brombya platynema* | Rutaceae | 38.0 [15.3; 94.4] | 3571 [1432; 8908] | 28.6 [12.7; 64.3] | 23.6 [10.5; 53.0] |
| *Dinosperma erythrococcum* | Rutaceae | 66.6 [52.2; 85.1] | 5318 [3835; 7375] | 85.0 [64.2; 112.5] | 65.0 [49.3; 85.6] |
| *Flindersia bourjotiana* | Rutaceae | 112.9 [88.2; 144.7] | 7300 [5630; 9466] | 75.6 [60.2; 95.1] | 53.0 [42.1; 66.7] |
| *Flindersia brayleyana* | Rutaceae | 86.9 [64.8; 116.6] | 6284 [4606; 8573] | 42.8 [31.8; 57.8] | 22.5 [16.0; 31.6] |
| *Flindersia pimenteliana* | Rutaceae | 38.9 [22.7; 66.7] | 3598 [1897; 6826] | 48.2 [31.1; 74.9] | 34.4 [22.6; 52.3] |
| *Castanospora alphandii* | Sapindaceae | 89.0 [65.9; 120.2] | 7683 [5657; 10433] | 71.6 [42.1; 121.8] | 46.8 [27.5; 79.7] |
| *Dendrocnide photinophylla* | Urticaceae | 16.8 [11.6; 24.2] | 3270 [2269; 4714] | 36.0 [26.9; 48.4] | 26.7 [18.9; 37.8] |

***Table S4*** *Species level branch biomass metrics estimated at a cross sectional area of 100 mm$^2$ (with 95 confidence interval shown in brackets).*

| Species | Family | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | n |
|---|---|---|---|---|---|---|
| *Alstonia muelleriana* | Apocynaceae | 63.2 [42.3; 94.5] | 4361 [2836; 6705] | 35.5 [19.0; 66.4] | 28.9 [15.7; 53.2] | 3 |
| *Alstonia scholaris* | Apocynaceae | 60.8 [49.5; 74.7] | 7107 [5548; 9103] | 28.4 [17.4; 46.3] | 22.8 [13.9; 37.6] | 3 |
| *Agathis robusta* | Araucariaceae | 42.1 [30.6; 57.9] | 4163 [2790; 6212] | 74.3 [58.8; 94.0] | 55.5 [43.9; 70.3] | 6 |
| *Daphnandra repandula* | Atherospermataceae | 28.2 [22.3; 35.6] | 1519 [1180; 1955] | 20.4 [15.9; 26.3] | 9.6 [7.5; 12.4] | 7 |
| *Gillbeea adenopetala* | Cunoniaceae | 24.7 [4.9; 124.7] | 2078 [416; 10374] | 1.9 [0.5; 6.8] | 1.5 [0.4; 5.6] | 3 |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 53.8 [45.1; 64.2] | 3599 [3230; 4009] | 24.4 [21.3; 27.8] | 17.6 [15.6; 19.8] | 3 |
| *Pullea stutzeri* | Cunoniaceae | 75.5 [62.5; 91.3] | 5849 [4800; 7128] | 30.2 [23.7; 38.5] | 19.5 [14.4; 26.3] | 7 |
| *Aleurites rockinghamensis* | Euphorbiaceae | 39.9 [30.7; 51.9] | 3762 [2821; 5016] | 58.9 [35.8; 96.7] | 45.5 [23.5; 88.0] | 7 |
| *Cleistanthus myrianthus* | Euphorbiaceae | 25.6 [18.9; 34.6] | 2383 [1751; 3244] | 12.4 [8.3; 18.6] | 8.8 [6.2; 12.6] | 3 |
| *Cleistanthus semiopacus* | Euphorbiaceae | 62.4 [42.8; 91.0] | 2487 [1465; 4223] | 25.3 [20.4; 31.4] | 14.7 [11.9; 18.1] | 3 |
| *Croton insularis* | Euphorbiaceae | 44.1 [18.6; 104.6] | 4123 [1687; 10079] | 34.8 [13.7; 88.3] | 28.7 [11.3; 72.8] | 3 |
| *Rockinghamia angustifolia* | Euphorbiaceae | 79.6 [63.9; 99.1] | 5535 [4311; 7106] | 17.2 [14.6; 20.2] | 13.1 [11.3; 15.2] | 3 |
| *Acacia celsa* | Fabaceae | 52.5 [45.3; 60.8] | 4543 [3898; 5296] | 28.6 [23.3; 35.1] | 18.7 [15.2; 23.0] | 6 |
| *Castanospermum australe* | Fabaceae | 41.9 [24.6; 71.5] | 3005 [1802; 5010] | 3.8 [1.1; 13.3] | 2.7 [0.8; 9.7] | 3 |
| *Homalium circumpinnatum* | Flacourtiaceae | 56.5 [46.8; 68.1] | 6519 [5356; 7934] | 40.4 [27.9; 58.6] | 31.4 [21.6; 45.6] | 4 |
| *Cinnamomum laubatii* | Lauraceae | 54.3 [37.4; 78.8] | 6912 [4588; 10412] | 41.3 [31.1; 54.8] | 32.7 [23.8; 45.0] | 3 |
| *Cryptocarya mackinnoniana* | Lauraceae | 33.9 [26.5; 43.5] | 3676 [2868; 4712] | 56.4 [47.6; 66.8] | 41.7 [35.3; 49.3] | 6 |
| *Cryptocarya murrayi* | Lauraceae | 40.5 [33.1; 49.5] | 4148 [3381; 5089] | 69.8 [54.4; 89.6] | 51.2 [39.9; 65.6] | 6 |
| *Endiandra leptodendron* | Lauraceae | 91.0 [48.3; 171.3] | 5111 [2514; 10393] | 35.3 [22.1; 56.3] | 20.2 [9.9; 41.1] | 4 |
| *Endiandra monothyra* | Lauraceae | 45.6 [20.8; 99.9] | 2949 [1337; 6506] | 18.5 [12.5; 27.5] | 14.8 [10.3; 21.3] | 3 |
| *Litsea leefeana* | Lauraceae | 37.6 [24.5; 57.8] | 6178 [4081; 9353] | 34.4 [22.4; 52.6] | 28.8 [18.7; 44.2] | 6 |
| *Neolitsea dealbata* | Lauraceae | 81.6 [64.7; 102.9] | 6024 [4782; 7588] | 35.1 [25.6; 48.2] | 26.2 [18.9; 36.3] | 6 |
| *Argyrodendron peralatum* | Malvaceae | 14.1 [11.0; 18.1] | 2791 [2181; 3572] | 16.6 [10.7; 25.7] | 12.8 [8.4; 19.5] | 7 |

| Species | Family | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | $LM_{xsa}$ [95% CI] | n |
|---|---|---|---|---|---|---|
| *Franciscodendron laurifolium* | Malvaceae | 52.5 [43.0; 64.1] | 4042 [3037; 5379] | 58.5 [49.3; 69.3] | 44.6 [37.5; 53.0] | 6 |
| *Tetrasynandra laxiflora* | Monimiaceae | 34.9 [23.2; 52.5] | 3313 [2140; 5130] | 30.3 [20.4; 45.1] | 24.7 [16.6; 36.8] | 3 |
| *Myristica insipida* | Myristicaceae | 64.4 [44.6; 93.2] | 6444 [4450; 9332] | 61.6 [47.4; 80.1] | 43.2 [31.6; 59.1] | 6 |
| *Gossia hillii* | Myrtaceae | 65.2 [56.5; 75.2] | 4242 [3679; 4890] | 31.5 [25.5; 38.9] | 21.9 [17.5; 27.4] | 6 |
| *Syzygium sayeri* | Myrtaceae | 59.2 [50.1; 70.0] | 4277 [3542; 5164] | 20.5 [17.2; 24.5] | 12.1 [9.9; 14.8] | 7 |
| *Cardwellia sublimis* | Proteaceae | 30.2 [21.1; 43.3] | 2947 [1947; 4462] | 32.0 [22.7; 45.2] | 22.5 [15.9; 31.8] | 5 |
| *Darlingia darlingiana* | Proteaceae | 37.6 [30.5; 46.2] | 3592 [2961; 4356] | 31.3 [23.6; 41.4] | 21.1 [15.9; 27.9] | 5 |
| *Alphitonia petriei* | Rhamnaceae | 50.5 [23.9; 106.6] | 3741 [1634; 8568] | 24.2 [17.3; 33.7] | 18.9 [13.3; 26.8] | 3 |
| *Alphitonia whitei* | Rhamnaceae | 41.6 [33.7; 51.4] | 2502 [2059; 3039] | 71.1 [48.2; 104.8] | 50.1 [33.9; 74.1] | 6 |
| *Acronychia acidula* | Rutaceae | 38.2 [33.5; 43.7] | 2834 [2425; 3312] | 53.0 [45.2; 62.1] | 31.5 [26.3; 37.8] | 6 |
| *Acronychia laevis* | Rutaceae | 61.0 [30.7; 121.0] | 4697 [2133; 10342] | 33.4 [26.9; 41.5] | 25.3 [19.7; 32.5] | 3 |
| *Brombya platynema* | Rutaceae | 39.5 [32.9; 47.4] | 3615 [3023; 4324] | 28.9 [23.9; 35.1] | 20.5 [15.8; 26.8] | 8 |
| *Dinosperma erythrococcum* | Rutaceae | 54.9 [39.6; 76.0] | 5915 [4048; 8643] | 46.5 [34.2; 63.2] | 34.5 [25.1; 47.5] | 3 |
| *Flindersia bourjotiana* | Rutaceae | 27.9 [19.1; 40.8] | 2142 [1482; 3095] | 57.6 [45.0; 73.8] | 37.5 [29.3; 48.0] | 6 |
| *Flindersia brayleyana* | Rutaceae | 52.7 [35.3; 78.8] | 5559 [3791; 8151] | 39.1 [25.6; 59.5] | 31.2 [19.2; 50.7] | 6 |
| *Flindersia pimenteliana* | Rutaceae | 61.3 [53.2; 70.5] | 5745 [4565; 7229] | 33.7 [22.1; 51.5] | 27.6 [18.4; 41.4] | 3 |
| *Castanospora alphandii* | Sapindaceae | 72.6 [28.5; 185.4] | 5592 [2352; 13293] | 47.6 [12.2; 185.5] | 33.8 [8.8; 130.0] | 3 |
| *Dendrocnide photinophylla* | Urticaceae | 46.6 [37.9; 57.4] | 7777 [6146; 9842] | 35.4 [25.1; 49.8] | 28.3 [20.0; 40.0] | 6 |

***Table S5*** *Details for linear regressions between traits and stem diameter growth rates (95th percentile and mean for trees of all sizes, and 95th percentile for trees between 10 and 30cm dbh).*

| **Regression functions** | **Growth Rate Measure** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **95$^{th}$ percentile (all sizes)** | | | **Mean (all sizes)** | | | **95$^{th}$ percentile (size restricted 10-30cm dbh)** | | |
| | **$R^2$** | **slope** | **p** | **$R^2$** | **slope** | **p** | **$R^2$** | **slope** | **p** |
| ***Leaf and wood traits*** | | | | | | | | | |
| log (GR) ~ log (SLA) | 0.21 | -0.75 | 0.002 | 0.34 | -1.1 | <0.001 | 0.25 | -0.75 | <0.001 |
| log (GR) ~ $A_{area}$ | 0.095 | 0.02 | 0.05 | 0.09 | 0.03 | 0.055 | 0.05 | 0.02 | 0.19 |
| log (GR) ~ log ($P_{area}$) | 0.22 | 0.6 | 0.002 | 0.22 | 0.67 | 0.002 | 0.13 | 0.61 | 0.02 |
| log (GR) ~ log ($N_{area}$) | 0.19 | 0.78 | 0.004 | 0.17 | 0.82 | 0.007 | 0.18 | 0.51 | 0.01 |
| log (GR) ~ Trunk WD | 0.17 | -0.59 | 0.007 | 0.11 | -0.52 | 0.04 | 0.07 | -0.36 | 0.10 |
| log (GR) ~ Branch WD | 0.09 | -0.56 | 0.054 | 0.04 | -0.43 | 0.2 | 0.02 | -0.25 | 0.39 |
| ***Branch biomass allocation metrics (****at a distance of 100cm from branch tip)* | | | | | | | | | |
| log (GR) ~ log (LM:WM) | 0.15 | 0.4 | 0.01 | 0.08 | 0.33 | 0.07 | 0.11 | 0.31 | 0.04 |
| log (GR) ~ log (LM:SM) | 0.27 | 0.55 | <0.001 | 0.18 | 0.5 | 0.006 | 0.20 | 0.44 | 0.001 |
| log (GR) ~ log (LA:WM) | 0.009 | 0.10 | 0.55 | 0.006 | -0.09 | 0.62 | 0.0001 | 0.01 | 0.95 |
| log (GR) ~ log (LA:SM) | 0.05 | 0.25 | 0.15 | 0.002 | 0.06 | 0.75 | 0.02 | 0.13 | 0.43 |
| ***Branch biomass allocation metrics (****at 100mm$^2$ cross sectional area)* | | | | | | | | | |
| log (GR) ~ log (LM:WM) | 0.29 | 0.39 | 0.0002 | 0.21 | 0.37 | 0.003 | 0.21 | 0.3 | 0.003 |
| log (GR) ~ log (LM:SM) | 0.34 | 0.41 | <0.0001 | 0.26 | 0.41 | 0.0006 | 0.25 | 0.32 | 0.001 |
| log (GR) ~ log (LA:WM) | 0.14 | 0.28 | 0.017 | 0.05 | 0.19 | 0.17 | 0.07 | 0.18 | 0.1 |
| log (GR) ~ log (LA:SM) | 0.19 | 0.34 | 0.004 | 0.088 | 0.26 | 0.059 | 0.11 | 0.23 | 0.04 |

***Table S6*** *Matrix of Pearson product-moment correlation coefficients between traits (LM:SM estimated at both a standard distance and a standard cross-sectional area).*

^ 0.05 < p < 0.1, * p < 0.05, **p < 0.001, *** p < 0.0001

| | log (SLA) | $A_{area}$ | log ($P_{area}$) | log ($N_{area}$) | WD | log (LM:SM dist) |
|---|---|---|---|---|---|---|
| $A_{area}$ | -0.38* | | | | | |
| log ($P_{area}$) | -0.27^ | 0.42* | | | | |
| log ($N_{area}$) | -0.35* | 0.64*** | 0.67*** | | | |
| WD | -0.15 | -0.04 | -0.17 | -0.19 | | |
| log (LM:SM dist) | -0.38* | 0.26^ | 0.35* | 0.24 | -0.17 | |
| log (LM:SM xsa) | -0.43* | 0.36* | 0.50** | 0.41* | -0.29^ | 0.89*** |

***Table S7*** *Axis loadings and explained variance of the first three components of a principal component analysis including all traits (LM:SM at a standard cross-sectional area).*

| Traits | PC1 | PC2 | PC3 |
|---|---|---|---|
| | Axis loadings | | |
| log (SLA) | 0.34 | -0.51 | -0.53 |
| WD | 0.15 | 0.82 | -0.18 |
| log (LM:SM) | -0.43 | -0.15 | 0.59 |
| $A_{area}$ | -0.44 | 0.18 | -0.38 |
| log ($P_{area}$) | -0.47 | -0.12 | -0.20 |
| log ($N_{area}$) | -0.51 | -0.03 | -0.40 |
| Eigen values | 2.84 | 1.17 | 0.79 |
| Variance explained | 47.3% | 19.5% | 13.2% |

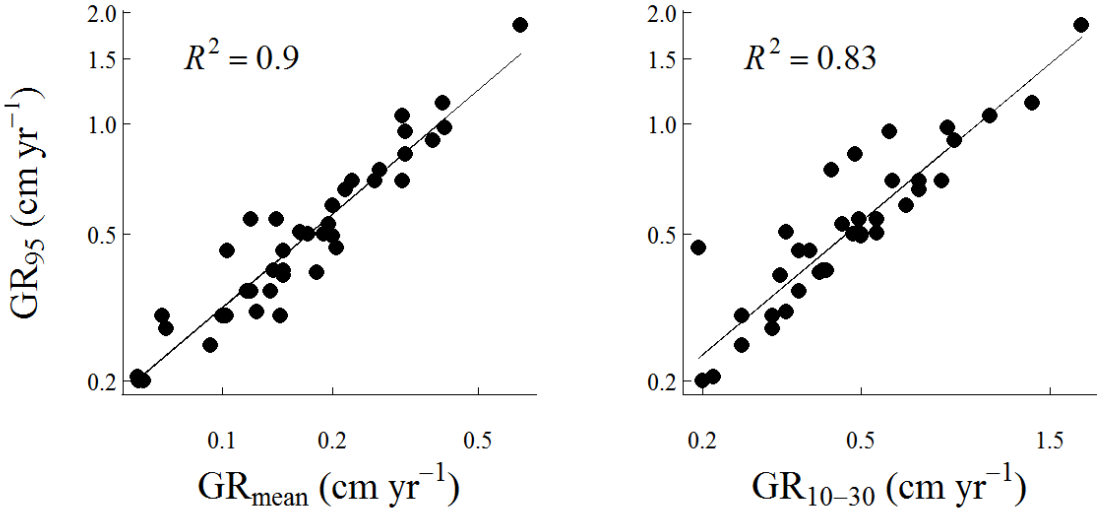



***Figure S1*** *Linear regression relationships between $GR_{95}$ and the two other estimates of growth rate, namely mean growth rate ($GR_{mean}$) and 95$^{th}$ percentile growth rate of individuals within a restricted sizeclass of 10-30 cm diameter ($GR_{10-30}$). Relationships are for 41 rainforest species, based on data in Table S1.*

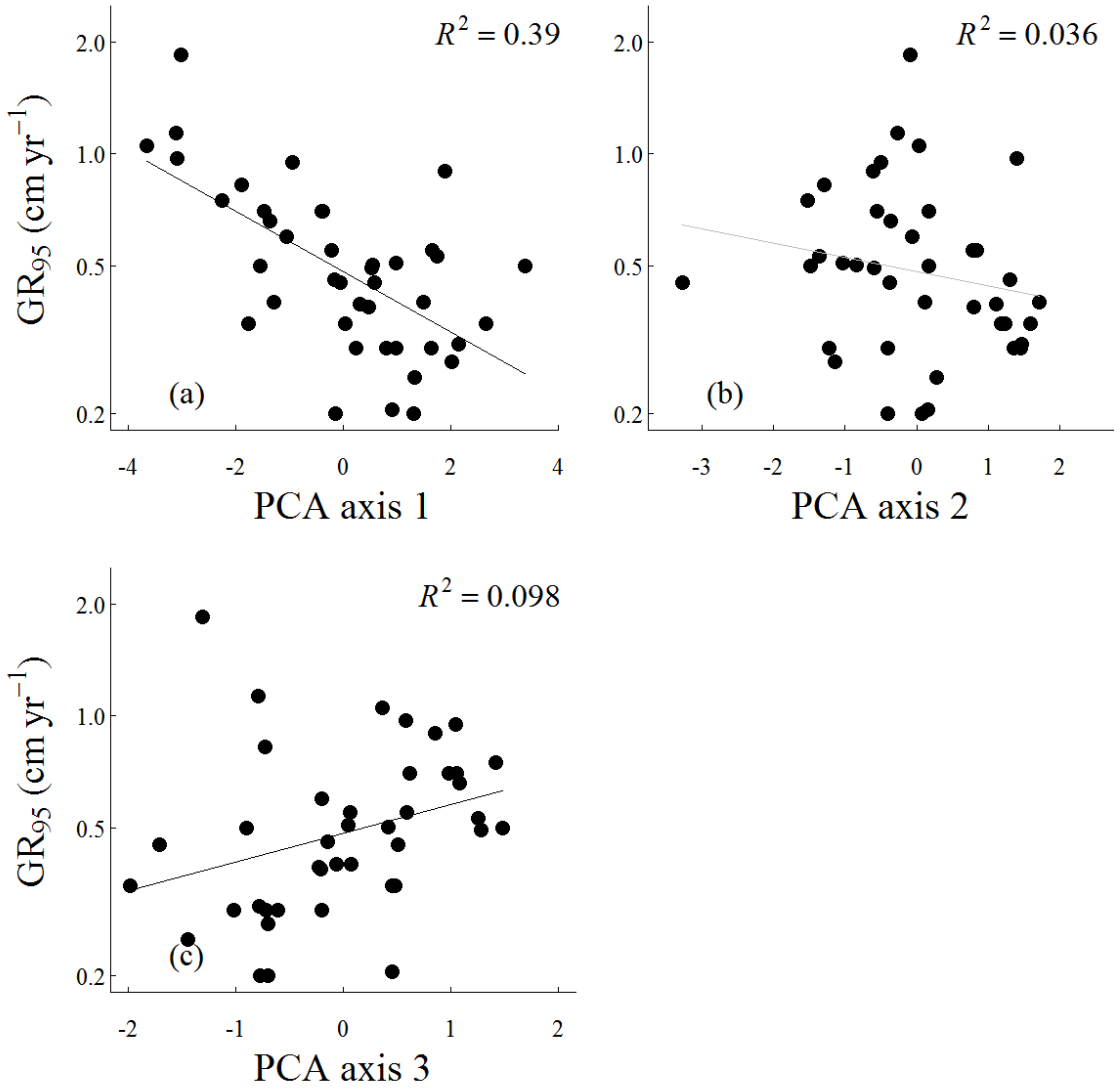



***Figure S2*** *Linear regression relationships between $GR_{95}$ and PCA axes (a) principal components axis 1, b) principal components axis 2, and c) principal components axis 3. Black trend lines indicate significant regression relationships, grey lines show non-significant relationships.*

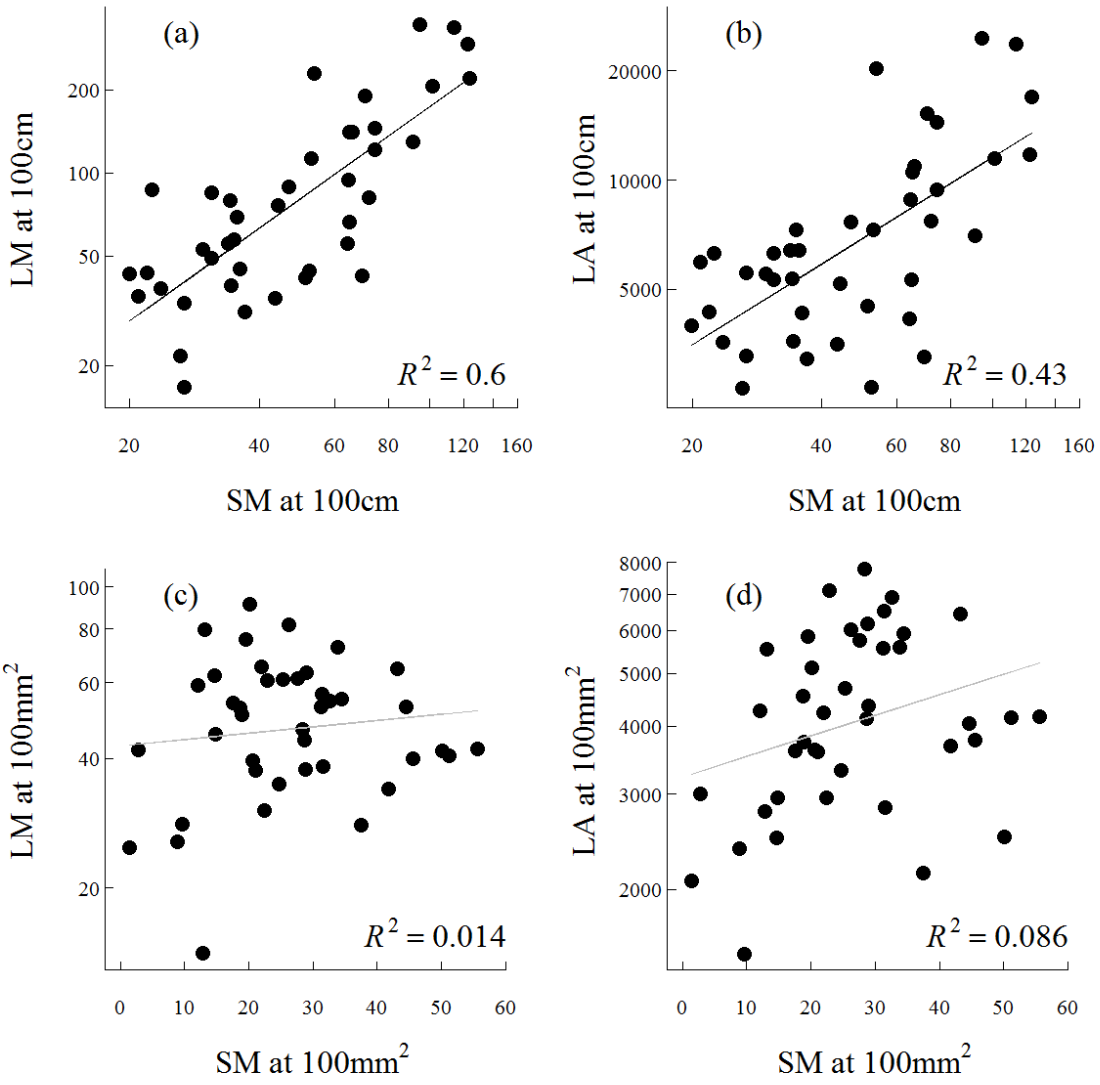



***Figure S3*** *Linear regression relationships between leaf and sapwood components (leaf mass (LM), leaf area (LA) and sapwood mass (SM)) at a standardised distance from tip (a, b) and a standardised cross sectional area (c, d). All variables except for sapwood mass at a standardised cross-sectional area are log transformed. Black trend lines indicate significant regression relationships, grey lines show non-significant relationships.*

# Chapter 3

## Testing the consistency of links between functional traits and adult stem diameter and height growth rates across three savanna regions

# Abstract

Variation in plant functional traits is assumed to underpin interspecific variation in species growth rates consistently across biomes, but most supporting evidence comes from experimental studies and, when from field studies, from closed forest vegetation. Here we quantified relationships between functional traits and growth rates for 58 savanna tree species from three biogeographically distinct regions, Australia, Brazil and South Africa. These savannas differ in climate, disturbance regimes and vegetation structure.

Diameter and height growth rates (DGR and HGR, respectively) were calculated from repeat-measurements of tree diameter and height made at each site. The functional traits we considered were light-saturated photosynthetic rate ($A_{area}$), specific leaf area (SLA), branch wood density (BWD) and branch-scale leaf mass:wood mass ratios (LM:WM). With no a priori expectations regarding how differences in disturbance regimes and resource availability would affect relationships, we expected growth rates in all sites would be positively related to $A_{area}$ and LM:WM, unrelated to SLA, and negatively related to BWD.

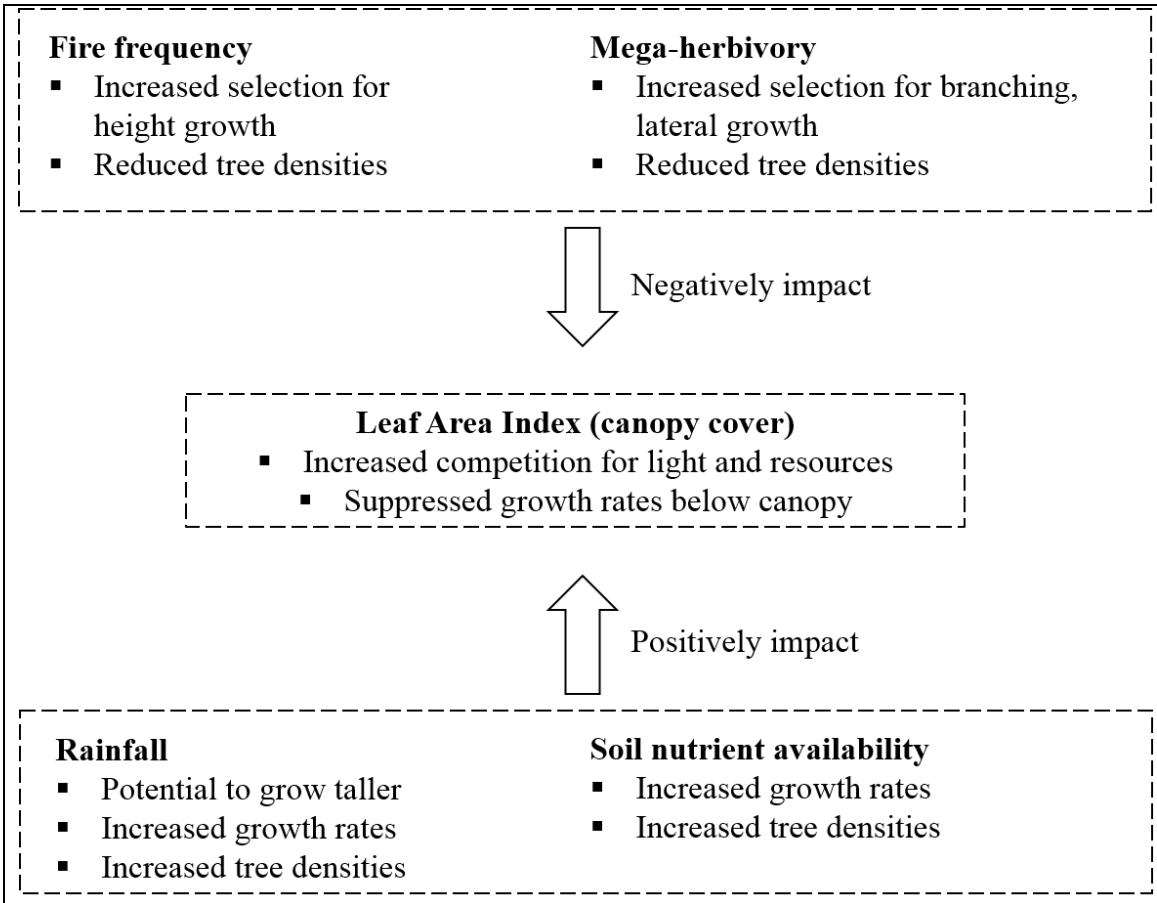
Mean stem diameter growth rates were highest in South Africa, mean height growth rates highest in Australia, with Brazil lowest in both. Although there was some variation in trait-growth relationships among sites, in general we found that: (i) SLA was unrelated to DGR or HGR; (ii) there was a general positive relationship between $A_{area}$ and HGR (but not DGR); (iii) there was a common negative slope between BWD and DGR; and (iv) there was a common positive slope between LM:WM and HGR. The explanatory power of traits (in combination) for growth rates varied between sites. At the Australian site, $A_{area}$ and SLA explained 40% (DGR) to 57 % (HGR) variation in growth rates. Explanatory power was considerably lower at the other two sites, ranging between 14 and 28%. For South African species, variation in growth rates was best explained by a negative relationship with BWD; for Brazilian species, growth rates were negatively related to BWD and positively related to LM:WM.

Ours is the first study to test the generality of trait – growth relationships across multiple savannas using field-based measurements, and the first to consider both height and diameter growth rates. Our analysis highlights the importance of considering both metrics of growth. We suggest that trait-growth relationships may be influenced by the prevailing disturbance regime, and that this will result in regional differences in vegetation response to future changes in climate and disturbance.

# Introduction

Plant growth rates differ among species, and understanding the drivers of these differences is essential to predicting vegetation dynamics and impacts of environmental change (Rees et al. 2001). Interspecific variation in growth rates should be underpinned by variation in plant functional traits related to carbon gains and losses, but most supporting evidence comes from experimental studies and, when from field-based studies, from closed forest vegetation (Gibert et al. 2016). Savannas cover more than 20% of the earth's surface, and contribute significantly to the global carbon cycle (Grace et al. 2006), yet few studies have considered how plant functional traits underpin variation in growth rates across these systems (Hoffmann & Franco 2003; Prior et al. 2004; Rossatto et al. 2009; Tomlinson et al. 2012; Tomlinson et al. 2014). Here, we take a comparative approach and examine interspecific variation in stem diameter and height growth rates and functional traits across three savannas.

Across much of the tropics the climate and soils are capable of supporting closed forest, but savannas are maintained by chronic disturbance such as fire and mammalian herbivory, which promote open-canopy ecosystems (Bond et al. 2005; Bond 2008; Moncrieff et al. 2011; Lehmann et al. 2011; Ratnam et al. 2011; Staver et al. 2011; Hoffmann et al. 2012; Dantas, Batalha, et al. 2013; Archibald & Hempson 2016). Nutrients and climate are considered bottom-up controls on tree cover, while fire and herbivory are top-down (Bond 2008). In isolation, the effects of each of these factors would be relatively easy to predict (Box 1), but in reality, they are all acting in combination. Tree density (and leaf area index) can thus be thought of as a site level product of the interactive effects of these factors on growth rates. Just as these factors affect landscape level vegetation characteristics, they also affect community structure. The type and frequency of disturbance within a savanna acts as an environmental filter, shifting the range of functional traits that are selected for, and the relative allocation of biomass (Gignoux et al. 1997; Tomlinson et al. 2012; Wigley et al. 2016), as well as growth rates (Archibald & Bond 2003; Murphy et al. 2010). For example, in savannas with frequent fire, rapid height growth enables escape above flame height (Higgins et al. 2000; Bond et al. 2012), while in herbivore-dominated systems wide and densely branched canopies maximise defence (Archibald & Bond 2003; Moncrieff et al. 2014). As such, the selective pressure for relatively faster height or diameter growth rates may vary between savannas, as might the associated range of functional trait values.




***Box 1.*** *Hypothetical individual effects of different environmental controls on growth rates, and tree cover. In reality, environmental factors do not act independently, and site differences in disturbance regimes and resource availability all combine to determine tree density in savannas (Lehmann et al. 2011). It is unclear how these factors in combination should influence traits and growth rates, and the interaction between them. Some factors (for example fire frequency) are likely to select preferentially for height growth over diameter growth, which may further influence trait-growth relationships.*

Resource availability has also been shown to affect the range of functional trait values (Diaz et al. 1998; McConnaughay & Coleman 1999; Ackerly 2003; Hoffmann et al. 2005; Ordoñez et al. 2009; Tomlinson et al. 2012; Jager et al. 2015; Wigley et al. 2016). Different savanna regions differ markedly in the relative importance of top-down vs bottom-up controls (Staver et al. 2011; Lehmann et al. 2011), which should impact the range of growth rates and traits present within a savanna, and potentially even the relationships between traits and growth rates. The extent of differences between savanna regions is unclear, as the majority of field-based studies investigating trait-growth relationships have been restricted to closed-canopy forests (Poorter et al. 2008; Wright et al. 2010; Hérault et al. 2011; Visser

et al. 2016), with one exception considering savanna species (Prior et al. 2004). No studies have considered field-based trait-growth relationships across multiple savanna regions (but see Tomlinson et al. (2012) comparing seedling growth rates of savanna species from Australia, Africa and South America).

Here we focus on four functional traits related to carbon gains and losses, namely: light-saturated photosynthetic rates ($A_{area}$), specific leaf area (leaf area per unit leaf mass, SLA), wood density (WD), and branch-scale leaf mass to wood mass ratios (LM:WM). The literature highlights certain expectations for each of these traits when variability in disturbance regimes and climate are not considered (outlined in Table 1). High $A_{area}$ should drive faster growth rates, because (all else equal) faster photosynthesis increases the rate of biomass production (Prior et al. 2004; Gibert et al. 2016). Species with high specific leaf area have lower dry mass construction costs per unit leaf area, which – all else equal – should drive faster growth rates, and this has been generally observed in seedling experiments (Poorter & Remkes 1990; Lambers & Poorter 1992; Wright & Westoby 2001). One study of adult savanna species has found a similar positive relationship (Prior et al. 2004). However, Gibert et al. (2016) suggest that as plants age, the relative growth benefit of low construction cost, high SLA leaves is counter-balanced by high tissue turnover costs and high biomass allocation to sapwood. As such, there may more commonly be no relation between adult growth rates and specific leaf area (and in certain cases a negative relationship, as in Chapter 2 of this thesis). Wood density should be negatively related to growth rates, because low wood density has lower construction costs (King et al. 2005; Roque & Fo 2007; Poorter et al. 2010; Wright et al. 2010; Ruger et al. 2012). At the landscape scale, higher leaf area index (LAI) drives higher net primary productivity (Webb et al. 1983; Luo et al. 2004), and similarly, at the individual plant scale higher LM:WM is expected to result in faster growth (Poorter et al. 2012). Here we go one step further and consider leaf mass to wood mass ratios at the branch scale, which are also expected to be positively related to growth (Pickup et al. 2005, and see Chapter 2 of this thesis). The consistency of these four expected relationships has not been systematically tested across different biogeographic regions.

**Table 1** Expected relationships between four functional traits and species growth rates, based on findings in literature, when differences in disturbance, climate, and resource availability are not considered.

| Trait (units) | Expected relationship in field-sampled savanna species | Relationships according to literature |
|---|---|---|
| Photosynthetic rate ($A_{area}$, $\mu mol\ m^{-2}\ s^{-1}$) | Positive | Generally positive (Gibert et al. 2016), though only one study on adult plants in savannas (Prior et al. 2004) |
| Specific Leaf Area ($cm^2\ g^{-1}$) | No relationship | Generally positive in seedlings, no relationship in adults (Gibert et al. 2016) |
| Wood density ($g\ cm^{-3}$) | Negative | Generally negative, though not always significant (Gibert et al. 2016) |
| Branch leaf mass to wood mass ratio (LM:WM, $g\ g^{-1}$) | Positive | Never tested (but see Chapter 2 of this thesis). Predicted to be positive (Pickup et al. 2005) |

Here we take a first step in reducing this knowledge gap by making inter-species comparisons of field-measured functional traits and stem diameter and height growth rates of common species in three savanna regions (one in Australia, one in Brazil and one in South Africa). These three savanna regions differ in all of fire frequency, rainfall, soil nutrient availability and mega-herbivore density (See Tables 2 and 3), and thus form a gradient of leaf area index (highest in Brazil and lowest in South Africa, see Figure 1). Here we estimate site-level trait-growth relationships, asking three questions: 1) Are the trait-growth relationships that have been observed in closed forest studies (and outlined in Table 1) also observed in these three savanna systems; 2) Are patterns of growth rates and traits consistent across the three savanna regions; and 3) Are patterns related to height growth rates the same as those for diameter growth rates?

# Methods

### Study Areas

We compiled growth data from three permanent plot datasets in South Africa, Australia and Brazil. These three sites represent some of the only permanent savanna tree measurement plots in existence. Highly replicated data on tree growth rates, particularly in savannas, are limited due to the problems with tracking stems in frequently disturbed landscapes. In addition, low tree densities in savannas mean that plots must cover a large spatial extent in order to sample enough individual trees to make reliable estimates of species level growth rates. Indeed, in the three datasets used in this study, many species are represented by as few as 10 individuals, despite plots covering large spatial extents. As such, while comparisons of species growth rates along fine scale resource gradients within a site would

be desirable, this is not possible in this study. Instead, we estimated coarse differences in disturbance regimes and resource availability between the three sites. Rainfall and temperature data for each site were extracted from the Worldclim dataset (www.worldclim.org/bioclim). Fire return intervals were obtained from Archibald et al. (2013). For both fire and climate datasets, we extracted data from the 1 degree x 1 degree area that encapsulated our sites, and a mean, minimum and maximum was calculated across these areas. Leaf Area Index (LAI) was extracted from MODIS within the same coordinates as the climate variables, and a protected areas GIS layer (http://maps.tnc.org/gis_data.html) was overlaid on the raster grid, to ensure that LAI was only estimated for natural vegetation within the area. This was particularly relevant for the Brazilian savanna which is highly transformed and dominated by crops (Hoekstra et al. 2005). For each site we fitted a sinusoidal model to LAI measurements as a function of time (2009 – 2014), to obtain an estimate of seasonal variation in LAI. Soil nutrient data were extracted from the SoilGrids dataset (www.soilgrids.org), and these data are at a 250 m resolution. The variables we considered were cation exchange capacity, soil organic carbon, pH and percentage sand content, all estimated to a depth of 30 cm (Table 3). We extracted data from the 1 degree x 1 degree encapsulating our site, and identified the median, minimum and maximum value for each variable (Table 3). Figure S1 shows frequency distributions within the sampled area of soil properties for each site.

The three savanna regions varied in mean annual precipitation (MAP), rainfall seasonality, mean annual temperature (MAT), and fire return intervals (Table 2), as well as soil nutrient availability (Table 3), and LAI (Fig. 1). MAP was highest in Australia but this site experienced the most seasonal rainfall. MAP was lowest in South Africa, while rainfall seasonality was lowest in Brazil. Temperatures were similar in Brazil and South Africa, and highest in Australia. Fire return intervals were shortest in Australia and longest in South Africa. Fire frequencies observed in this dataset are presumed to be substantially manipulated by people, and so not necessarily truly reflective of historical fire regimes (Archibald et al. 2013). LAI was on average highest in Brazil, and lowest in South Africa, with reduced seasonal variation in Australia (Fig.1). No large scale spatial data quantifying large mammal herbivory levels exist for all three continents, but qualitatively the sites differ strongly in that mega-herbivores are present in South Africa, extinct since the end of the last ice age in Brazil, and historically absent in Australia (Archibald & Hempson 2016; Metcalf et al. 2016). Mega-herbivores should have a significant impact on tree architecture, growth rates and densities (Archibald & Bond 2003; Lehmann et al. 2011).

**Table 2** Mean climate and fire return interval (number of years between fire) for each site, with the range across the entire area provided in brackets.

| | MAP (mm) | Rainfall in driest quarter (mm) | MAT (°C) | Fire return interval (years) | Mega-herbivory effects |
|---|---|---|---|---|---|
| **Australia** | 1392 (1303 – 1569) | 8 (6 – 12) | 27.1 (26.2 – 27.4) | 0.80 (0.57 – 1.01) | Evolutionarily absent |
| **Brazil** | 1268 (1199 – 1352) | 133 (119 – 150) | 21.8 (20.9 – 22.3) | 1.40 (1.2 – 1.6) | Extinct for ~12000 years |
| **South Africa** | 625 (515 – 1050) | 24 (17 – 44 ) | 21.3 (15.2 – 22.0) | 5.98 (4.9 – 7.5) | Present |

Soil properties showed different patterns in each site (Table 3, Fig S1) South Africa and Australia had similarly high cation exchange capacity, but South Africa had the lowest levels of soil organic carbon. Brazil had the lowest cation exchange capacity, but the highest soil organic carbon levels. Brazil also had the lowest pH and the lowest percentage sand content, while South Africa had a pH close to neutral, and a similar sand content to Australia.

**Table 3** Median soil properties for each site, with the range across the entire area provided in brackets.

| Soil property | Australia | Brazil | South Africa |
|---|---|---|---|
| Cation Exchange Capacity ($cmol_c\ kg^{-1}$) | 10 [2; 35] | 8 [2; 30] | 10 [5; 43] |
| Soil Organic Carbon ($g\ kg^{-1}$) | 8 [0; 116] | 10 [5; 135] | 5 [0; 42] |
| pH | 5.8 [5.1; 6.6] | 5.5 [5; 6.5] | 6.5 [5.3; 7.6] |
| Sand content (%) | 60 [30; 72] | 52 [17; 73] | 61 [37; 74] |

## Growth rate datasets

Savanna tree measurement datasets are often sparsely replicated within species due to low tree densities, and difficulty in tracking individual trees over long periods of time. As such, we selected species based solely on their replication within the datasets. Once data were cleaned we included species if they were represented by 10 or more individuals across all plots. For all three datasets, we cleaned data by excluding individuals smaller than 1 cm in diameter or 0.5 m in height. We also excluded a growth increment if it was negative, if the diameter increment was greater than 2.5 cm $yr^{-1}$, or if the height increment was greater than 2 m $yr^{-1}$. After cleaning, we were able to quantify mean height growth rates for 68 species and diameter growth rates for 72 species in total. Species were selected based on their prevalence in permanent plots, and figure S2 shows the height-diameter allommetries of each sampled species. Permanent plots in each region were established independently, prior

to our study, and so differ in plot size, aerial extent, and time since establishment.

*Australian savanna*

Data for this site came from two sources: the "Kapalga" dataset (Andersen et al. 2003) and the "Three Parks" dataset (Murphy et al. 2010). At Kapalga (located in Kakadu National Park, 12.8°S, 132.8°E) woody species stem diameters (repeat-censused) and heights were measured in numerous 30 m x 30 m study plots as part of various experiments from the 1970s to the 1990s. For the early experiments all individuals greater than 1.4 m height were measured; for the later studies all individuals greater than 3 m height were measured. Stem diameters were measured at 1.3 m height and re-censused every 12 months. The "Three Parks" dataset contains stem-increment (diameter at breast height) repeat census data for 163 sites (20 m x 40 m) spread across three National Parks in Northern Territory (Kakadu 86, Litchfield 38 and Nitmiluk 39 sites). All individuals with diameter at breast height greater than 5 cm were measured between 1994 and 1997, and then twice more five years apart. We combined the two datasets and used data from all sites except those that were recorded as experiencing severe and frequent fires. Based on these data we calculated annual diameter increments of 2604 individuals from 21 species and annual height increments of 2043 individuals from 18 species.

*Brazilian savanna*

Stem increment data were obtained from permanent plots established by the Forestry Institute of Sao Paolo State at the Assis Research Station established in 2006. There were 30 plots each 50 m x 20 m in size, situated at 22.6°S and 50.4°W. Heights and diameters of all woody plants greater than 5 cm in diameter were measured in 2006, and then again in 2011. We calculated annual diameter increments for 2860 individuals of 35 species, and annual height increments for 2163 individuals of 35 species.

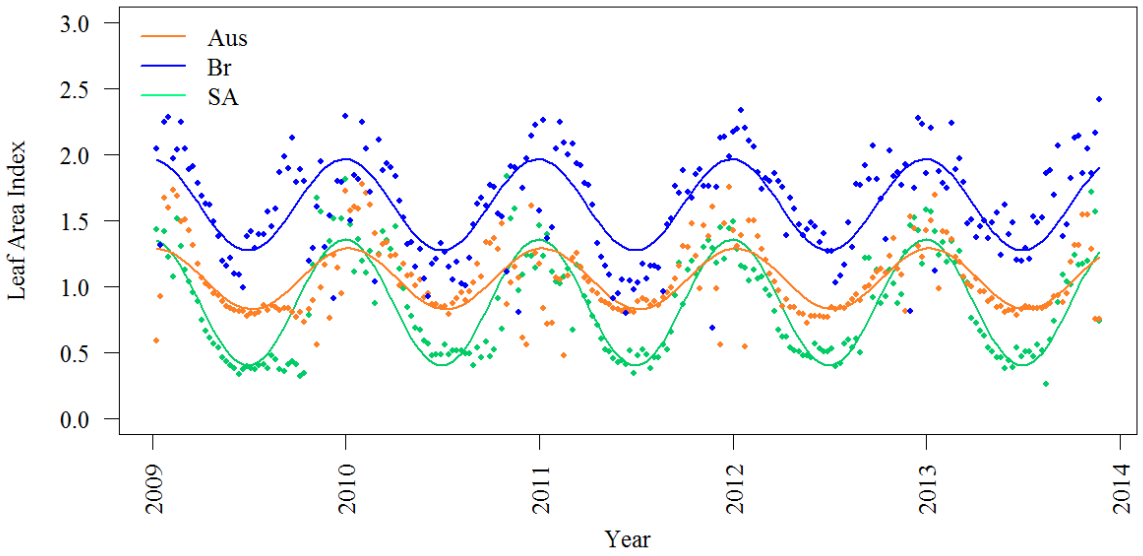



**Figure 1.** Mean leaf area index as a function of time for each study area (Aus = Australia, Br = Brazil, SA = South Africa.). LAI shows strongly seasonal trends at each of the three sites; a sinusoidal line-fit captured much of this variation ($R^2$ = 0.74, 0.41 and 0.34 for SA, Br and Aus respectively).

**South African savanna**

Species-level growth data were obtained from 84 permanent plots established by the South African Environmental Observation Network, located between 23.6°S, 30.8°E and 24.6°S, 31.5°E, and remeasured annually between 2008 and 2015. Fourteen plots were square (20 m x 20 m), while the remaining 70 plots were circular. In circular plots all trees > 30cm tall and within 5m from the centre-point were marked and remeasured annually. At least 3 replicate individuals for each species were required, so in order to achieve this replication some additional individuals were tagged up to a distance of 20m from the centre. These plots were remeasured annually between 2008 and 2015. Based on these data we calculated annual diameter increments from 1295 individuals of 16 species, and annual height increments from 1204 individuals of 15 species. Throughout the measurement period fire was actively excluded in only 20% of plots, but only six (experimentally planned) plots burnt over the course of the study, and we excluded burnt trees from this study.

**Growth rate calculations**

We calculated height and diameter annual increments for each individual using the formula $GR = (size_{y2} – size_{y1})/ (y2 – y1)$, where GR is annual absolute growth increment, and size is diameter or height of an individual at y1 and y2, which are the dates (in years) at which measurements were made. When multiple measurements existed for the same individual we took the mean of all positive annual increments for that individual (as negative increments are assumed to be years where trees are damaged due to fire or herbivory, and we are interested in potential growth rates, not actual growth rates). We then calculated the mean diameter growth rate (DGR) and height growth rate (HGR) of each species using the mean annual increment across all individuals of that species. We used the mean growth rate of each species as we considered this to be the most robust measure, due to the high levels of variation within each species, and the low levels of replication. This is evidenced by figure S3 showing the relationship between diameter and diameter growth rate for each species, and figure S4 showing the relationship between height and height growth rate for each species.

**Leaf and wood traits**

We sampled traits for 58 (17 in Australia, 25 in Brazil and 16 in South Africa) of the species for which growth data was quantified. All traits were sampled within or adjacent to the tree measurement plots. Traits measured were light-saturated photosynthetic rate ($A_{area}$), SLA, branch wood density (dry mass per fresh volume), and branch-level leaf dry mass:wood dry mass ratio. For all traits, three to eight individuals (with a minimum stem

diameter of 5 cm) of each species were sampled (see Table S1 for species mean trait and growth rate estimates, as well as numbers of replicates). Figure S2 indicates the mean size of individuals sampled for traits, relative to the size of individuals used to estimate growth rates for each species. Photosynthetic rate ($A_{area}$) measurements were made on one canopy leaf per individual, under ambient $CO_2$ concentrations (approx. 400 ppm) and temperature (25–27°C), and high light (1800-2000 $\mu mol\ m^{-2}s^{-1}$), using a Li-Cor 6400XT portable infrared gas analyser (LICOR Inc., Lincoln, NE, USA). SLA was calculated by dividing leaf area by dry mass, for three outer canopy leaves from each individual. Leaves were scanned and leaf area calculated using ImageJ software (U. S. National Institutes of Health, Bethesda, Maryland, USA). Leaves were oven dried at 60-70°C for at least five days and reweighed to determine dry mass. We measured branch wood density (BWD) for all individuals by removing a small section of outer canopy branch approximately 10mm in diameter and 40mm in length, and measuring fresh volumes of the sapwood by water displacement. Pith and bark were removed and branch wood density was determined by dividing dry sapwood mass by fresh sapwood volume. We sampled leaf:wood ratios at the branch scale. Measuring whole plant biomass allocation for adult trees is necessarily destructive and very difficult. Pickup et al. (2005) argued that species with higher relative allocation to leaf mass at the branch scale would either show faster branch-scale growth rate, and/or export more photosynthate to the rest of the plant, both of which would influence whole plant growth. To our knowledge this has not been tested (but see Chapter 2 of this thesis). One terminal, outer-canopy branch was sampled per individual. Leaves and wood on the terminal 80 cm were separated and dried in an oven at 70 °C for at least five days. Any side branches extending from the 80 cm segment were included with that segment. Fruit and flowers were generally absent, but when present they were discarded to allow direct comparison of leaf and wood material. We then calculated the ratio between leaf dry mass (LM) and wood dry mass (WM).

**Data analysis**

We performed all statistical analyses using R version 3.3.0 (R Development Core Team 2015). ANOVA was used to compare species mean diameter growth rates, height growth rates, and trait values of species across the three study areas. We compared the relationships between stem diameter and height growth rates in the three sites by fitting standardised major axes (SMA), which describe variation in both x and y ('smatr' R package, Warton et al. 2012).

We used ordinary least squares multiple linear regression to compare trait-growth

relationships among sites, and test for slope heterogeneity among sites. When slopes were found to be non-heterogeneous (indicated by a non-significant interaction between site and the independent variable) we re-ran the model without an interaction term, fitting a common slope, asking whether this common slope differed significantly from zero. Significance in these analyses was specified as $p <= 0.05$, but marginal significance at $0.05 < p <= 0.1$ was also noted. We also fitted trait-growth linear regressions to the full dataset (all species and sites together) to determine if there was a general relationship between traits and growth rates, regardless of site.

Backward stepwise regression (using the 'leaps' R package) was used to identify the best models (i.e. most influential traits) for the two growth rate metrics, both across all sites and within individual sites. These stepwise reduced models were compared to full models using Akaike's Information Criterion (AIC). A lower AIC implies the model is a better fit, and penalises a model for additional parameters (Hooten & Hobbs 2015).

# Results

*Growth rates*

Stem diameter growth rates (DGR) varied widely among species, from 0.14 to 0.96 cm $yr^{-1}$, and the three sites differed in mean DGR (ANOVA, $F= 29.0$, $p < 0.0001$, Table 4). On average, South African species had the fastest mean DGR (0.63 cm $yr^{-1}$, Fig. 2a), followed by Australian and Brazilian species (0.38 and 0.29 cm $yr^{-1}$ respectively). Stem height growth rates (HGR) also differed significantly between sites (ANOVA, $F = 9.82$, $p < 0.0001$, Fig. 2b), but here Australian species had the highest mean (0.46 m $yr^{-1}$, $p < 0.0001$), while South African and Brazilian species had similar, lower mean HGR (0.32 and 0.3 m $yr^{-1}$ respectively).

Height and diameter GRs were significantly correlated among species at each of the three sites ($R^2 = 0.18$, 0.42 and 0.72 for Brazil, Australia and South Africa respectively; all $p < 0.01$; Fig. 3). Considered another way, 28% (South Africa) to 82% (Brazil) of variation in HGR was independent from that in DGR, indicating that the two metrics convey substantially complementary information. In South Africa height and diameter GRs scaled almost in direct proportion (SMA slope = 1.06). In Australia the slope was 1.26, while the slope in Brazil was less than half this (0.58).

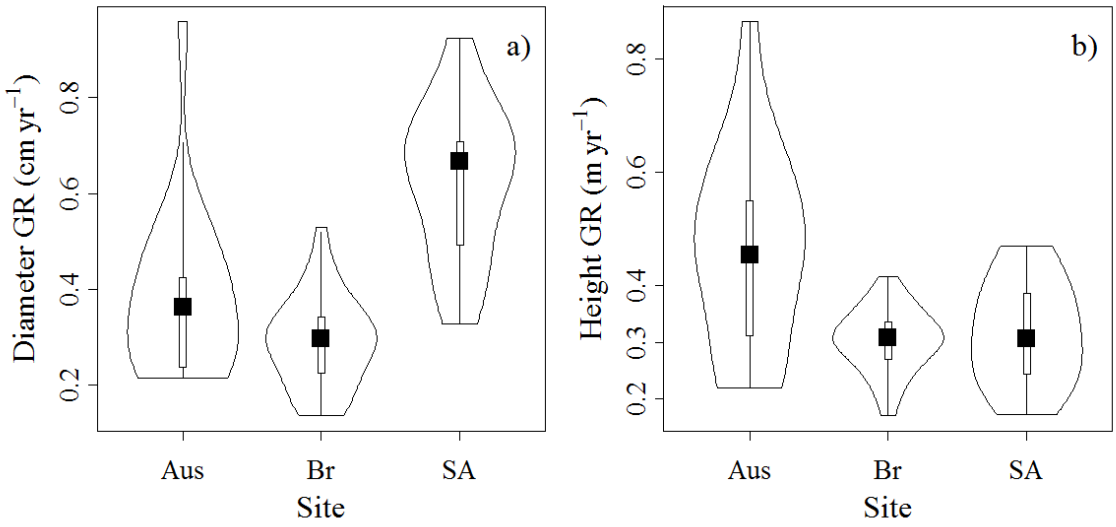



**Figure 2** Violin plots showing the probability density of different values of (a) species-mean stem-diameter growth rates, and b) species-mean height growth rates at the three sites. Black squares indicate the median while white box shows the inter-quartile range. Details of species and sample sizes for each site can be found in Table S1. Site abbreviations as for Figure 1.

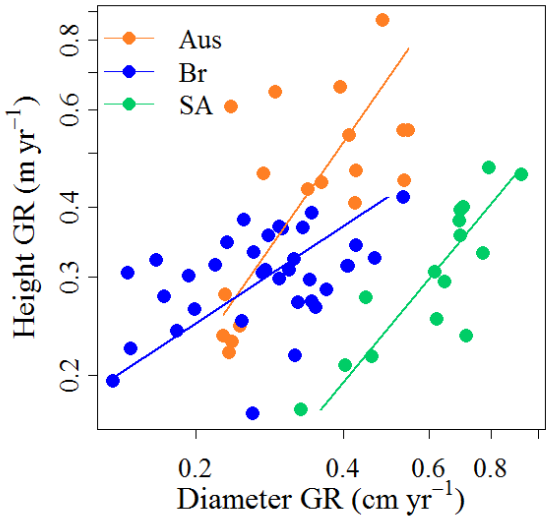



**Figure 3** Positive relationships between species-mean height growth rate and stem diameter growth rate across species in three savannas (axes are log-scaled). Fitted lines are site-specific SMA lines, with significant heterogeneity between the fitted slopes ($p = 0.003$). SMA slopes were 1.26 (Aus), 0.58 (Br) and 1.06 (SA). Details of species and sample sizes for each site can be found in Table S1. Site abbreviations as for Figure 1.

*Relationships between growth rates and traits*

Specific leaf area (SLA) varied significantly between sites ($p = 0.0001$; Fig. 4a). Mean SLA decreased from Brazil (110.7 $cm^2\ g^{-1}$) to South Africa (101.5 $cm^2\ g^{-1}$) to Australia (79.4 $cm^2\ g^{-1}$). SLA and DGR were unrelated at each site (all $p > 0.35$; Fig. 5a), and also considered as a whole: while the three slopes were deemed not to differ ($p = 0.9$), the common fitted slope was not significantly different from zero ($p = 0.21$; Table 4, Table 5). By contrast, SLA and HGR were negatively related across the full dataset (slope = -0.4, $R^2 = 0.12$, $p = 0.01$, Table 4). That said, within-site relationships were all non-significant (all $p > 0.2$), did not differ ($p = 0.26$), and the common slope fitted across them was again not significantly different from zero ($p = 0.4$, Table 5).

Light-saturated photosynthetic rate, $A_{area}$ , varied significantly among sites ($p < 0.0001$; Fig 4b). On average $A_{area}$ was highest for Australian species (17.6 µmol $m^{-2}\ s^{-1}$) and lowest for South African species (9.8 µmol $m^{-2}\ s^{-1}$). In Australia, photosynthetic rates were positively related to DGR with marginal significance ($p = 0.08$), and significantly positively related to HGR ($p = 0.004$, Table 4). Photosynthetic rates were unrelated to growth rates in other sites (All $p > 0.5$, Fig. 5b,d). There was a general positive relationship between $A_{area}$ and HGR across all sites ($p = 0.02$, Table 4). A regression including both $A_{area}$ and site explained 46 % of the variation in HGR, with $A_{area}$ contributing more to this variation than site (F-values 9.1 and 5.2 respectively), and a significant interaction between site and $A_{area}$ ($p = 0.0005$, Table 5).

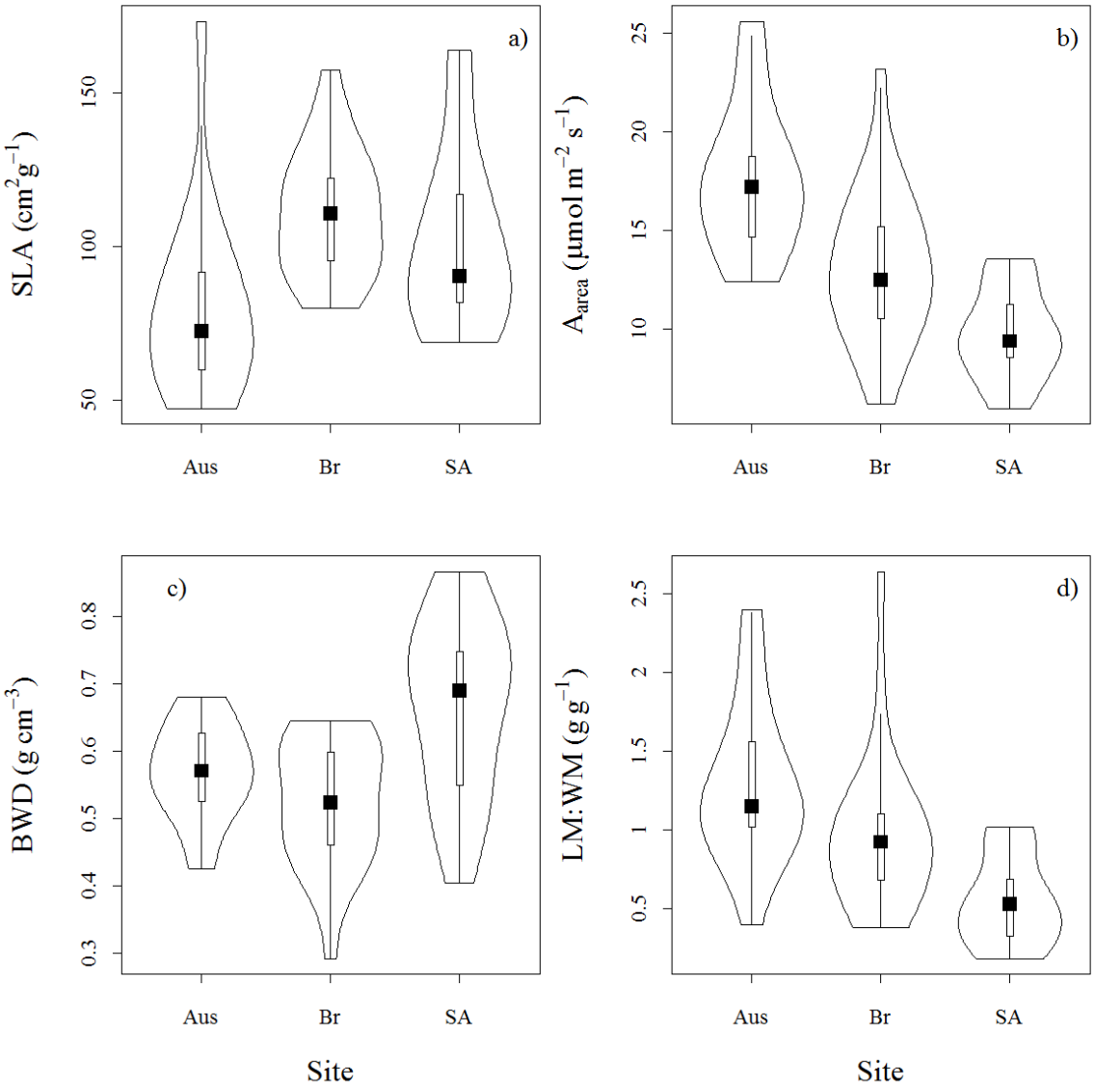



**Figure 4** Violin plots showing the probability density of different values of (a) Specific leaf area (SLA), (b) Light-saturated photosynthetic rate ($A_{area}$), (c) Branch sapwood density (BWD) and (d) Branch leaf mass:wood mass (LM:WM) ratio at the different sites. Black squares indicate the median while white box shows the inter-quartile range. Details of species and sample sizes for each site can be found in Table S1. Site abbreviations as for Figure 1.

Branch wood density (BWD) varied significantly among sites (p = 0.0002; Fig 4c), being significantly higher in the South African site (0.67 g $cm^{-3}$) than in Australia (0.57 g $cm^{-3}$) or Brazil (0.52 g $cm^{-3}$). When sites were considered separately, DGR was negatively related to BWD in both Brazil and South Africa (both p = 0.04, Fig. 6a, Table 4). Slopes did not differ among sites (p = 0.38), and the common fitted slope was significantly negative (slope = -0.45, p = 0.03; Table 5). HGR and BWD were unrelated at all three sites (All p > 0.3, Fig. 6c, Table 4). The three slopes did not differ (p = 0.28), and the common fitted slope was not different to zero (p = 0.85, Table 5).

**Table 4** Linear regression results with height and diameter growth rates as response variables and traits as predictor variables, first using the full dataset across all sites, and then data from each individual site. Details of species and sample sizes for each site can be found in Table S1. Significance is indicated by stars, marginal significance by † († p <= 0.1, * p <= 0.05, ** p <= 0.01, *** p <= 0.001).

| Response | Predictor | Site | slope | $R^2$ |
|---|---|---|---|---|
| Diameter Growth Rate | SLA | All | 0.04 | 0.001 |
| | | Aus | 0.30 | 0.06 |
| | | Br | 0.1 | 0.003 |
| | | SA | 0.23 | 0.05 |
| | $A_{area}$ | All | -0.28 | 0.05 |
| | | Aus | 0.86 | 0.22 † |
| | | Br | -0.1 | 0.008 |
| | | SA | -0.1 | 0.003 |
| | BWD | All | 0.27 | 0.02 |
| | | Aus | 0.18 | 0.006 |
| | | Br | -0.65 | 0.17 * |
| | | SA | -0.48 | 0.28 * |
| | LM:WM | All | -0.16 | 0.04 |
| | | Aus | 0.45 | 0.18 |
| | | Br | 0.1 | 0.02 |
| | | SA | 0.08 | 0.02 |
| Height Growth Rate | SLA | All | -0.4 | 0.12 ** |
| | | Aus | -0.63 | 0.14 |
| | | Br | 0.06 | 0.004 |
| | | SA | 0.02 | 0.0003 |
| | $A_{area}$ | All | 0.32 | 0.11 * |
| | | Aus | 1.64 | 0.57 ** |
| | | Br | -0.08 | 0.02 |
| | | SA | -0.08 | 0.004 |
| | BWD | All | -0.02 | 0.0004 |
| | | Aus | 0.77 | 0.08 |
| | | Br | -0.05 | 0.003 |
| | | SA | -0.2 | 0.04 |
| | LM:WM | All | 0.22 | 0.14 ** |
| | | Aus | 0.28 | 0.06 |
| | | Br | 0.15 | 0.14 † |
| | | SA | 0.12 | 0.05 |

Site abbreviations: Aus = Australia, Br = Brazil, SA = South Africa. Trait abbreviations: specific leaf area (SLA), light-saturated photosynthetic rate ($A_{area}$), branch sapwood density (BWD), branch leaf mass:wood mass ratio (LM:WM).

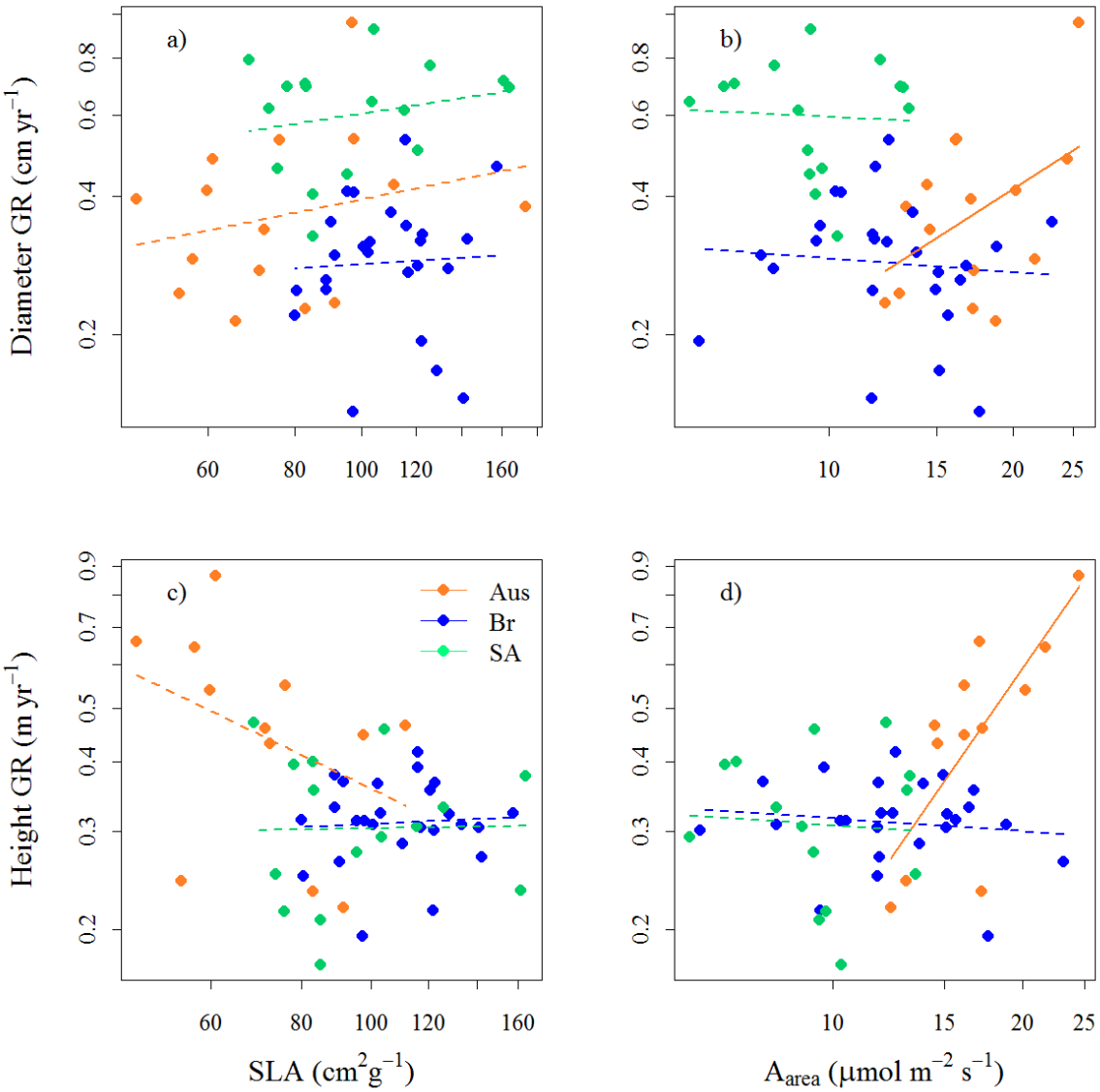



**Figure 5** Diameter (a-b) and height (c-d) growth rates as a function of traits (a,c) Specific leaf area (SLA) and (b,d) light-saturated photosynthetic rate ($A_{area}$), separated by site. Solid lines indicate slopes are significantly different from zero (at $p < 0.1$) and dashed lines indicate non-significant slopes. Details of species and sample sizes for each site can be found in Table S1. Model slopes and explained variance can be found in Table 4. Site abbreviations as for Figure 1.

Branch-scale leaf:wood mass ratios (LM:WM) differed significantly between sites ($p < 0.0001$, Fig. 4d). Mean LM:WM decreased from Australia (1.28) to Brazil (0.96), to South Africa (0.55). LM:WM was not significantly related to DGR in any sites (All $p > 0.1$, Fig. 6b). The three slopes were non-heterogeneous ($p = 0.39$), and their common slope not significantly different from zero ($p = 0.12$). By contrast, LM:WM was positively related to HGR across the full dataset ($p = 0.007$, Table 4), and also within Brazil with marginal significance ($p = 0.06$, Fig. 6d). HGR - LM:WM slopes did not differ significantly between the three sites ($p = 0.83$) and the common-fitted slope was positive with marginal significance ($p = 0.06$, Table 5).

**Table 5** ANOVA output from linear models of growth rate measures with individual traits and site as predictor variables. Details of species and sample sizes for each site can be found in Table S1. Significance is indicated by stars, marginal significance by † († p <= 0.1, * p <= 0.05, ** p <= 0.01, *** p <= 0.001)

| Response | Predictors | $R^2$ | F (trait) | F (site) | F (trait x site) | Common slope |
|---|---|---|---|---|---|---|
| Diameter Growth Rate | Site | 0.46 *** | | 29.0 *** | | |
| | SLA, site | 0.49 *** | 0.1 | 24.5 *** | | n.s. |
| | $A_{area}$, site | 0.46 *** | 4.3 * | 19.2 *** | | n.s. |
| | BWD, site | 0.52 *** | 2.7 | 26.9 *** | | -0.45 * |
| | LM:WM, site | 0.49 *** | 3.9 * | 23.4 *** | | n.s. |
| Height Growth Rate | Site | 0.23 *** | | 9.82 *** | | |
| | SLA, site | 0.24 ** | 7.8 ** | 3.6 * | | n.s. |
| | $A_{area}$, site | 0.46 *** | 9.1 ** | 5.2 ** | 9.13 *** | |
| | BWD, site | 0.23 ** | 0.02 | 7.1 ** | | n.s. |
| | LM:WM, site | 0.28 *** | 9.1 ** | 4.7 * | | 0.16 † |

Site and trait abbreviations as for Table 4.

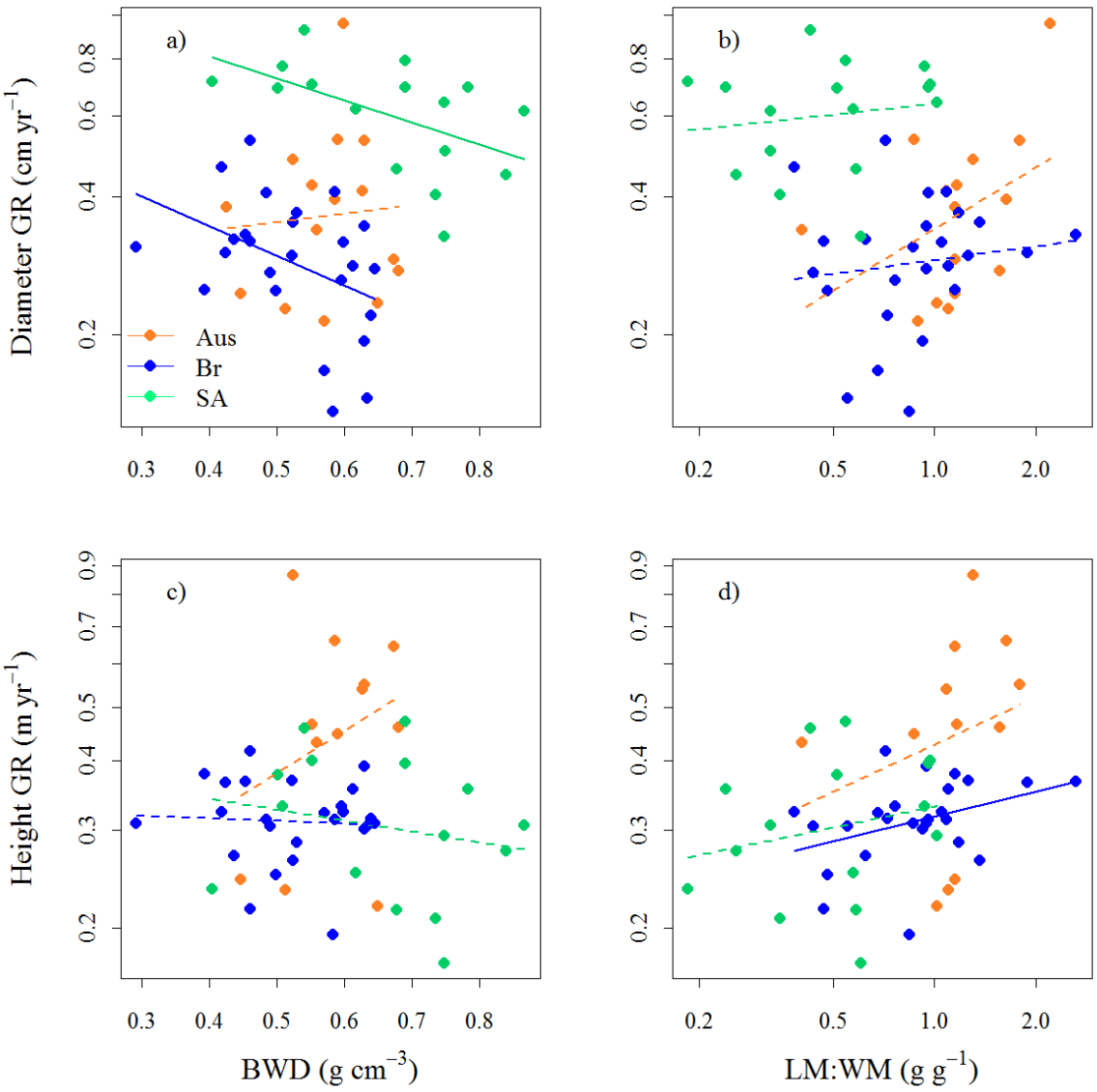



**Figure 6** Diameter (a-b) and height (c-d) growth rates as a function of traits (a,c) branch sapwood density (BWD) and (b,d) branch leaf mass to wood mass ratio (LM:WM), separated by site. Solid lines indicate slopes are significantly different from zero (at $p < 0.1$) and dashed lines indicate non-significant slopes. Details of species and sample sizes for each site can be found in Table S1. Model slopes and explained variance can be found in Table 4. Site abbreviations as for Figure 1.

*Multivariate trait-growth relationships*

We used backward stepwise regression to identify trait combinations which best explained variation in growth rates across all sites (Table 6a), and also in each individual site (Table 6b-d). DGR (across all sites) was not well explained by traits (Table 6a). A model including all traits explained only 7% of the variation in DGR, and this was captured fully by $A_{area}$ and BWD (Table 6a). In contrast, significant variation in HGR was explained by traits. The best model of HGR included SLA and LM:WM as predictors, which together explained 18% of the variation in HGR. This model explained almost as much variation in HGR as site alone ($R^2 = 0.23$, Table 5).

The most influential traits driving GR varied among sites. SLA and $A_{area}$ together explained 40% of the variation in DGR of Australian species (Table 6b), while variation in HGR of Australian species was most parsimoniously explained by just $A_{area}$ ($R^2 = 0.57$). BWD best explained variation in DGR in both Brazilian ($R^2 = 0.17$) and South African species ($R^2 = 0.28$) as well as HGR in South African species, though this was not significant ($R^2 = 0.16$, Table 6c-d). HGR variation in Brazilian species was best explained by LM:WM, though the relationship was only marginally significant ($p = 0.06$, $R^2 = 0.14$).

**Table 6** Multiple linear regressions of diameter and height growth rate. Full models including all traits (SLA, $A_{area}$, LM:WM and BWD) are on left and best models identified using backward stepwise regression are on right. Models were run separately using (a) the full dataset with all sites, and (b-d) data from each individual site. Amount of variance explained by the model is indicated by $R^2$. Best stepwise models were identified using AIC, a lower AIC suggests a more parsimonious model. F-values of each trait in the reduced model are given, and the direction of the coefficient shown in brackets. Details of species and sample sizes for each site can be found in Table S1. Significance is indicated by stars, marginal significance by †

(† p <= 0.1, * p <= 0.05, ** p <= 0.01, *** p <= 0.001)

| | Site | Growth metric | Full model | | Best model | | | |
|---|---|---|---|---|---|---|---|---|
| | | | AIC | $R^2$ | Predictors | F | AIC | $R^2$ |
| a) | All | Diameter | -15.3 | 0.07 | $A_{area}$<br>BWD | 2.5 (-)<br>1.3 (+) | -19.7 | 0.07 |
| | | Height | -57.4 | 0.22 * | SLA<br>LM:WM | 6.3 (-) *<br>4.4 (+) * | -59.1 | 0.18 ** |
| b) | Aus | Diameter | -7.2 | 0.44 | SLA<br>$A_{area}$ | 1.2 (+) †<br>6.7 (+) * | -10.0 | 0.40 * |
| | | Height | -5.9 | 0.60 | $A_{area}$ | 13.5 (+) ** | -11.2 | 0.57 ** |
| c) | Br | Diameter | -21.5 | 0.24 | BWD | 4.9 (-) * | -25.6 | 0.17 * |
| | | Height | -51.9 | 0.19 | LM:WM | 3.9 (+) † | -56.5 | 0.14 † |
| d) | SA | Diameter | -14.5 | 0.30 | BWD | 5.0 (-) * | -20.1 | 0.28* |
| | | Height | -9.4 | 0.22 | BWD | 2.2 (-) | -14.3 | 0.16 |

Site and trait abbreviations as for Table 4.

# Discussion

Based on studies undertaken in closed forest systems, ecologists often make assumptions about the way in which traits influence growth rates more generally (Table 1). Here we aimed to test the generality of field-measured trait – growth relationships across three distinct savanna regions, which differed in all of rainfall, soil quality, fire frequency, mega-herbivore density, and thus leaf area index. Species mean growth rates and trait values differed significantly among the three savannas, but there were some consistencies regarding trait – growth relationships. The most consistent results regarding each trait, and supporting expectations in Table 1, were: (i) SLA was unrelated to diameter growth rate in any site; (ii) there was a general positive relationship between $A_{area}$ and height growth rate across the full dataset; (iii) there was a common negative slope between branch wood density and diameter growth rate in all sites; and (iv) there was a common positive slope between LM:WM and height growth rate in all sites, and a general positive relationship between those variables across the full dataset. Despite these general consistencies, the specifics for each site varied, both regarding the relative influence of each trait, and the direction of growth that was most influenced. These results present a first investigation into how traits are related to both diameter and height growth rates of adult plants in three biogeographically distinct savannas, and here we discuss both general consistencies as well as potential reasons for observed inconsistencies.

*Growth rates and site conditions*

The three savannas vary with respect to both top-down (disturbance regimes, here represented by mega-herbivory and fire frequency) and bottom-up (resource availability, here represented by soil quality and rainfall) controls on tree growth, all of which are known to influence tree cover (Bond 2008; Lehmann et al. 2011; Dantas et al. 2016). Fire is most frequent at the Australian site (Table 2), and Australian species had the highest mean height growth rates, a growth strategy normally associated with fire escape in savannas (Higgins et al. 2000; Bond et al. 2012). In a region dominated by megaherbivores, South African species had relatively low mean height growth rates but much higher mean diameter growth rates than either Australian or Brazilian species. Such patterns of growth have been previously linked to mammalian herbivory, as well as aridity (Archibald & Bond 2003). The fast diameter growth rates in South Africa may be linked to the higher cation exchange capacity and pH of the soils, but surprisingly, South African species also had significantly higher branch wood density on average than species in other sites, and wood

density has been shown to be lower when nutrients are more readily available (Mäkinen et al. 2002; Slik et al. 2010). But wood density has also been linked to drought tolerance (Hacke et al. 2001), and South Africa receives only half the mean annual precipitation of other sites. Further, relatively lower investment in height growth should reduce water transport costs and associated hydraulic risks, such as cavitation due to increased trunk length (Ryan & Yoder 1997). Brazilian species on average had the lowest mean height and diameter growth rates. The trees in this site have been protected from fire for decades, due to a general policy of fire exclusion in the Brazilian savanna (Durigan & Ratter 2016). Under low levels of disturbance, tree cover is expected to increase (Lehmann et al. 2014), and indeed the Brazilian site had the highest canopy cover (LAI, Fig. 1) and this may suppress species growth rates due to limited access to light (Hoffmann et al. 2012). The slower growth rates in Brazil could also be linked to lower soil quality, and this should be further investigated.

*Site differences in trait - growth relationships*

While at first glance the observed trait – growth relationships appear highly variable across sites, we found important consistencies, many of which were only apparent because we considered both height and diameter growth rates. The only prior field study we know of concerning savanna species found a positive relationship between growth rates and SLA (Prior et al. 2004), though this study was not restricted to savanna species. We expected a generally non-significant relationship, as has been more often observed for adult plants (Gibert et al. 2016). Indeed, this was the case in all sites when considering diameter growth rate, but we found a general negative relationship between SLA and height growth rate across the full dataset. On closer inspection this appeared to be largely due to site level differences in both variables: the fast height growth rates of Australian species coupled with their significantly lower SLA (within sites HGR and SLA were unrelated, and the common fitted slope was not different to zero). While Gibert et al. (2016) predict that in general there should be no effect of SLA on growth in adult plants, they also highlight that in large plants, low SLA can favour fast growth rates because the marginal cost of building sapwood to support new leaf area negates any potential growth benefits from higher SLA leaves (Falster et al. 2011; Gibert et al. 2016, and see chapter 2 of this thesis). Indeed, Australian savanna species have been shown to be taller at a given diameter than species in African savannas (Moncrieff et al. 2014). Further, low SLA species tend to have longer leaf lifespans, and so have the potential to, over time, build more massive canopies than high SLA species. This can lead to total canopy productivity at least as high as that of high SLA species, thus increasing overall growth (Matyssek 1986; Bond 1989; Gower et al. 1993;

Reich 1998), but of course, this benefit of leaf longevity is irrelevant if leaves are regularly removed by deciduousness. The Australian savanna had the least seasonal variation in LAI (Fig. 1), suggesting a greater proportion of evergreen species, which has been previously observed (Bowman & Prior 2005), and may promote the importance of leaf traits in this site (Tomlinson et al. 2014).

We expected a positive relationship between photosynthetic rates and growth rates across all sites, but we only observed this in Australia where the relationship was convincingly positive, particularly with regards to height growth rate (photosynthetic rate explained 57 % variation in Australian species HGR). It is unclear why there should be such a strong relationship observed in the Australian site, and not elsewhere. In South Africa, it may be because photosynthetic rates were measured in a year of drought, and plants have been shown to reduce stomatal conductance, and thus photosynthetic rate, at such times (Yordanov et al. 2000). There is no similar explanation for Brazil, and at this site the measured photosynthetic rates were not particularly low (Franco et al. 2005). Perhaps the relative importance of traits shifts as a result of site conditions, and in Brazil and South Africa we found that branch wood density and LM:WM explained more variation in growth rates than leaf traits.

In South Africa, branch wood density explained more variation in diameter growth rate than any other trait. Wood density may contribute to drought tolerance (Hacke et al. 2001) as well as defend against damage from megaherbivores (Hemborg & Bond 2006), though there is no clear evidence that higher wood density reduces herbivore damage. Either way, high wood density is an important survival trait, and past studies have shown strong trade-offs between growth and survival (Kraft et al. 2010; Wright et al. 2010). As a result, one would expect South African species to be slow growing overall, but in fact they had the fastest diameter growth rates of all sites. However, at any given diameter growth rate species had a lower height growth rate than species in other sites, so in terms of overall biomass accumulation there may not be any great disparity between sites. Interestingly, in South Africa height growth rate was not significantly related to any traits.

With regards to Brazilian species there were a few points of interest. Firstly, while branch wood density explained most variation in diameter growth rate, and LM:WM explained most variation in height growth rate, these relationships were both relatively weak. In fact traits explained less than 20% of the variation in growth rate in either direction. Secondly, Brazilian species were the slowest growing with respect to both height and diameter. This

is surprising because this region is thought to have a historically frequent fire regime (Dantas, Pausas, et al. 2013), and so we might expect species to invest in rapid height growth to escape flame height just as in Australia (Higgins et al. 2000; Bond et al. 2012). However, previous studies have suggested that species in this region invest heavily in fire resistance traits such as bark thickness, which is assumed to reduce their growth rates, and also removes the need for rapid growth to avoid fire (Hoffmann & Franco 2003; Hoffmann et al. 2012; Dantas & Pausas 2013). Heavy bark investment may be decoupling growth from the traits measured here. Alternatively, as mentioned above, the higher canopy cover in this site (due to reduced fire) may act to suppress height growth rates. Support for this theory lies in the amount of variation in height growth rates that is independent of diameter growth rates at this site (82 %) while they are more tightly linked in other sites, with slopes close to 1. We might expect more variation in the diameter - height growth relationships if species are not achieving their maximum potential growth rates.

*Branch leaf mass:wood mass ratios*

Logic suggests that, all else equal, higher whole plant biomass allocation to leaves relative to wood should result in faster growth (Walters et al. 1993; Pickup et al. 2005; Tomlinson et al. 2014). However, in frequent fire savannas, biomass allocation to roots (for stored reserves of carbohydrates to enable resprouting after fire) should also be of importance (Bell et al. 1996; Wigley et al. 2009; Tomlinson et al. 2012). In seedlings, Tomlinson et al. (2012) found that the relative allocation of carbon to roots differs among species from the three regions; in African and South American species, allocation to roots was relatively high, while in Australian species, the persistent nature of evergreen leaves prevented increased investment below ground (Tomlinson et al. 2012). The generally weaker relationships between leaf traits and growth rates in South Africa and Brazil compared to Australia may be a result of higher allocation to below ground biomass in these sites (Tomlinson et al. 2012). Tomlinson et al. (2012) suggest leaf traits should be of most importance in Australia. Indeed we found this, but we also suspected that, particularly in Australia, higher biomass allocation to leaves would drive faster growth. We estimated leaf:wood ratios at the branch scale, and found a positive relationship with both diameter and height growth rates in all sites. However, the only marginally significant relationship was in Brazil, not Australia. The general positive relationship between LM:WM and growth was predicted by Pickup et al. (2005) and to our knowledge has not previously been tested (but see Chapter 2 for a similar result in rainforest vegetation). Here we showed that in combination with SLA, LM:WM ratio measured on a branch could explain 18 % of the variation in height growth rate across all sites. In other words, knowledge of leaf tissue

properties (in the form of SLA), and the relative amount of these tissues on a branch, can explain significant variation in growth rates across three biogeographically distinct savanna regions.

*Future directions*

The issue of how disturbance regimes and resource availability interact to drive growth rates and select for different trait combinations in savannas is a fascinating, and very much open, topic of research (Tomlinson et al. 2014; Wigley et al. 2016). Here our results suggest continental-scale differences in trait-growth strategies, but we were unable to definitively attribute these differences to any given factor. This is largely because we were limited to just three sites. Ideally, in a study such as this, we would have a much larger number of sites spanning a broad gradient of environmental conditions, which we are able to measure (for example quantitative estimates of herbivore densities). Unfortunately, the three sites in this study represent some of the only permanent savanna tree measurement plots in existence. To accurately estimate a species growth rate, one needs to make repeat measures of a large number of individuals. Or at least, if this is not possible, to measure a smaller number of individuals regularly over a much greater time period. But savannas are subject to two key constraints in this regard; firstly, they are highly disturbed systems, and tracking individual trees over long periods is problematic; and secondly, tree densities are low, and so large spatial extents must be sampled in order to obtain sufficient replication within species. This immediately makes fine-scale comparisons of environmental conditions more difficult. These considerations do not make it impossible to undertake the fine-scale comparisons that are sorely lacking in savanna literature (Parr et al. 2014), but they undoubtedly highlight the need for the establishment of more permanent tree measurement plots, as well as the need for collaboration between study groups. Only once we address the sever lack of data within savanna systems, can we begin to address more in-depth questions such as impacts of phylogenetic relatedness and environmental gradients on trait-growth relationships.

## Conclusion

This is the first known study to test the generality of trait-growth relationships across multiple savanna systems using field-measured data, and also the first to consider both height and growth rates. Site specific relationships appeared to be tightly linked to the prevailing disturbance regime. Fast height growth rates in Australia were linked to high fire frequency, and were most tightly related to leaf traits. Here, the higher prevalence of evergreen species may have contributed to the relative importance of leaf traits for growth.

Wood density, on the other hand, was most tightly linked to diameter growth rates in South Africa. South African species had the fastest diameter growth rates, and investment in growing wide has previously been linked to the presence of mega-herbivores (Archibald & Bond 2003; Moncrieff et al. 2014). Branch LM:WM ratios explained most variation in height growth rates of Brazilian species, which were not tightly linked to any other traits. This measure of biomass allocation has never been compared across savanna systems, nor has its effect on growth rates. We found that branch LM:WM explained significant variation in height growth rates across all sites, regardless of site. Our results suggest that leaf- and wood-related functional traits do underpin growth across savanna regions, but that the relative strength of relationships varies between sites, and consistency with general expectations is only apparent when both height and diameter growth rates are considered. Trait – growth strategies appear linked to the nature of disturbance regimes. Hence, human mediated changes in both fire (ie. fire suppression or increased fire) and herbivore pressures (i.e the loss of megaherbivores via hunting and poaching in South Africa, or the increase in feral megaherbivores in places like Australia) along with climate change will undoubtedly impact vegetation dynamics, but in ways that are difficult to predict without a region-specific appreciation of the ecology of savannas.

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# Supplementary Information

***Table S1*** *Species mean diameter growth rate (DGR) and height growth rate (HGR) values, with the number of individuals used to calculate this value shown in brackets. Species mean specific leaf area (SLA), branch wood density (BWD), leaf mass to wood mass ratio at 80 cm along the branch (LM:WM) and photosynthetic rate ($A_{area}$). The number of individuals sampled to obtain trait values is in the final column (n).*

| Site | Species | Family | DGR (n) cm $yr^{-1}$ | HGR (n) m $yr^{-1}$ | SLA $cm^2$ $g^{-1}$ | BWD g $cm^{-3}$ | LM:WM g $g^{-1}$ | $A_{area}$ µmol $m^{-2}$ $s^{-1}$ | n |
|---|---|---|---|---|---|---|---|---|---|
| Aus | *Buchanania obovata* | Anacardiaceae | 0.25 (72) | 0.24 (32) | 54.6 | 0.45 | 1.2 | 13.1 | 5 |
| Br | *Tapirira guianensis* | Anacardiaceae | 0.41 (44) | 0.31 (23) | 97.7 | 0.48 | 1.0 | 10.5 | 5 |
| SA | *Lannea schweinfurthii* | Anacardiaceae | 0.77 (22) | 0.33 (21) | 126.0 | 0.51 | 0.9 | 8.2 | 5 |
| SA | *Sclerocarya birrea* | Anacardiaceae | 0.71 (48) | 0.40 (43) | 83.0 | 0.55 | 1.0 | 7.0 | 5 |
| Br | *Annona crassiflora* | Annonaceae | 0.31 (24) | 0.31 (18) | 100.7 | 0.29 | 0.9 | 18.8 | 5 |
| Br | *Xylopia aromatica* | Annonaceae | 0.25 (124) | 0.38 (90) | 89.1 | 0.39 | 1.2 | 15.0 | 5 |
| Aus | *Livistona inermis* | Arecaceae | 0.23 (16) | 0.28 (17) | NA | NA | NA | NA | 5 |
| Br | *Gochnatia polymorpha* | Asteraceae | 0.35 (60) | 0.26 (45) | 90.4 | 0.52 | 1.4 | 23.2 | 5 |
| Aus | *Cochlospermum fraseri* | Bixaceae | 0.38 (18) | NA | 173.1 | 0.43 | 1.2 | 13.4 | 5 |
| Br | *Eriotheca gracilipes* | Bombacaceae | 0.25 (54) | 0.25 (54) | 80.6 | 0.50 | 0.5 | 11.8 | 4 |
| Br | *Protium heptaphyllum* | Burseraceae | 0.17 (152) | 0.28 (94) | NA | NA | NA | NA | NA |
| SA | *Commiphora mollis* | Burseraceae | 0.72 (27) | 0.23 (29) | 161.1 | 0.40 | 0.2 | NA | 4 |
| Aus | *Erythrophloem chlorostachys* | Caesalpiniaceae | 0.53 (114) | 0.45 (268) | 97.6 | 0.59 | 0.9 | 16.2 | 5 |
| Aus | *Terminalia ferdinandiana* | Combretaceae | 0.42 (188) | 0.41 (229) | NA | NA | NA | NA | 5 |
| Br | *Terminalia glabrescens* | Combretaceae | 0.22 (22) | 0.31 (14) | 80.0 | 0.64 | 0.7 | 15.7 | 3 |
| SA | *Combretum apiculatum* | Combretaceae | 0.64 (177) | 0.29 (165) | 103.5 | 0.75 | 1.0 | 5.9 | 5 |
| SA | *Combretum hereroense* | Combretaceae | 0.33 (37) | 0.17 (42) | 85.2 | 0.75 | 0.6 | 10.3 | 5 |
| SA | *Terminalia sericea* | Combretaceae | 0.70 (50) | 0.40 (48) | 78.1 | 0.69 | 1.0 | 6.8 | 5 |
| SA | *Diosphyros mespiliformis* | Ebenaceae | 0.92 (23) | 0.46 (24) | 104.4 | 0.54 | 0.4 | 9.4 | 5 |
| Aus | *Petalostigma pubescens* | Euphorbiaceae | 0.23 (42) | 0.22 (19) | 91.5 | 0.65 | 1.0 | 12.4 | 5 |
| Br | *Mabea fistulifera* | Euphorbiaceae | 0.33 (60) | 0.37 (37) | 122.7 | 0.45 | 2.6 | 11.8 | 5 |

| Site | Species | Family | DGR (n) cm $yr^{-1}$ | HGR (n) m $yr^{-1}$ | SLA $cm^2$ $g^{-1}$ | BWD g $cm^{-3}$ | LM:WM g $g^{-1}$ | $A_{area}$ µmol $m^{-2}$ $s^{-1}$ | n |
|---|---|---|---|---|---|---|---|---|---|
| Br | *Maprounea guianensis* | Euphorbiaceae | 0.43 (19) | 0.34 (12) | NA | NA | NA | NA | NA |
| Br | *Pera obovata* | Euphorbiaceae | 0.30 (66) | 0.30 (48) | NA | NA | NA | NA | NA |
| SA | *Croton megalobotrys* | Euphorbiaceae | 0.69 (37) | 0.38 (40) | 163.9 | 0.50 | 0.5 | 13.2 | 5 |
| Aus | *Acacia difficilis* | Fabaceae | 0.96 (16) | NA | 97.0 | 0.60 | 2.2 | 25.6 | 5 |
| Aus | *Acacia latescens* | Fabaceae | 0.53 (64) | 0.55 (60) | 76.0 | 0.63 | 1.8 | 16.1 | 5 |
| Aus | *Acacia mimula* | Fabaceae | 0.28 (26) | 0.46 (11) | 71.2 | 0.68 | 1.6 | 17.3 | 5 |
| Br | *Acosmium subelegans* | Fabaceae | 0.14 (25) | 0.19 (18) | 97.2 | 0.58 | 0.8 | 17.6 | 5 |
| Br | *Anadenanthera falcata* | Fabaceae | 0.41 (70) | 0.31 (56) | 95.4 | 0.59 | 1.1 | 10.3 | 5 |
| Br | *Copaifera langsdorffii* | Fabaceae | 0.27 (412) | 0.30 (303) | 117.1 | 0.49 | 0.4 | 15.1 | 5 |
| Br | *Dimorphandra mollis* | Fabaceae | 0.46 (31) | 0.32 (25) | 157.3 | 0.42 | 0.4 | 11.9 | 4 |
| Br | *Machaerium acutifolium* | Fabaceae | 0.35 (78) | 0.39 (57) | 116.2 | 0.63 | 0.9 | 9.7 | 4 |
| Br | *Platypodium elegans* | Fabaceae | 0.28 (11) | 0.36 (18) | 120.8 | 0.61 | 1.1 | 16.8 | 5 |
| Br | *Stryphnodendron rotundifolium* | Fabaceae | 0.32 (103) | 0.27 (104) | 142.3 | 0.44 | 0.6 | 11.9 | 5 |
| SA | *Albizia harveyi* | Fabaceae | 0.62 (144) | 0.25 (127) | 73.6 | 0.62 | 0.6 | 13.6 | 5 |
| SA | *Colophospermum mopane* | Fabaceae | 0.46 (158) | 0.22 (147) | 75.7 | 0.68 | 0.6 | 9.8 | 7 |
| SA | *Dalbergia melanoxylon* | Fabaceae | 0.45 (74) | 0.28 (45) | 95.5 | 0.84 | 0.3 | 9.3 | 5 |
| SA | *Dichrostachys cinerea* | Fabaceae | 0.62 (130) | 0.31 (126) | 115.6 | 0.87 | 0.3 | 8.9 | 5 |
| SA | *Philenoptera violacea* | Fabaceae | 0.79 (55) | 0.47 (61) | 68.7 | 0.69 | 0.5 | 12.1 | 5 |
| SA | *Senegalia nigrescens* | Fabaceae | 0.69 (139) | 0.36 (134) | 83.3 | 0.78 | 0.2 | 13.1 | 5 |
| SA | *Vachellia exuvialis* | Fabaceae | 0.40 (163) | 0.21 (152) | 85.0 | 0.74 | 0.3 | 9.5 | 4 |
| Br | *Nectandra cuspidata* | Lauraceae | 0.30 (67) | 0.37 (52) | 102.3 | 0.42 | 1.9 | 13.9 | 5 |
| Br | *Ocotea corymbosa* | Lauraceae | 0.32 (427) | 0.32 (323) | 103.1 | 0.60 | 1.1 | 12.5 | 5 |
| Br | *Persea wildenovii* | Lauraceae | 0.35 (24) | 0.27 (14) | NA | NA | NA | NA | NA |
| Aus | *Planchonia careya* | Lecythidaceae | 0.23 (70) | 0.23 (85) | 82.9 | 0.51 | 1.1 | 17.2 | 5 |
| Br | *Byrsonima laxiflora* | Malpighiaceae | 0.37 (54) | 0.29 (40) | 110.5 | 0.53 | 1.2 | 13.7 | 5 |
| Br | *Pseudolmedia laevigata* | Moraceae | 0.23 (15) | 0.35 (11) | NA | NA | NA | NA | NA |
| Br | *Rapanea umbellata* | Myrsinaceae | 0.26 (31) | 0.33 (19) | 89.0 | 0.60 | 0.8 | 16.4 | 5 |
| Aus | *Corymbia bleeseri* | Myrtaceae | 0.29 (100) | 0.64 (16) | 56.9 | 0.67 | 1.2 | 21.7 | 5 |

| Site | Species | Family | DGR (n) cm $yr^{-1}$ | HGR (n) m $yr^{-1}$ | SLA $cm^2$ $g^{-1}$ | BWD g $cm^{-3}$ | LM:WM g $g^{-1}$ | $A_{area}$ µmol $m^{-2}$ $s^{-1}$ | n |
|---|---|---|---|---|---|---|---|---|---|
| Aus | *Corymbia polysciada* | Myrtaceae | 0.36 (146) | 0.44 (34) | NA | NA | NA | NA | NA |
| Aus | *Corymbia porrecta* | Myrtaceae | 0.41 (203) | 0.54 (263) | 59.8 | 0.63 | 1.1 | 20.2 | 5 |
| Aus | *Eucalyptus miniata* | Myrtaceae | 0.48 (667) | 0.87 (454) | 60.9 | 0.52 | 1.3 | 24.5 | 5 |
| Aus | *Eucalyptus tetrodonta* | Myrtaceae | 0.40 (543) | 0.66 (343) | 47.3 | 0.59 | 1.6 | 17.1 | 5 |
| Aus | *Xanthostoemon paradoxus* | Myrtaceae | 0.34 (92) | 0.43 (139) | 72.4 | 0.56 | 0.4 | 14.6 | 5 |
| Br | *Myrcia bella* | Myrtaceae | 0.32 (19) | 0.22 (18) | 122.0 | 0.46 | 0.5 | 9.6 | 5 |
| Br | *Myrcia lingua* | Myrtaceae | 0.15 (38) | 0.31 (19) | 140.9 | 0.63 | 0.6 | 11.8 | 6 |
| Br | *Myrcia multiflora* | Myrtaceae | 0.18 (56) | 0.24 (45) | NA | NA | NA | NA | NA |
| Br | *Myrcia venulosa* | Myrtaceae | 0.15 (16) | 0.22 (13) | NA | NA | NA | NA | NA |
| Br | *Ouratea spectabilis* | Ochnaceae | 0.26 (13) | 0.17 (10) | NA | NA | NA | NA | NA |
| Aus | *Pandanus spiralis* | Pandanaceae | 0.24 (120) | 0.61 (18) | NA | NA | NA | NA | NA |
| Aus | *Grevillea decurrens* | Proteaceae | 0.42 (26) | 0.47 (19) | 111.7 | 0.55 | 1.2 | 14.5 | 5 |
| Aus | *Persoonia falcata* | Proteaceae | 0.21 (21) | NA | 65.9 | 0.57 | 0.9 | 18.7 | 5 |
| SA | *Ziziphus mucronata* | Rhamnaceae | 0.50 (11) | NA | 120.6 | 0.75 | 0.3 | 9.3 | 5 |
| Aus | *Gardenia megasperma* | Rubiaceae | 0.24 (37) | 0.23 (10) | NA | NA | NA | NA | NA |
| Br | *Amaioua intermedia* | Rubiaceae | 0.28 (51) | 0.31 (35) | 133.5 | 0.65 | 0.9 | 8.1 | 5 |
| Br | *Faramea montevidensis* | Rubiaceae | 0.19 (142) | 0.30 (95) | 122.3 | 0.63 | 0.9 | 6.2 | 4 |
| Br | *Pouteria ramiflora* | Sapotaceae | 0.34 (30) | 0.30 (26) | NA | NA | NA | NA | NA |
| Br | *Siparuna guianensis* | Sipuranaceae | 0.20 (53) | 0.26 (32) | NA | NA | NA | NA | NA |
| Aus | *Brachychiton diversifolious* | Sterculiaceae | 0.54 (23) | 0.55 (26) | NA | NA | NA | NA | NA |
| Br | *Qualea cordata* | Vochysiaceae | 0.17 (63) | 0.32 (50) | 128.5 | 0.57 | 0.7 | 15.2 | 5 |
| Br | *Qualea grandiflora* | Vochysiaceae | 0.30 (26) | 0.37 (25) | 91.6 | 0.52 | 1.3 | 7.8 | 4 |
| Br | *Vochysia tucanorum* | Vochysiaceae | 0.53(380) | 0.42 (320) | 115.9 | 0.46 | 0.7 | 12.6 | 4 |

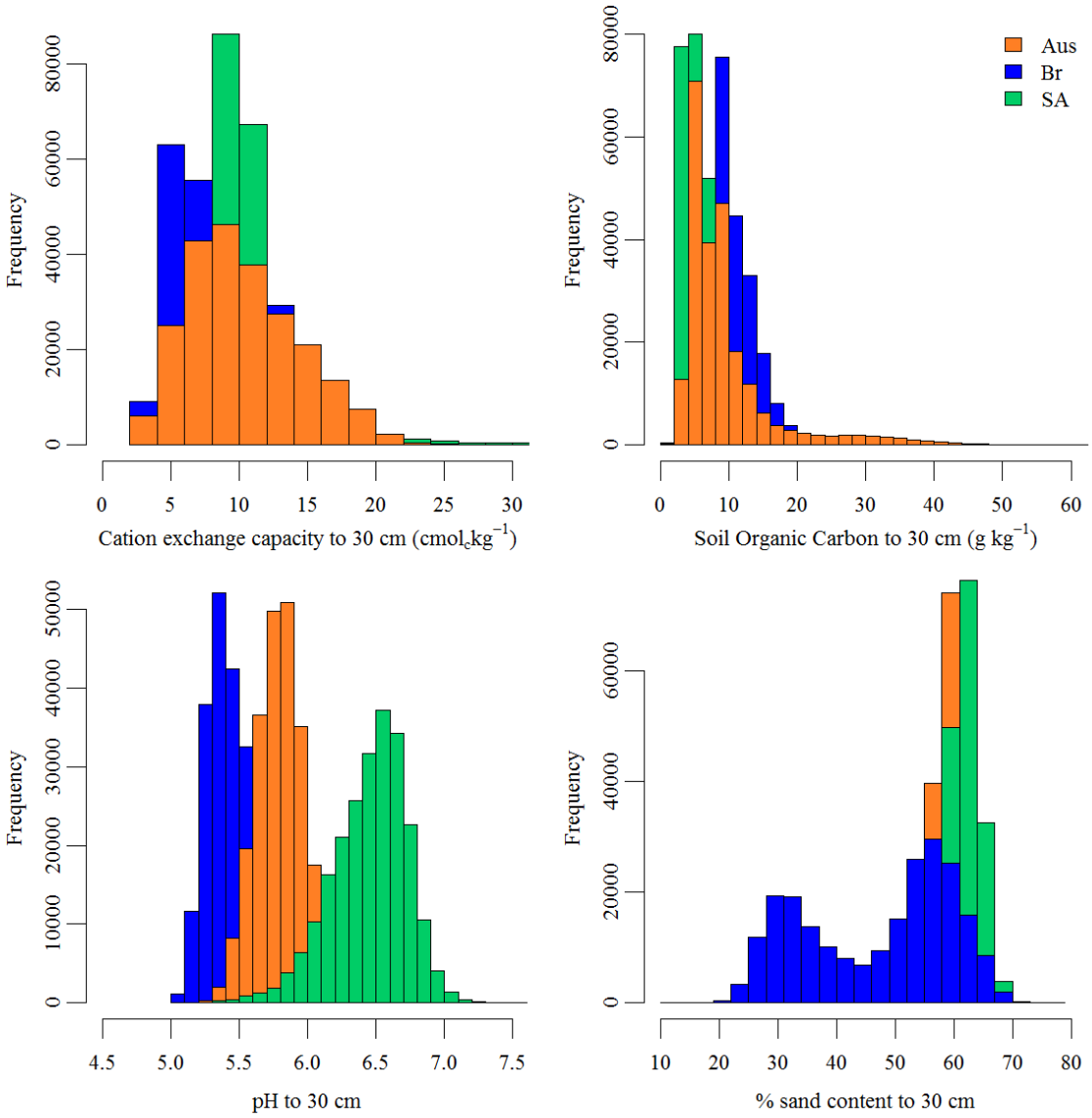



***Figure S1*** *Frequency distribution of soil properties (cation exchange capacity, soil organic carbon, pH and percentage sand content) in the top 30 cm of soil. Data were obtained from www.soilgrids.org, and are gridded at a resolution of 250 m. Data were extracted from the 1 degree x 1 degree area that encapsulated our sites.*

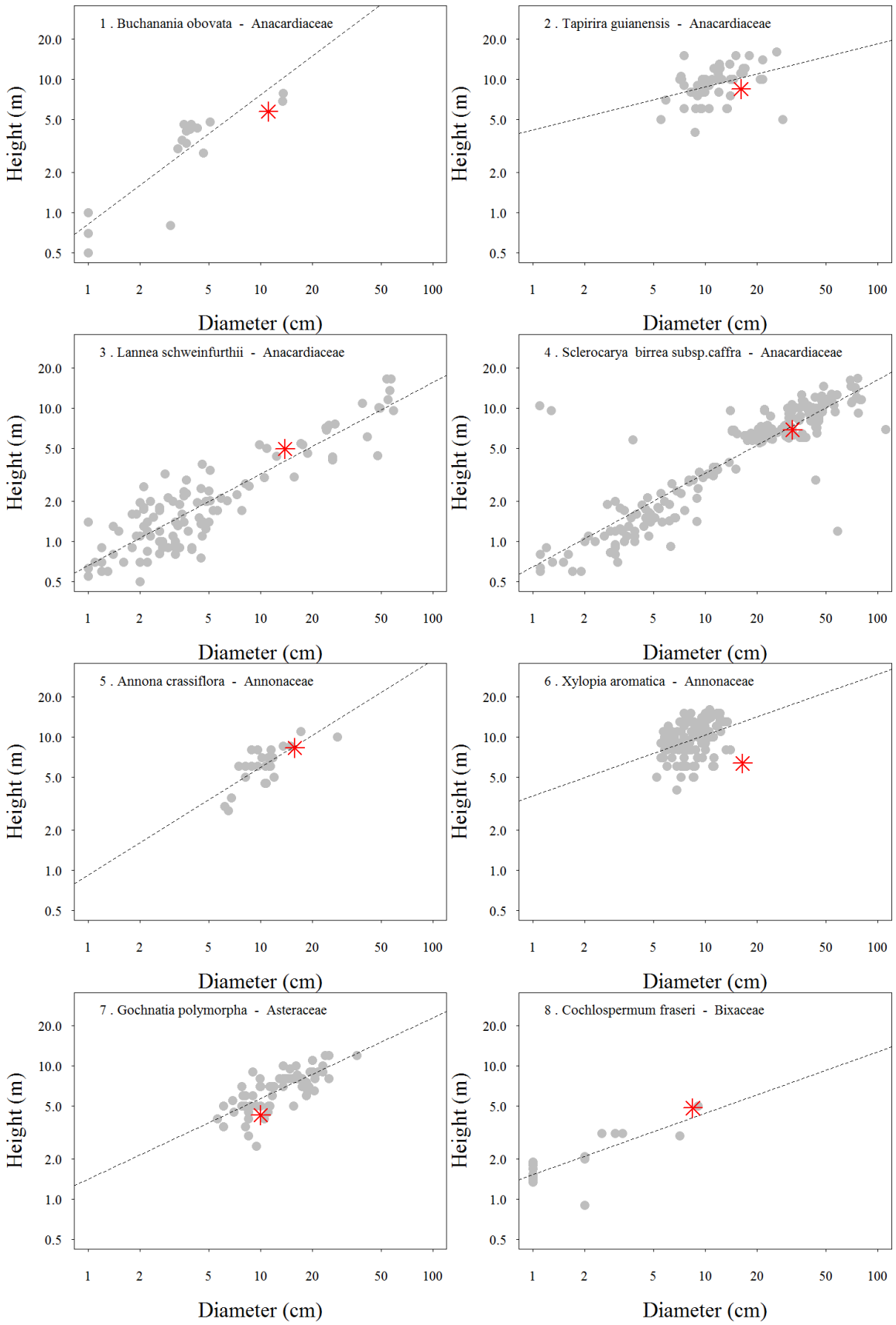



***Figure S2*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

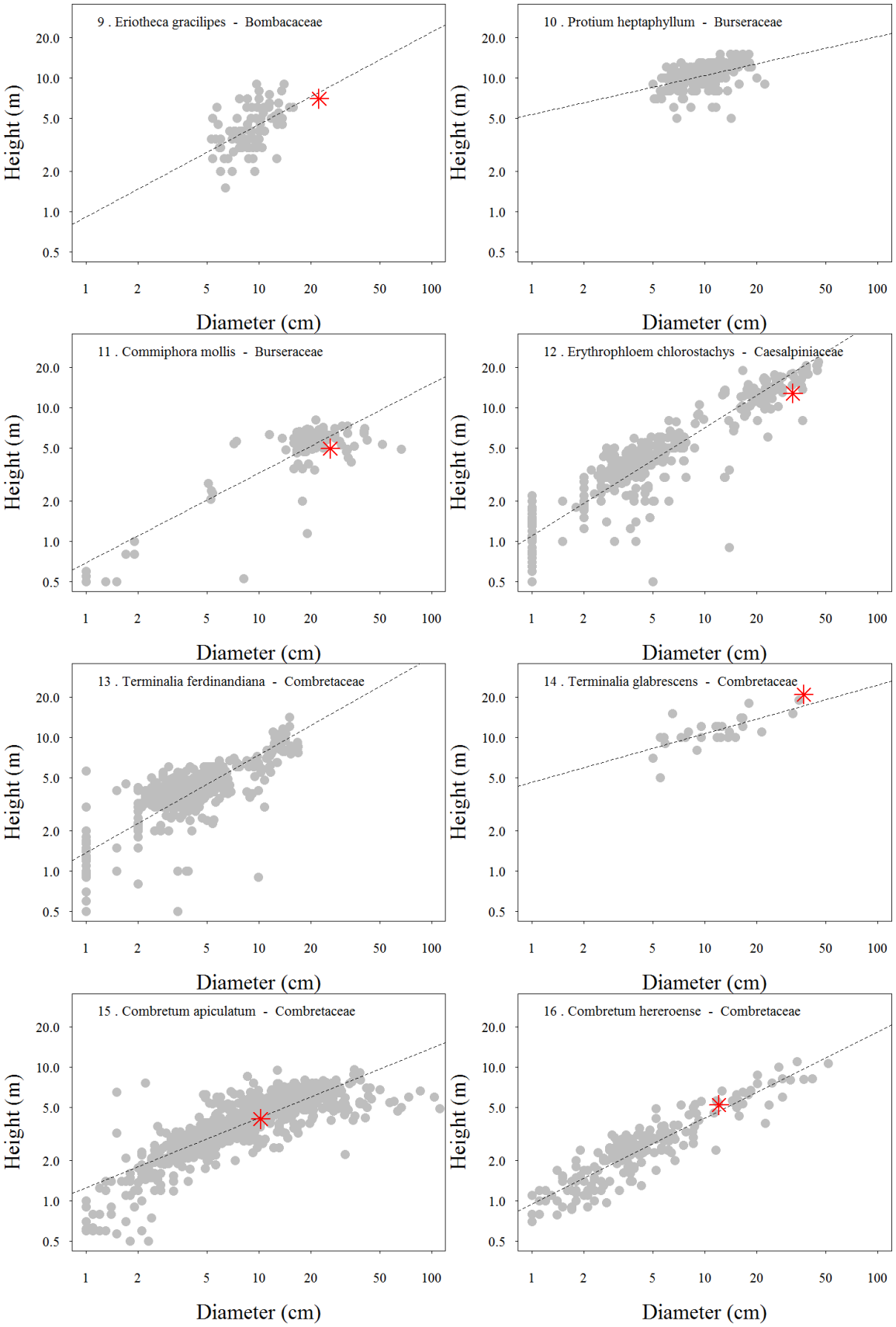



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

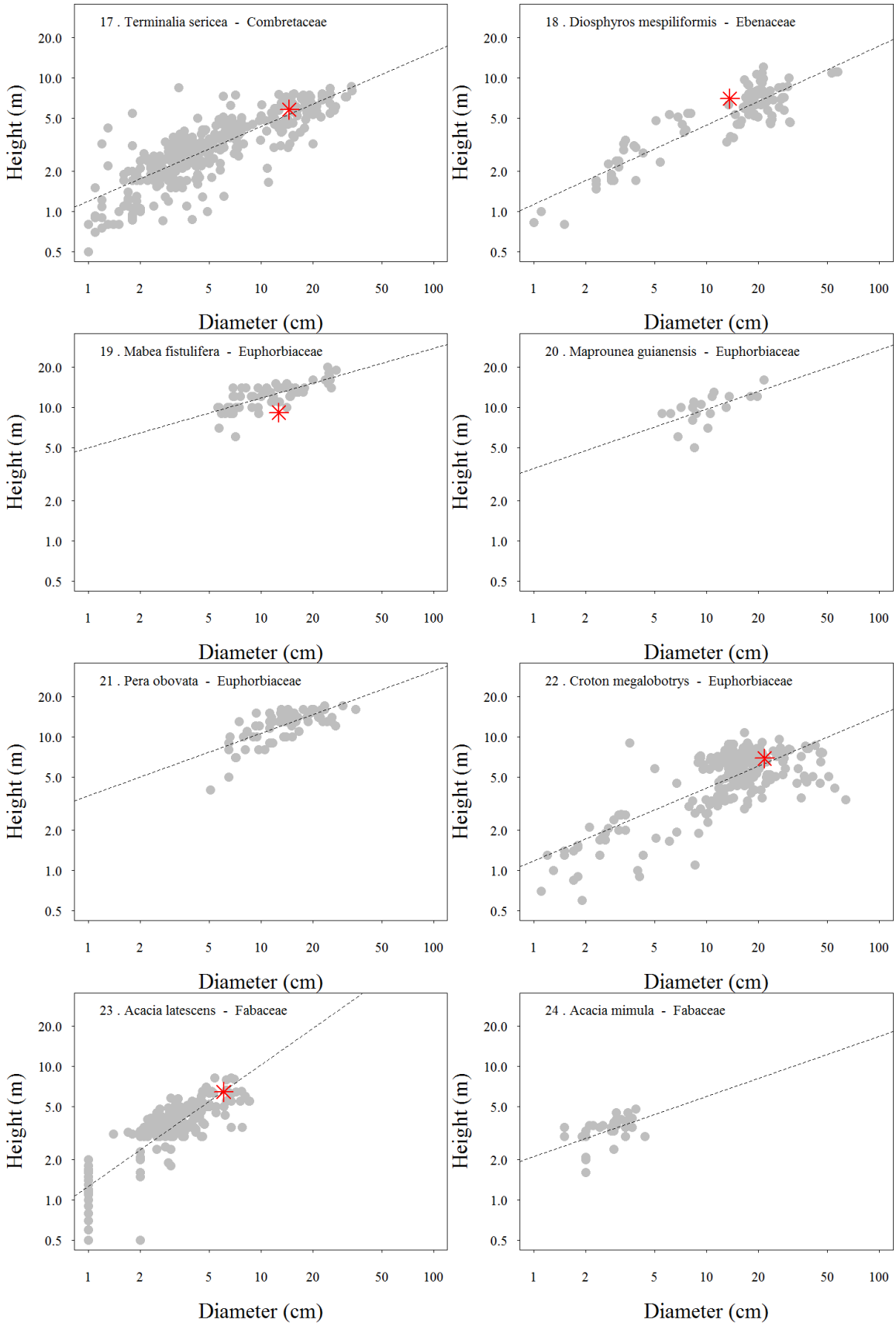



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

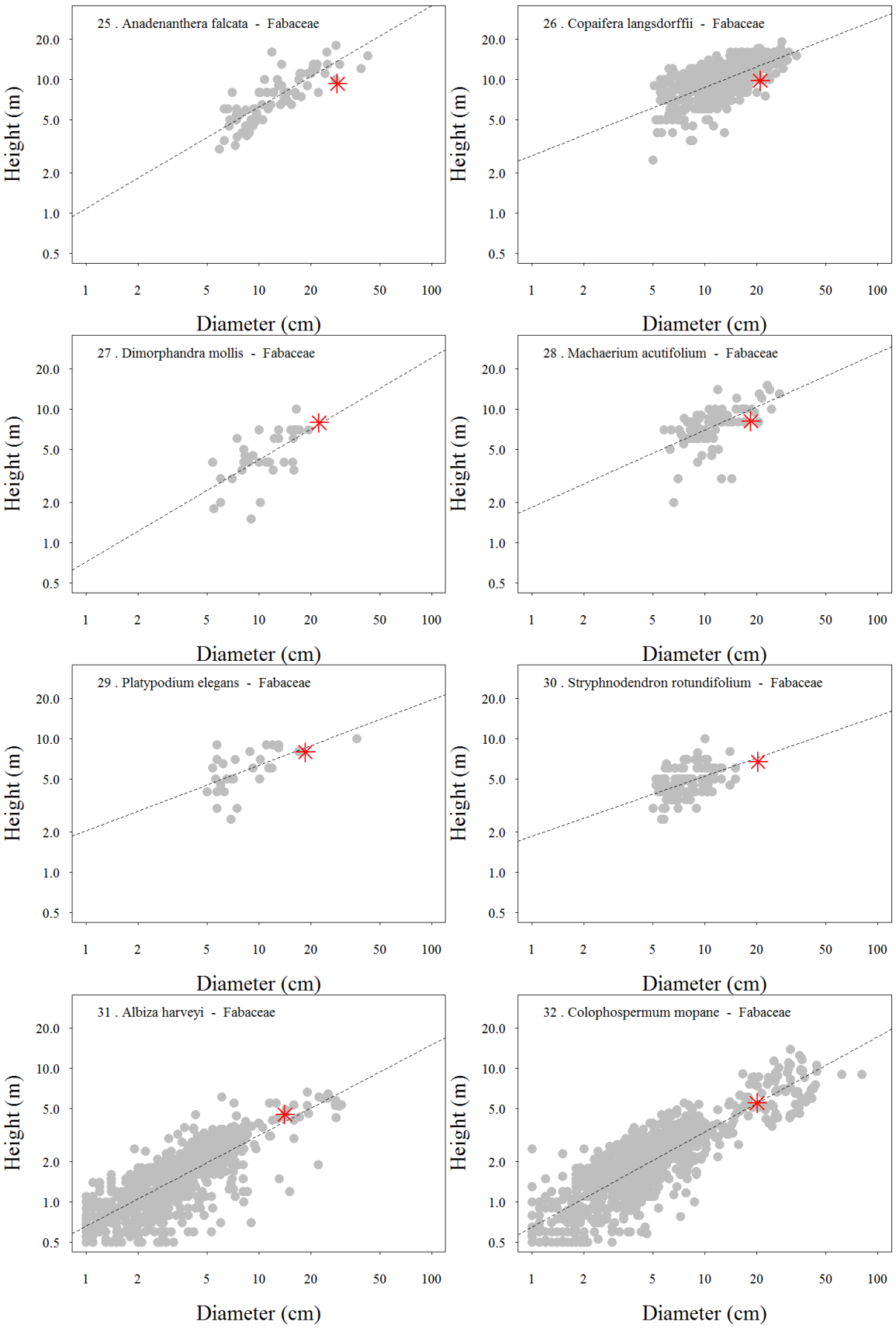



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

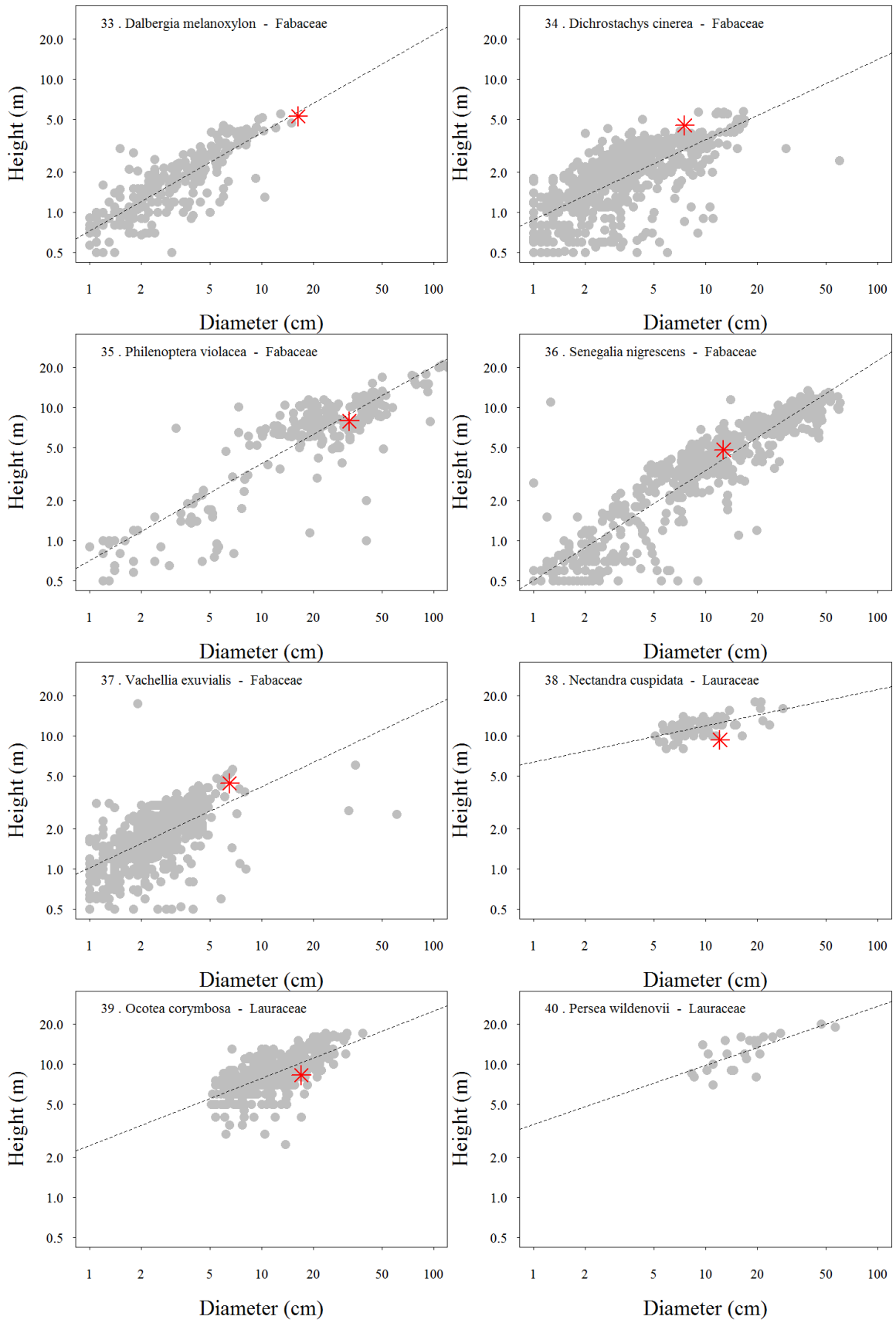



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

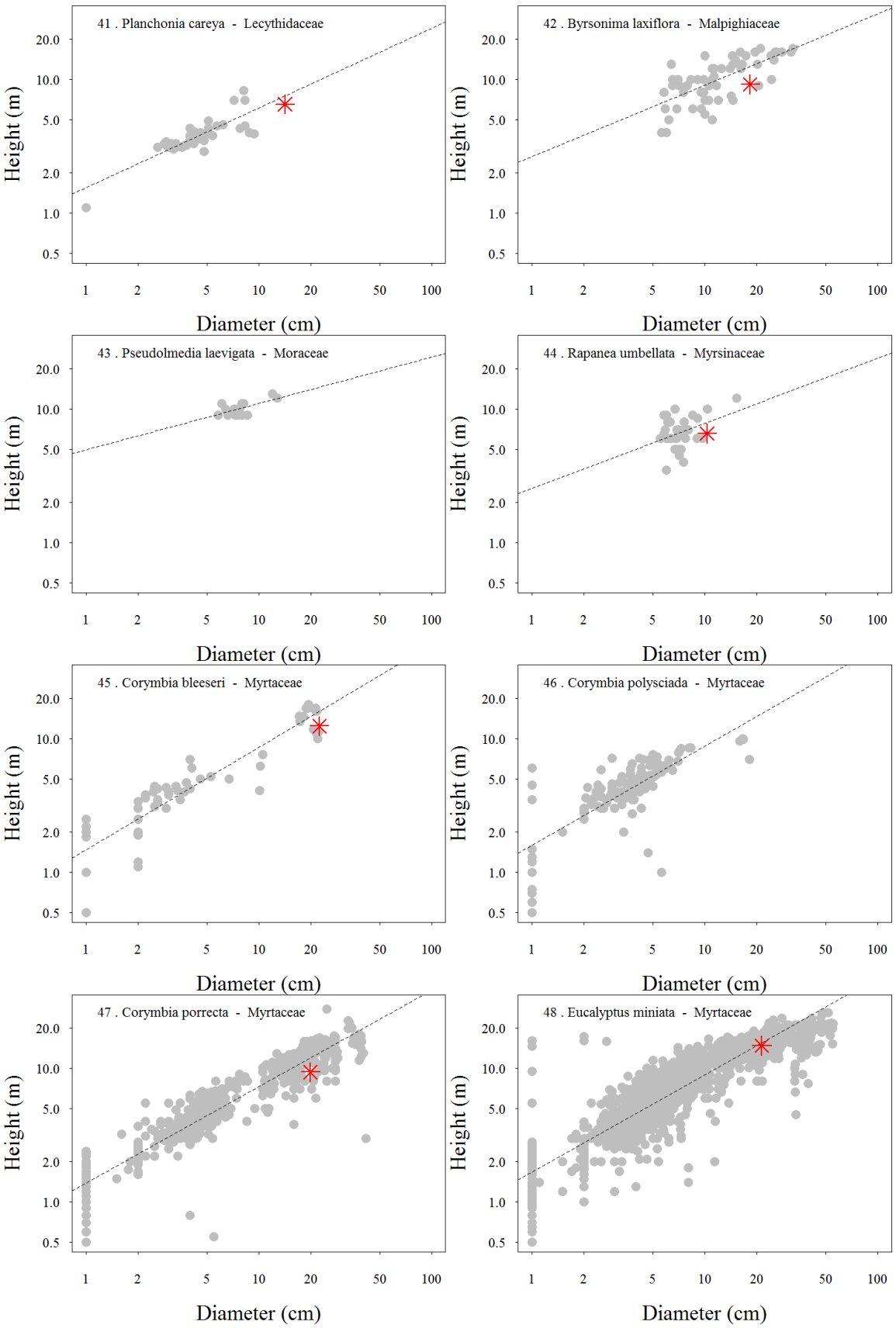



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

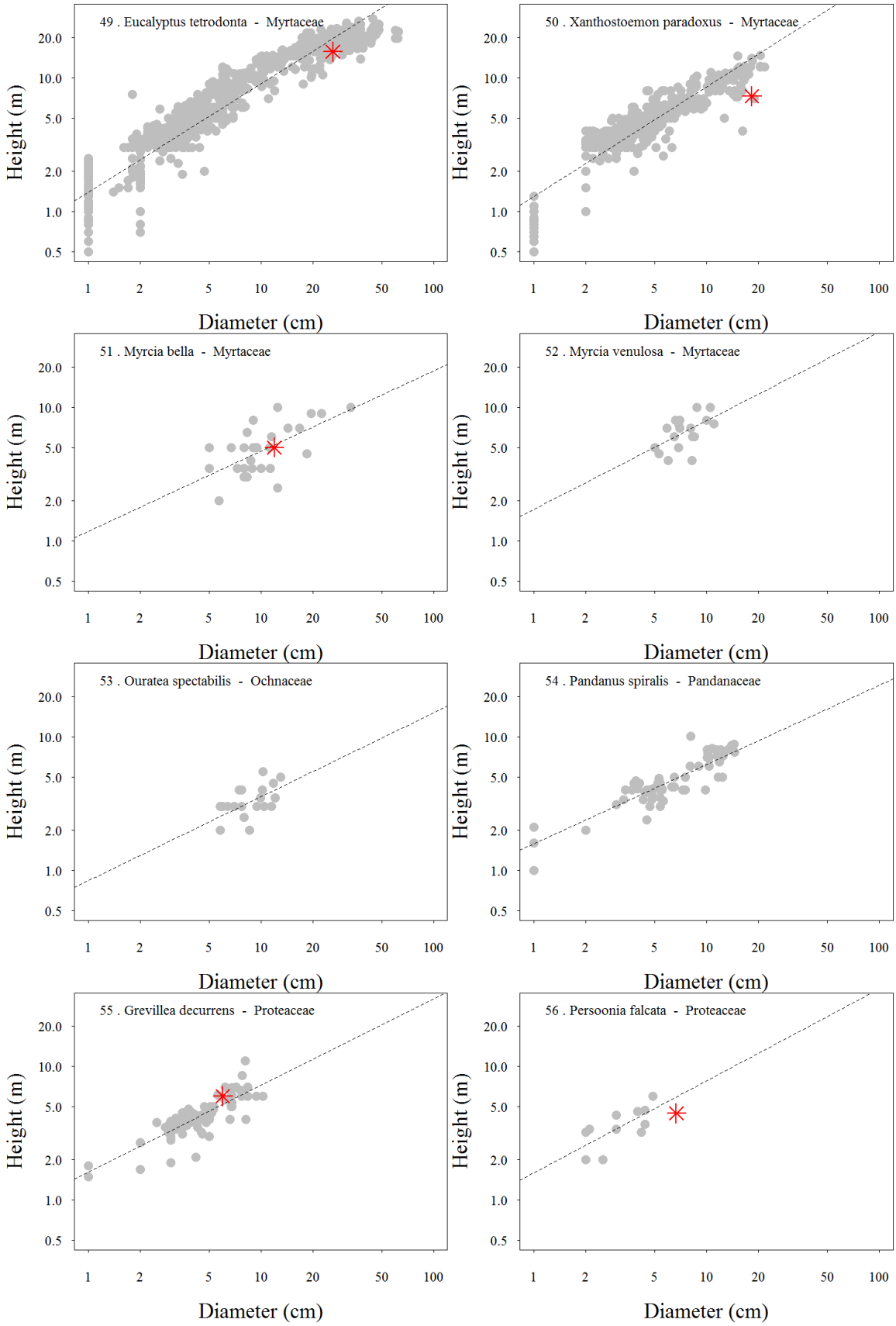



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

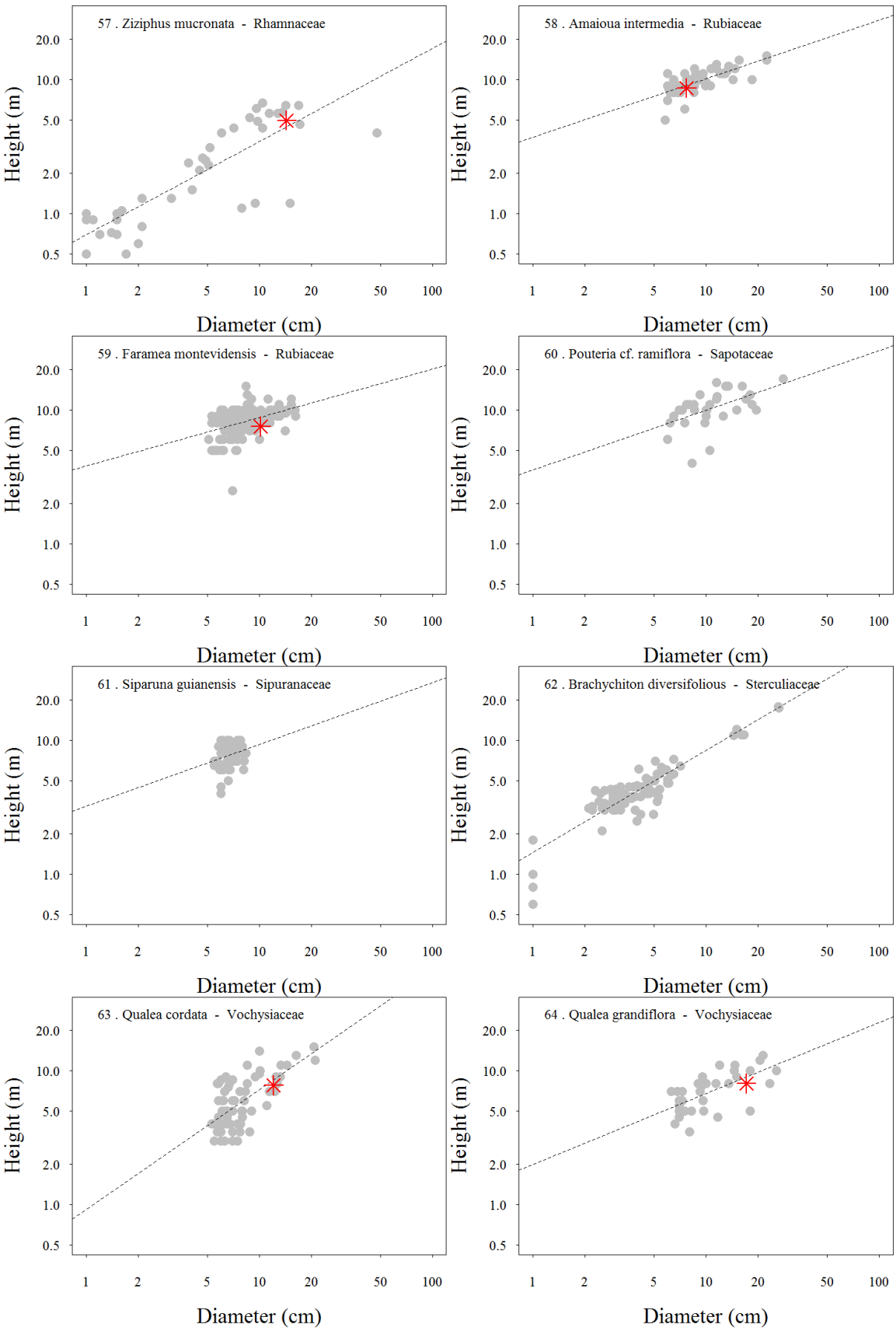



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

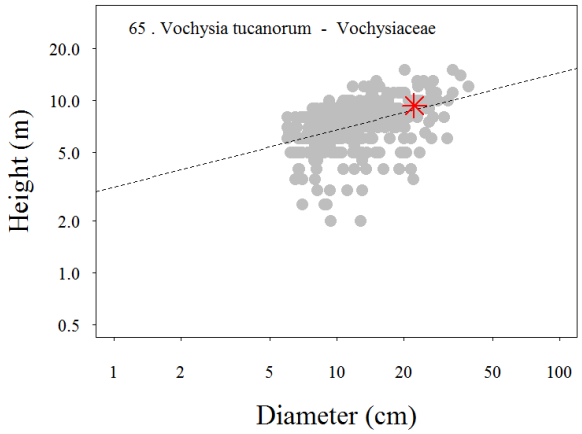



***Figure S2 cont.*** *Diameter-height allometries for each species. Each point is an individual. For those species for which we sampled traits, the mean size of the sampled individuals is indicated with a red star.*

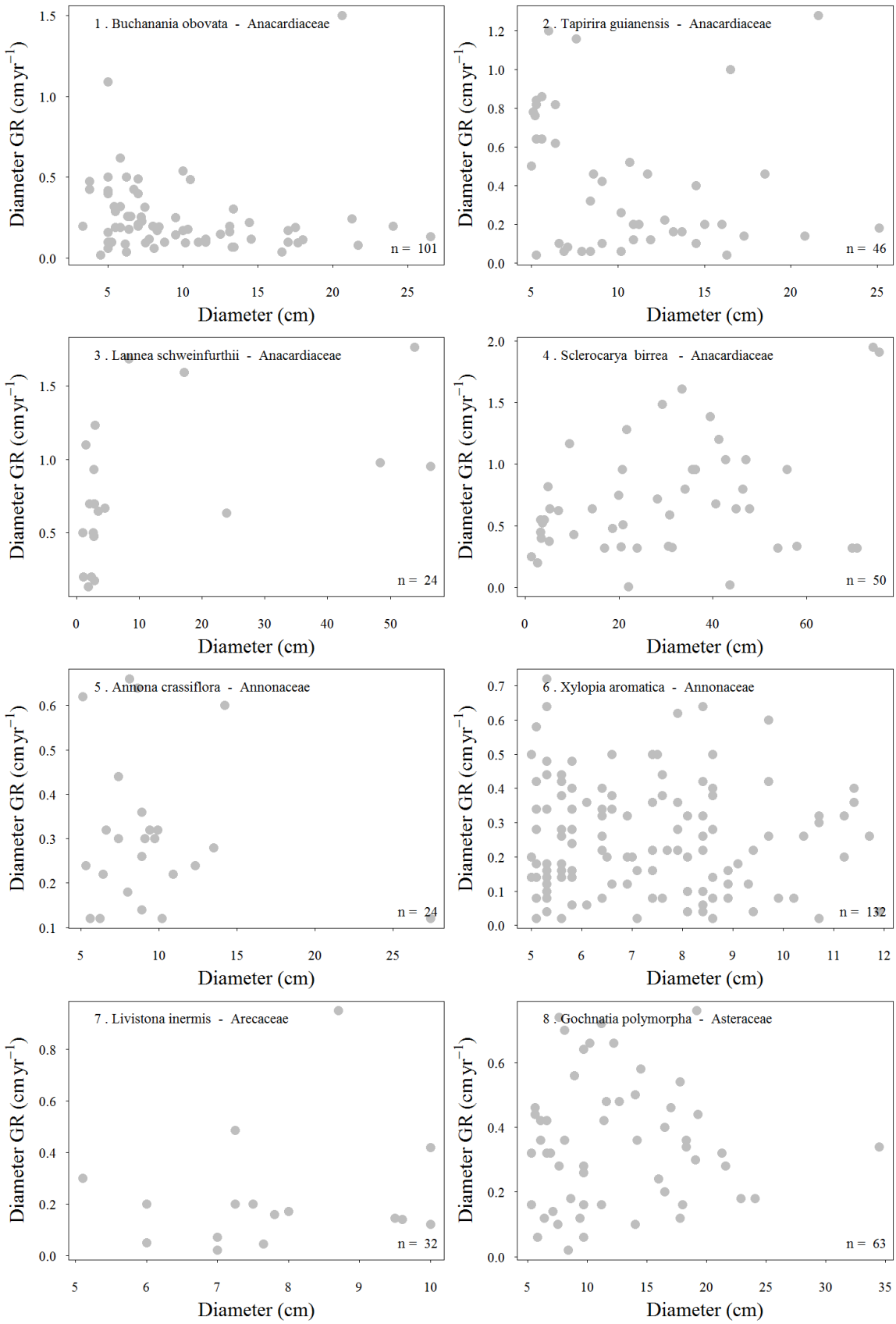



***Figure S3*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

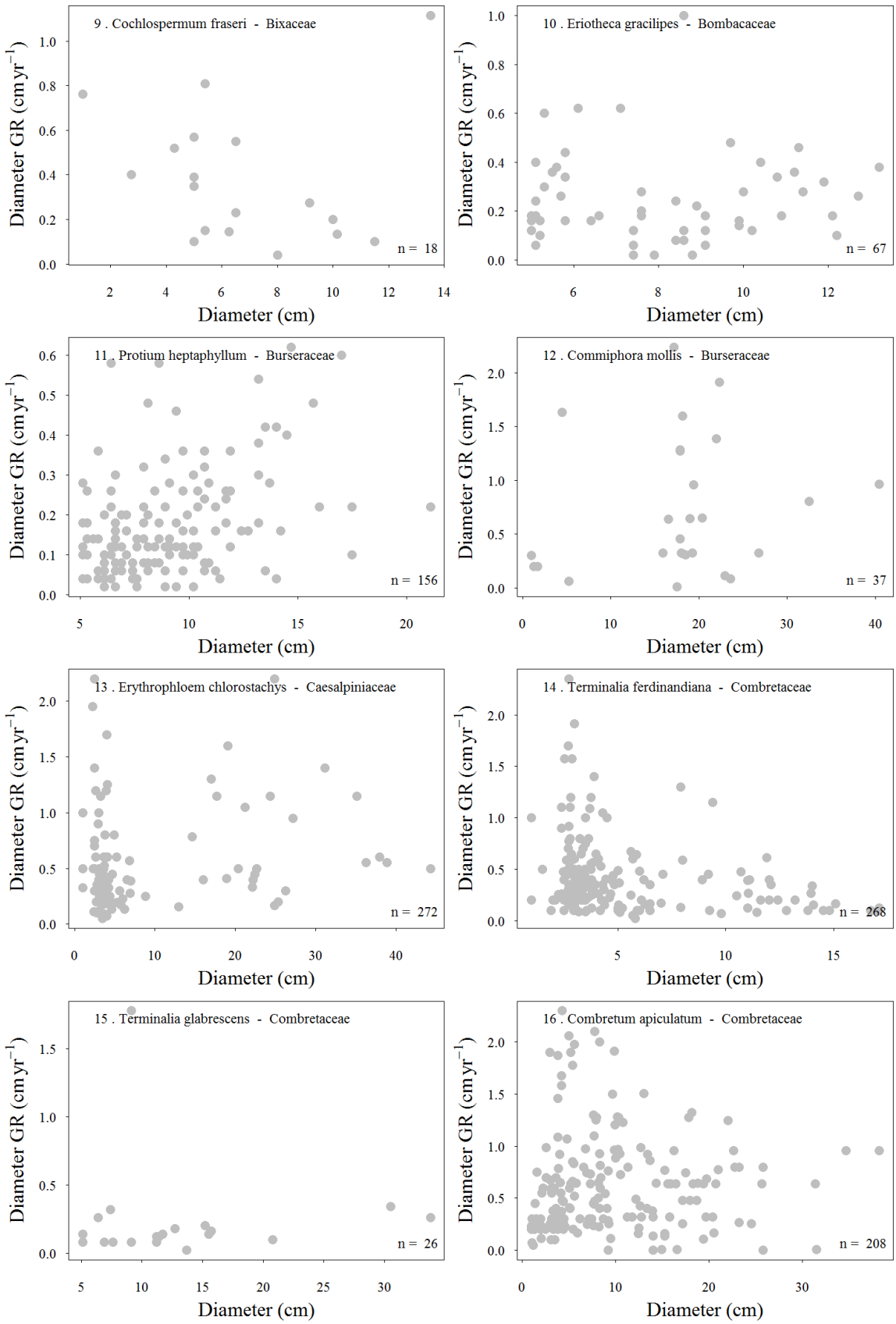



***Figure S3 cont****. Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

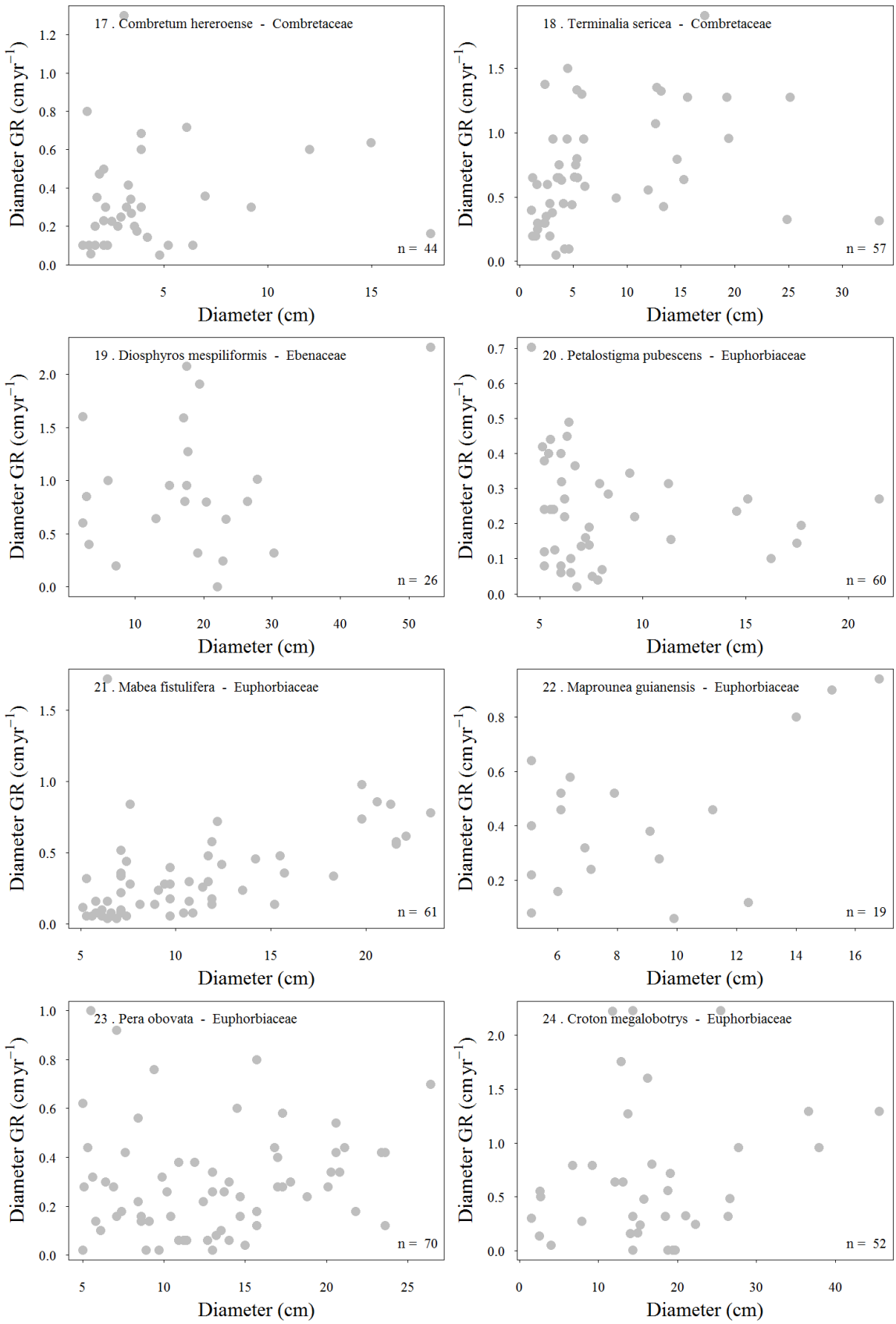



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

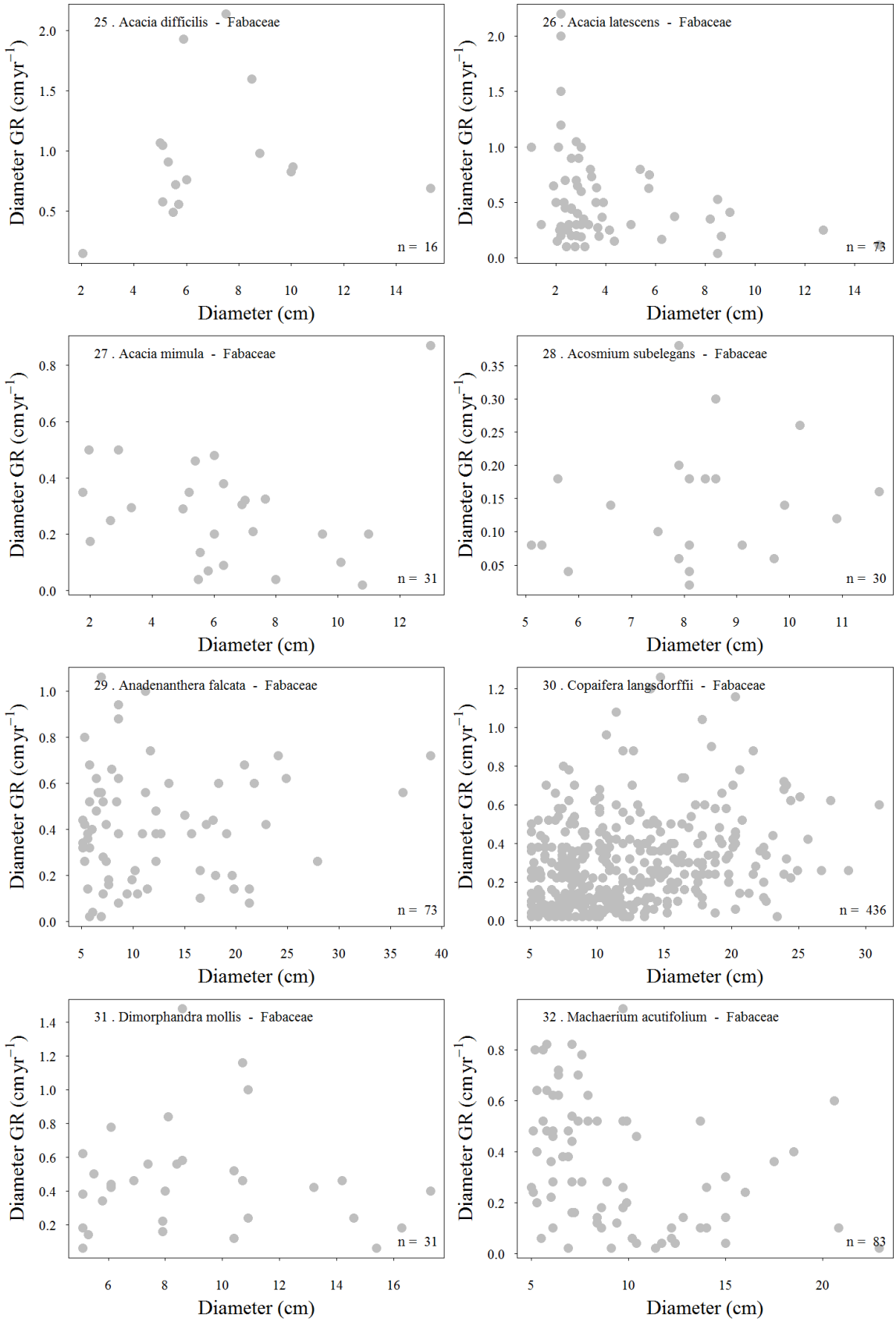



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

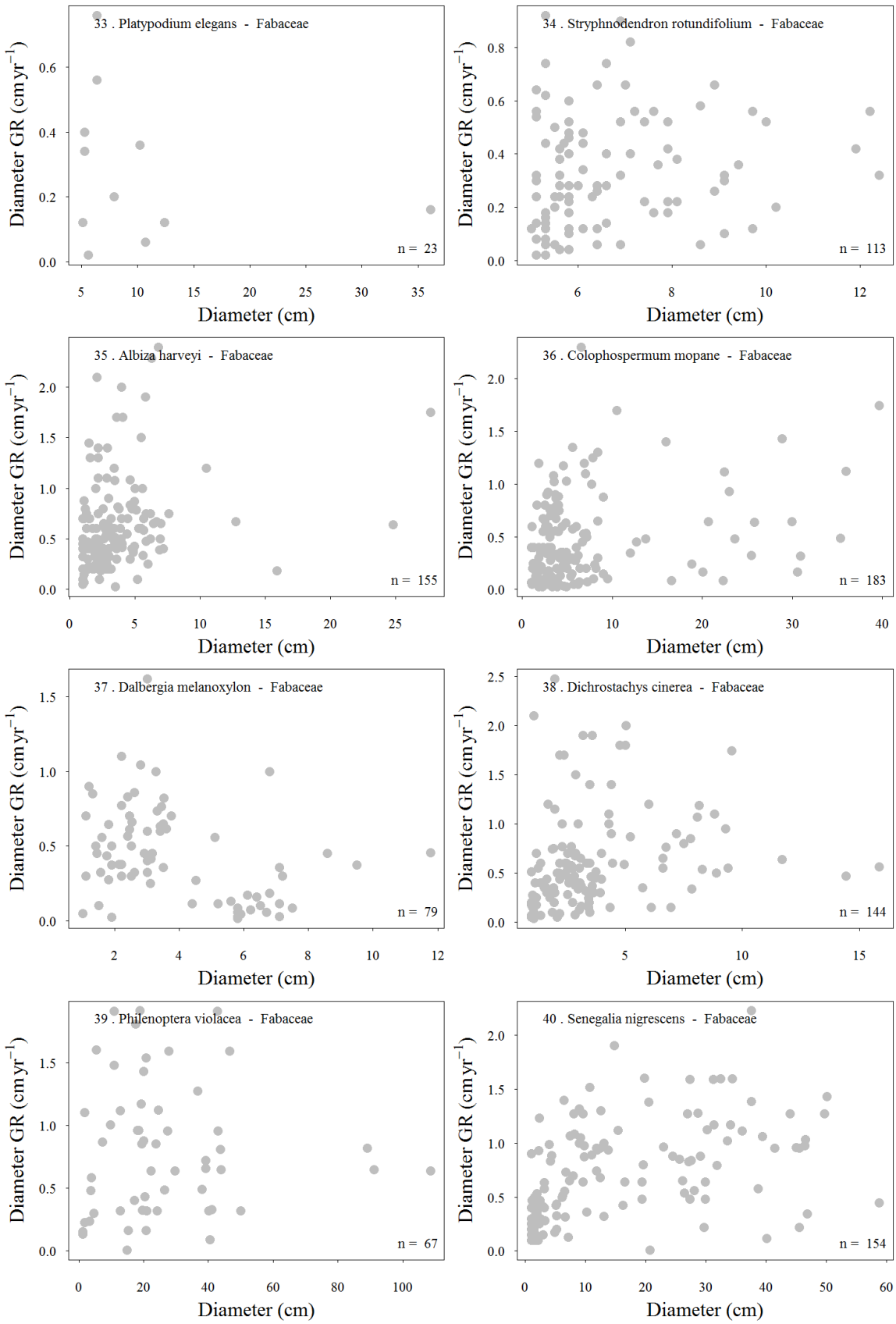



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

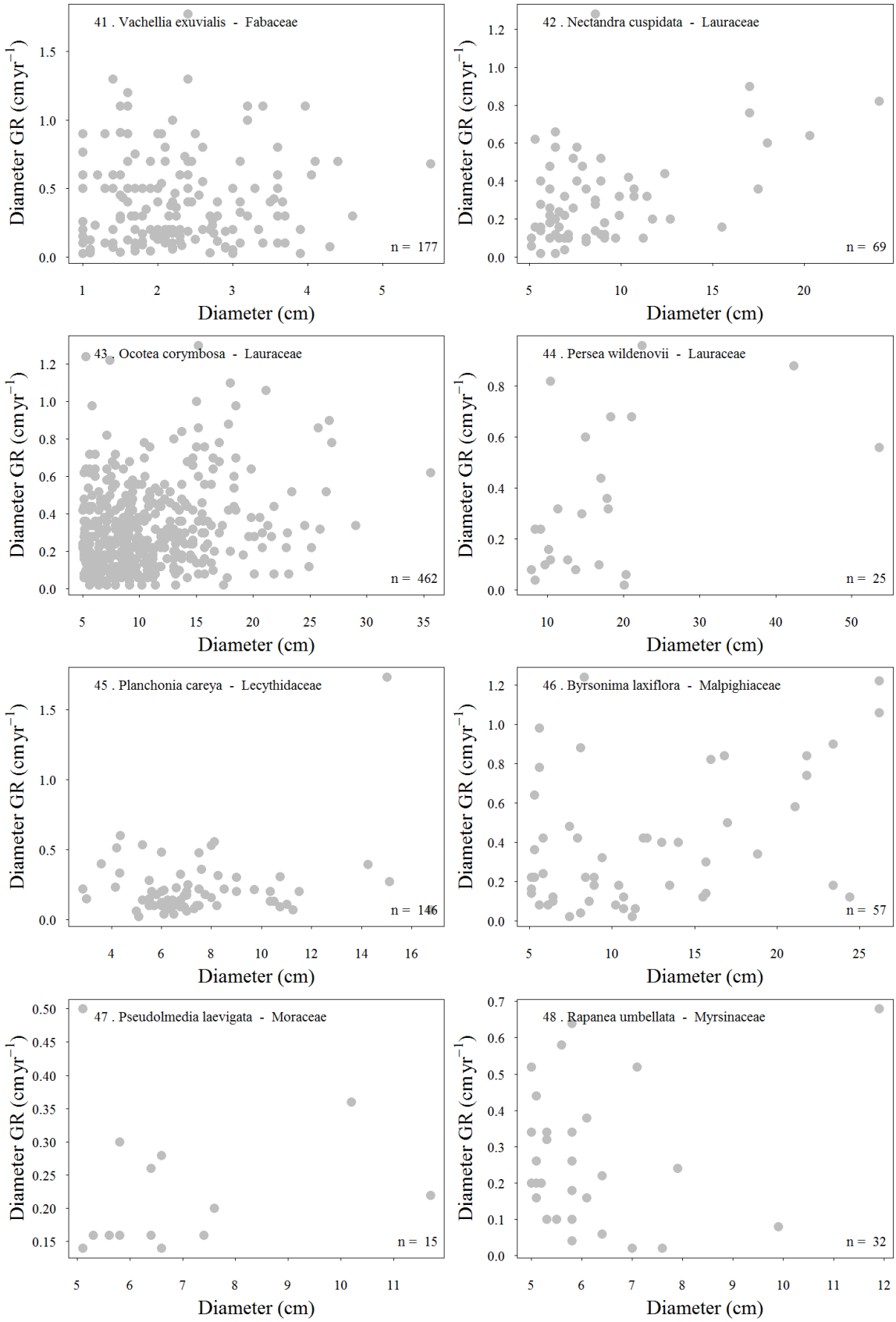



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

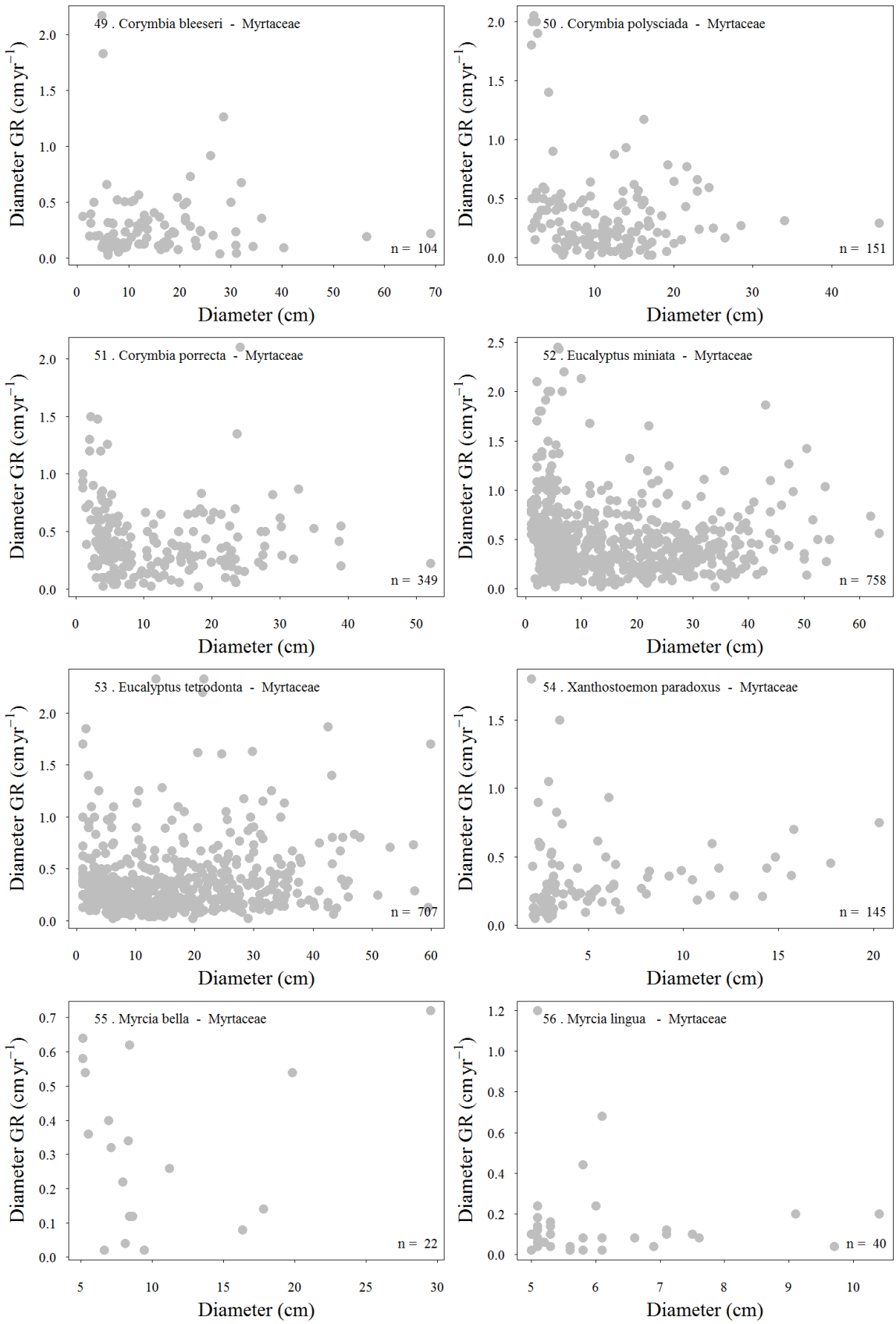



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

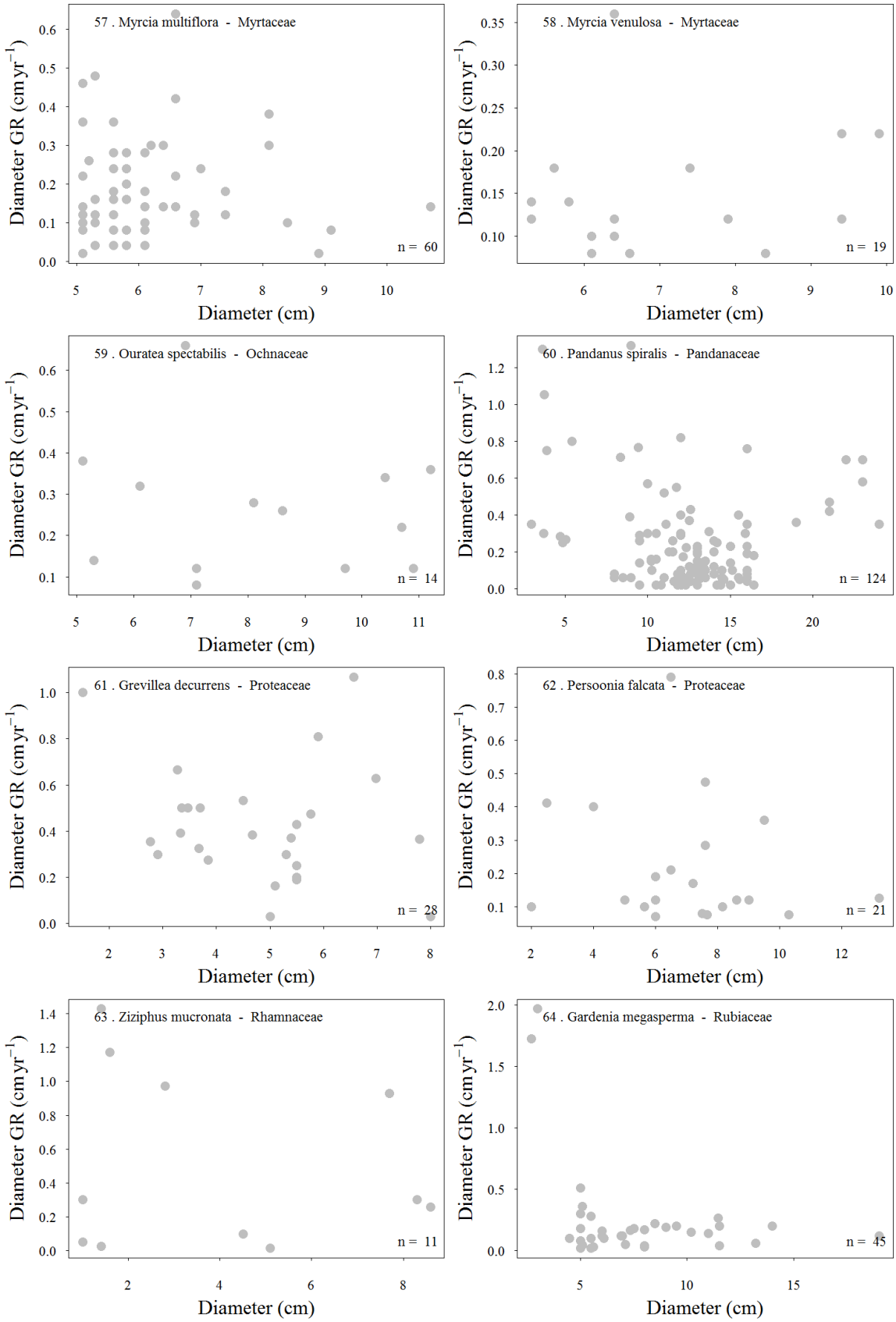



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

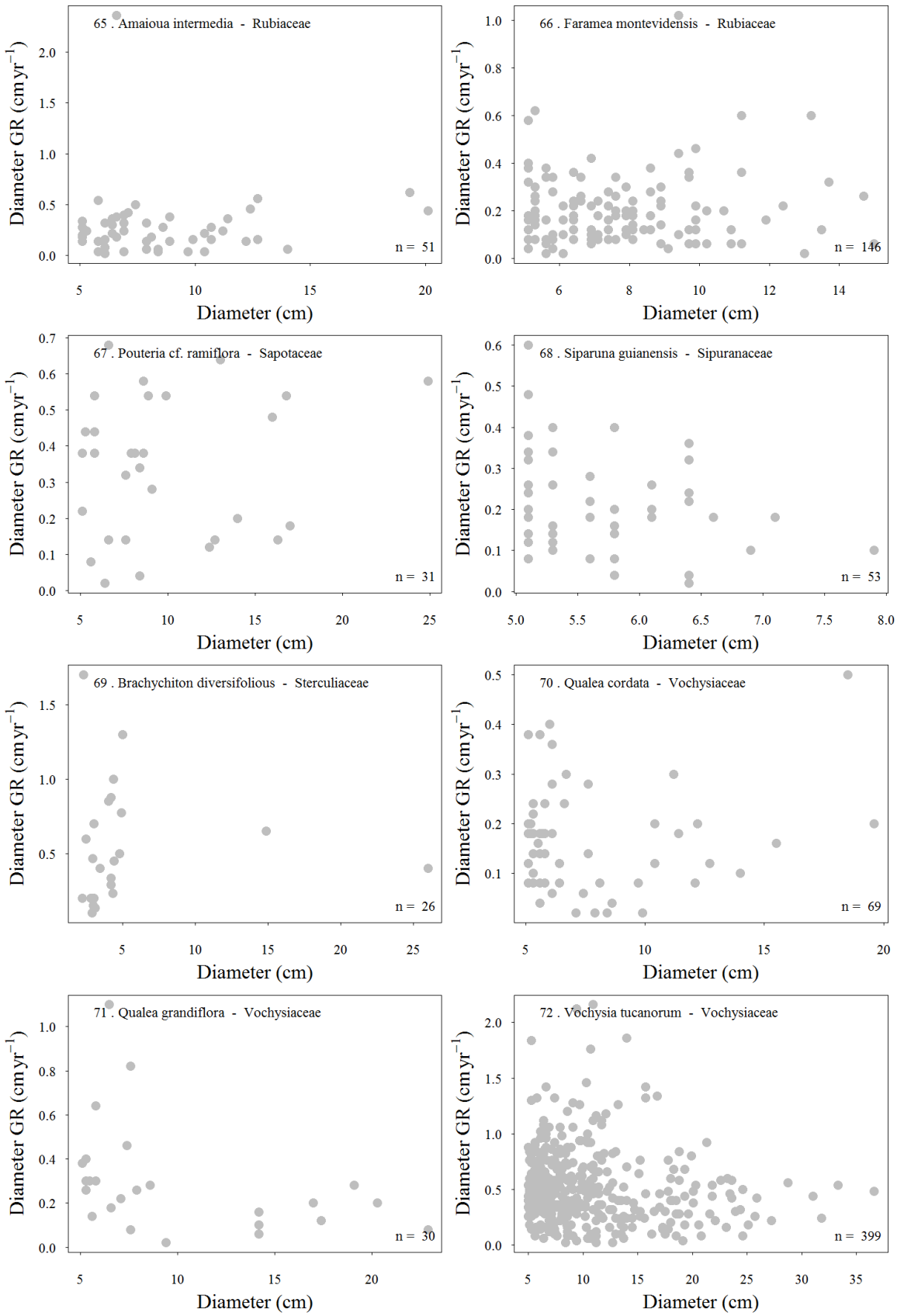



***Figure S3 cont.*** *Diameter size – diameter growth rate data spread for each species. Each point is an individual.*

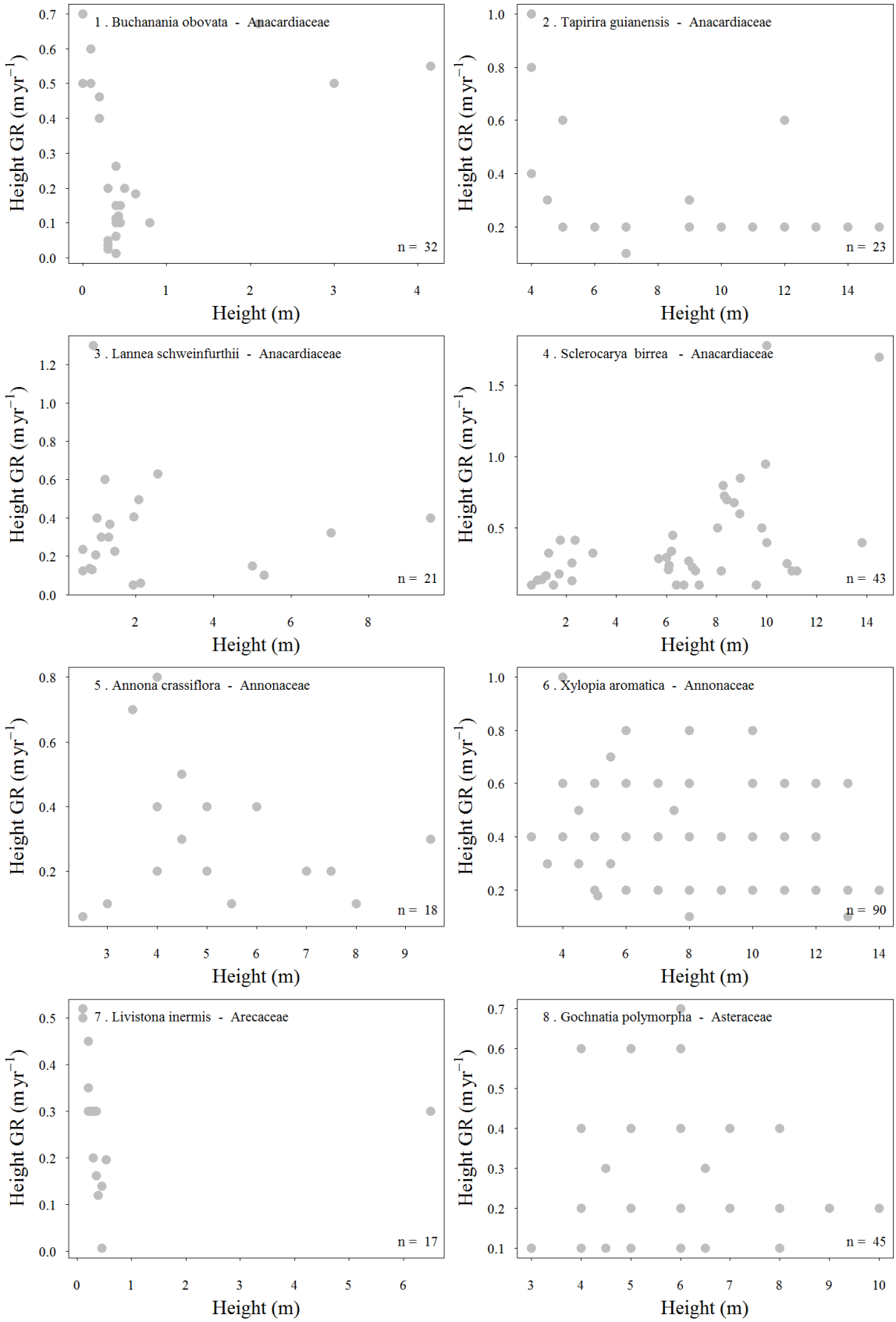



***Figure S4*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

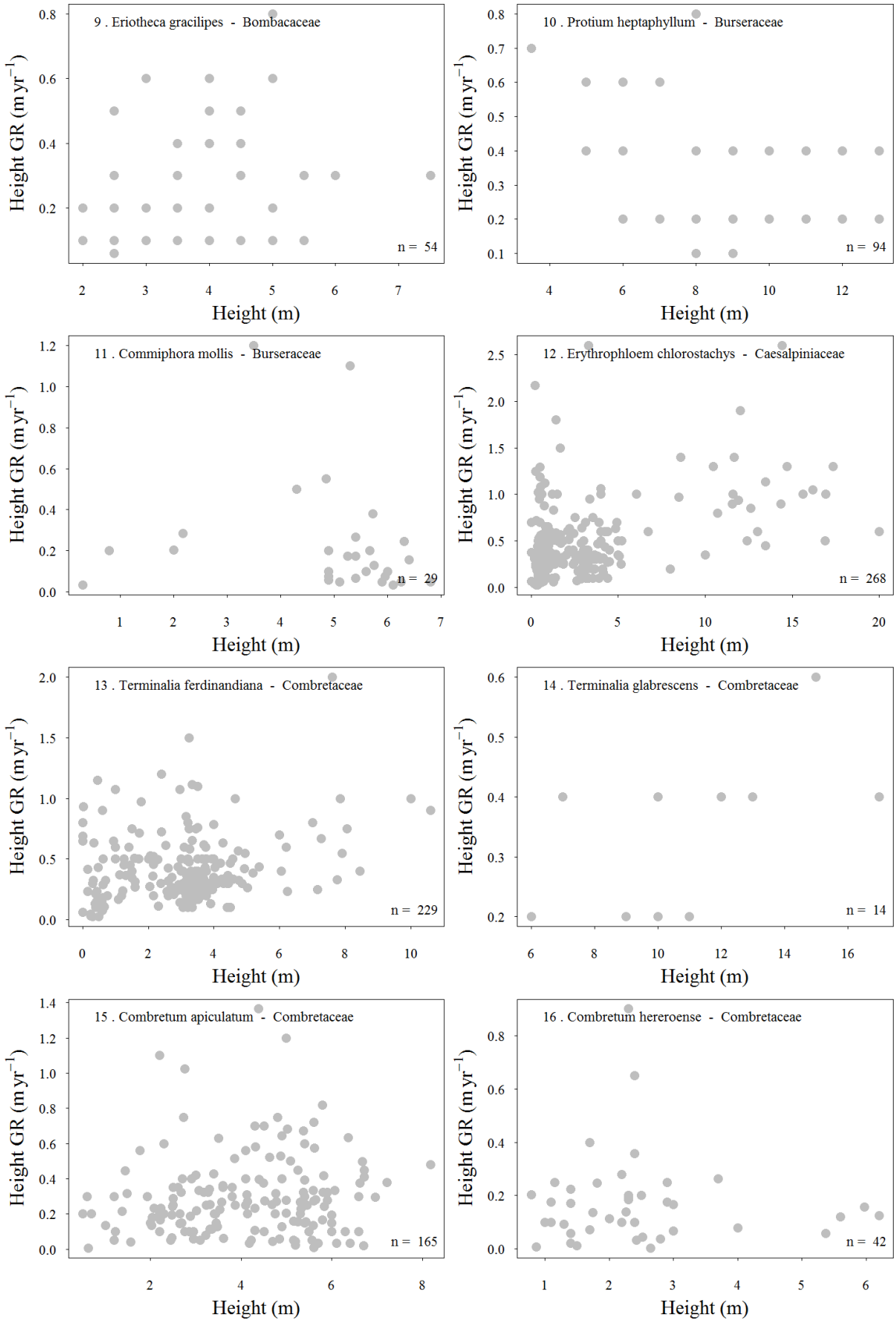



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

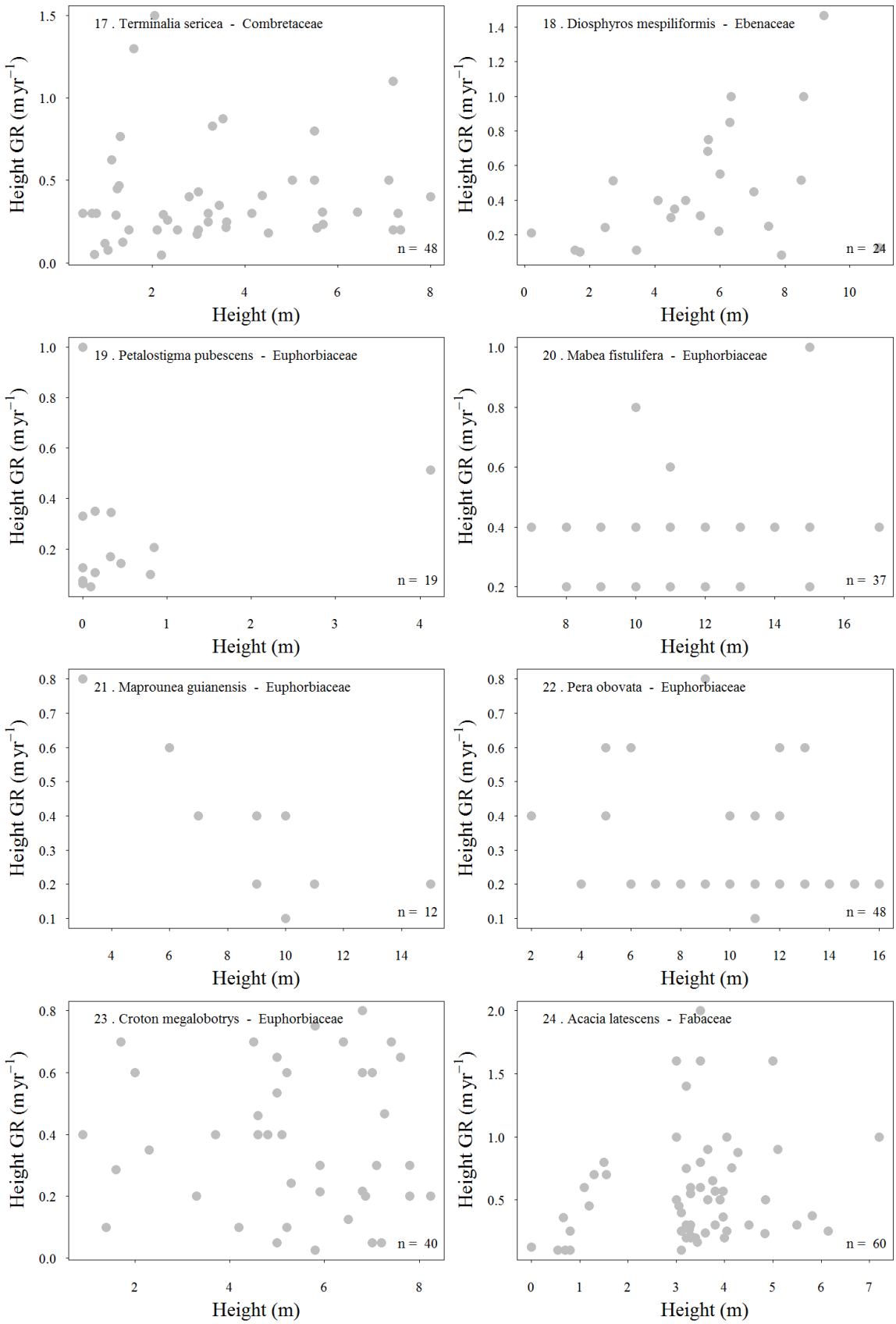



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

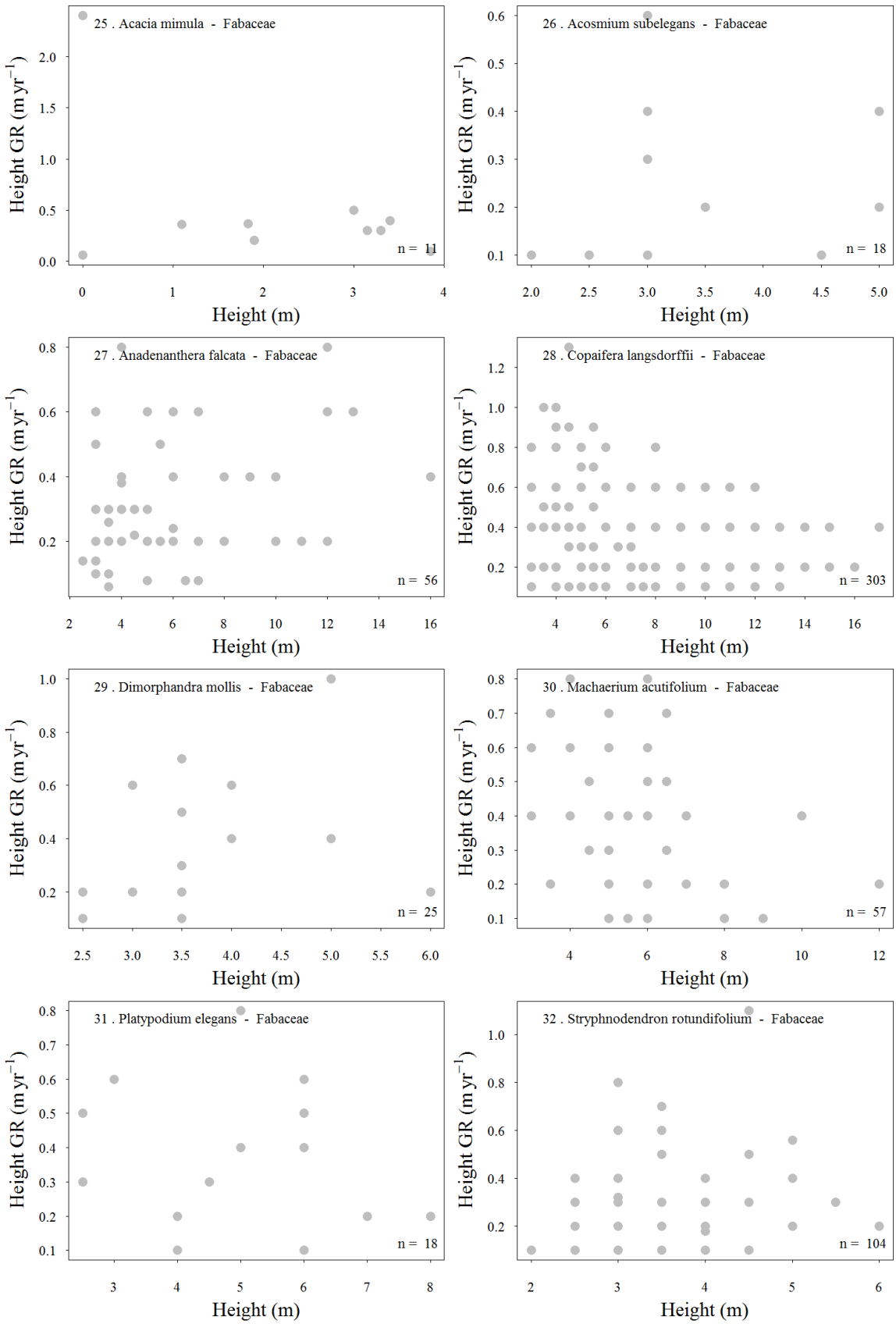



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

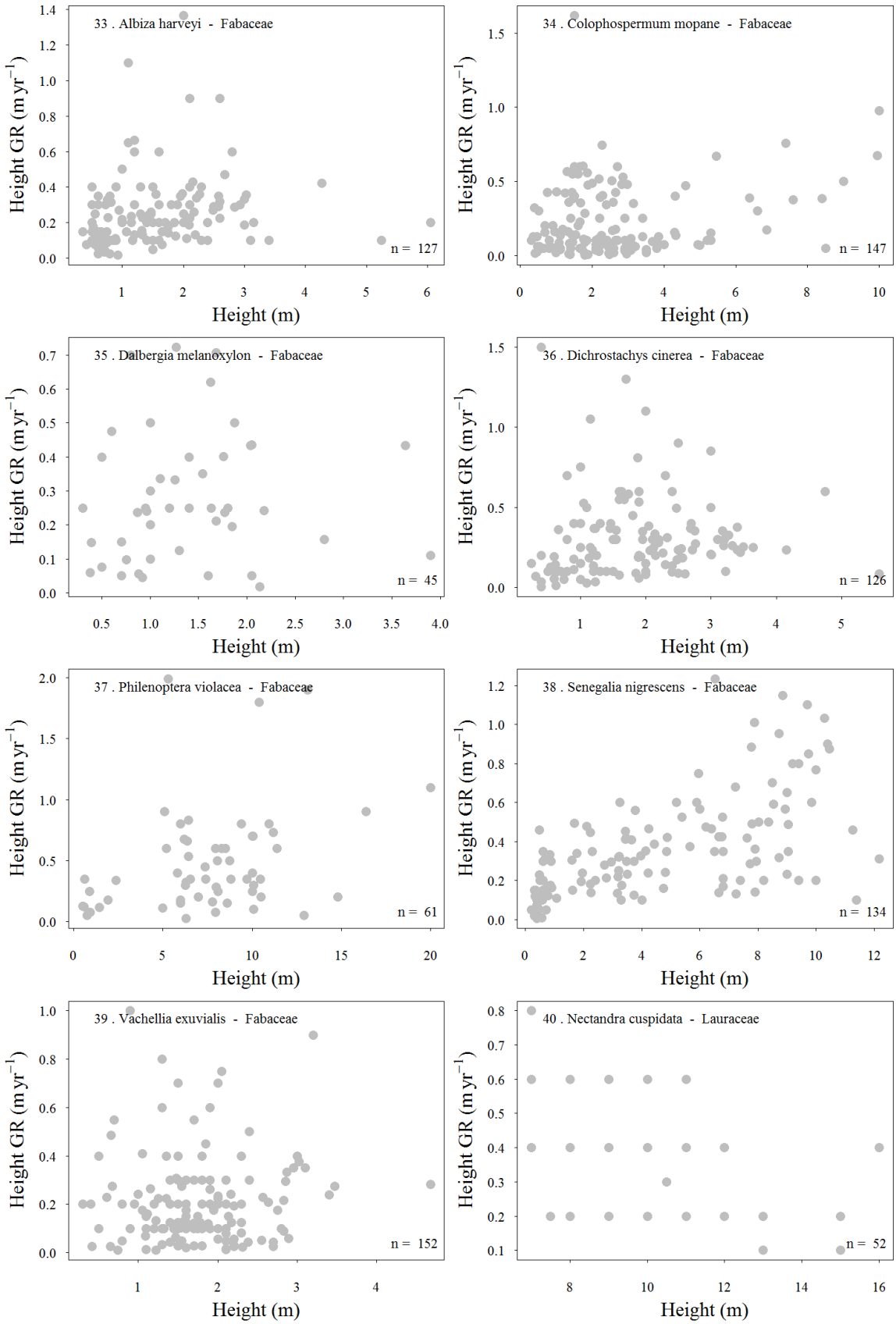



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

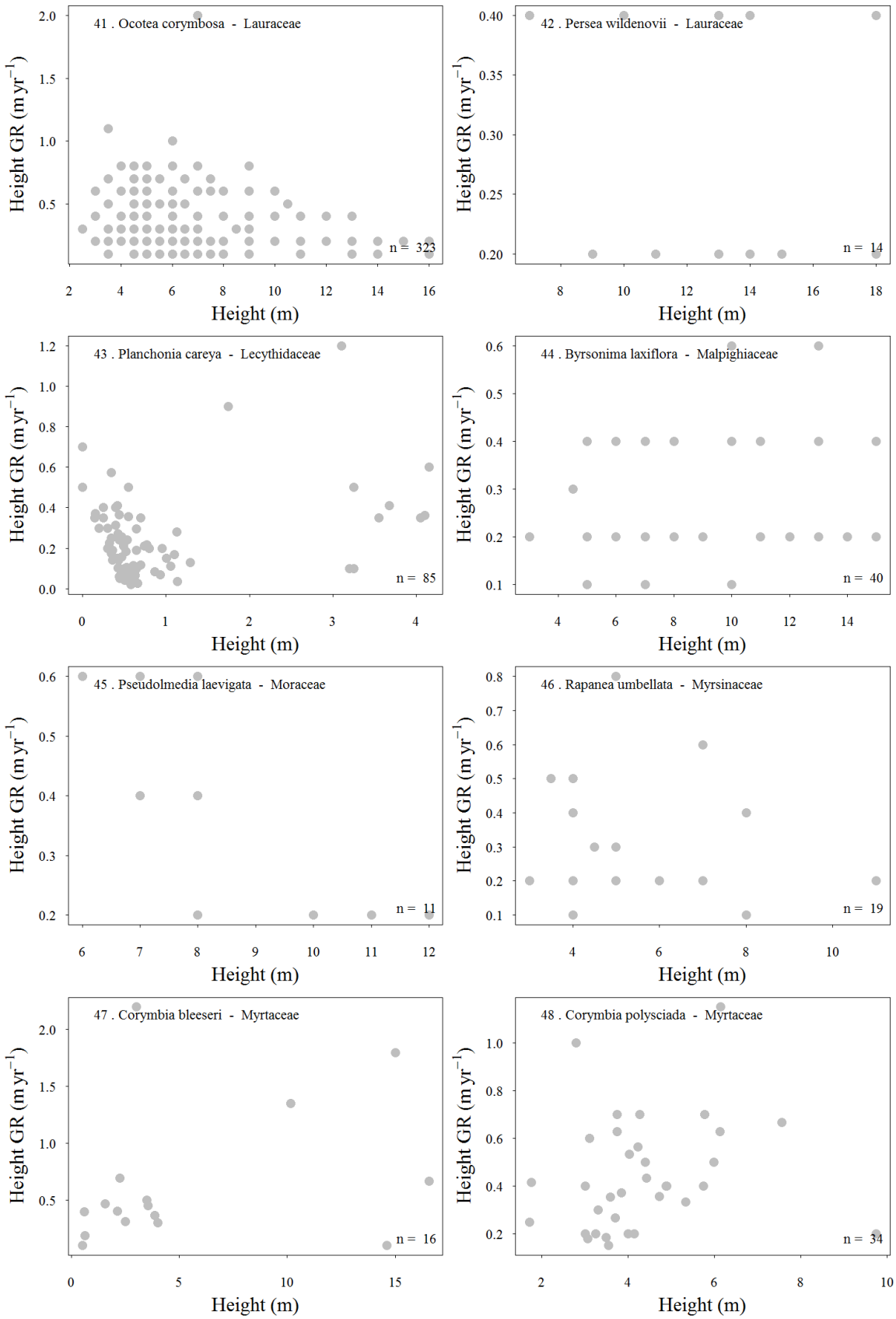



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

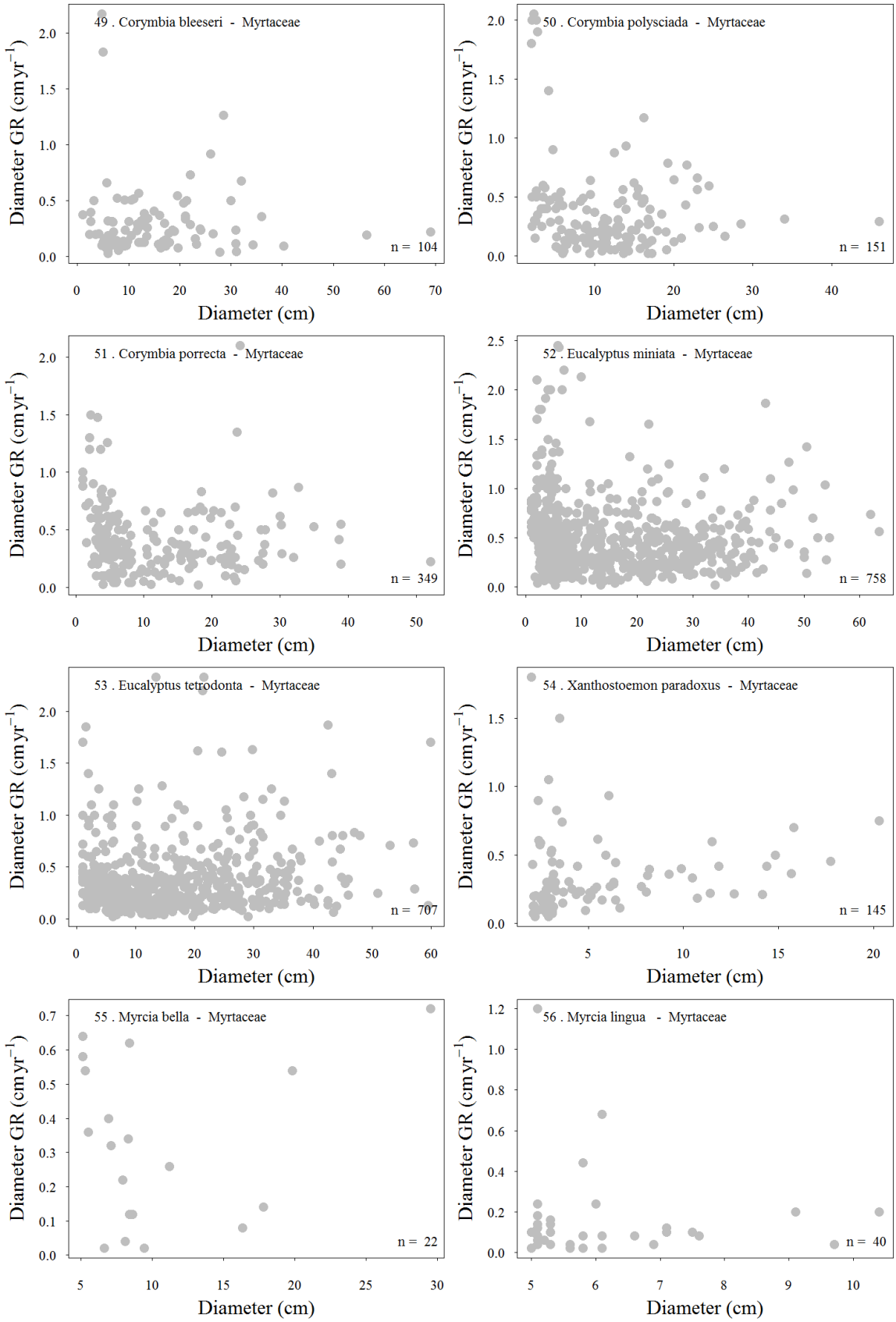



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

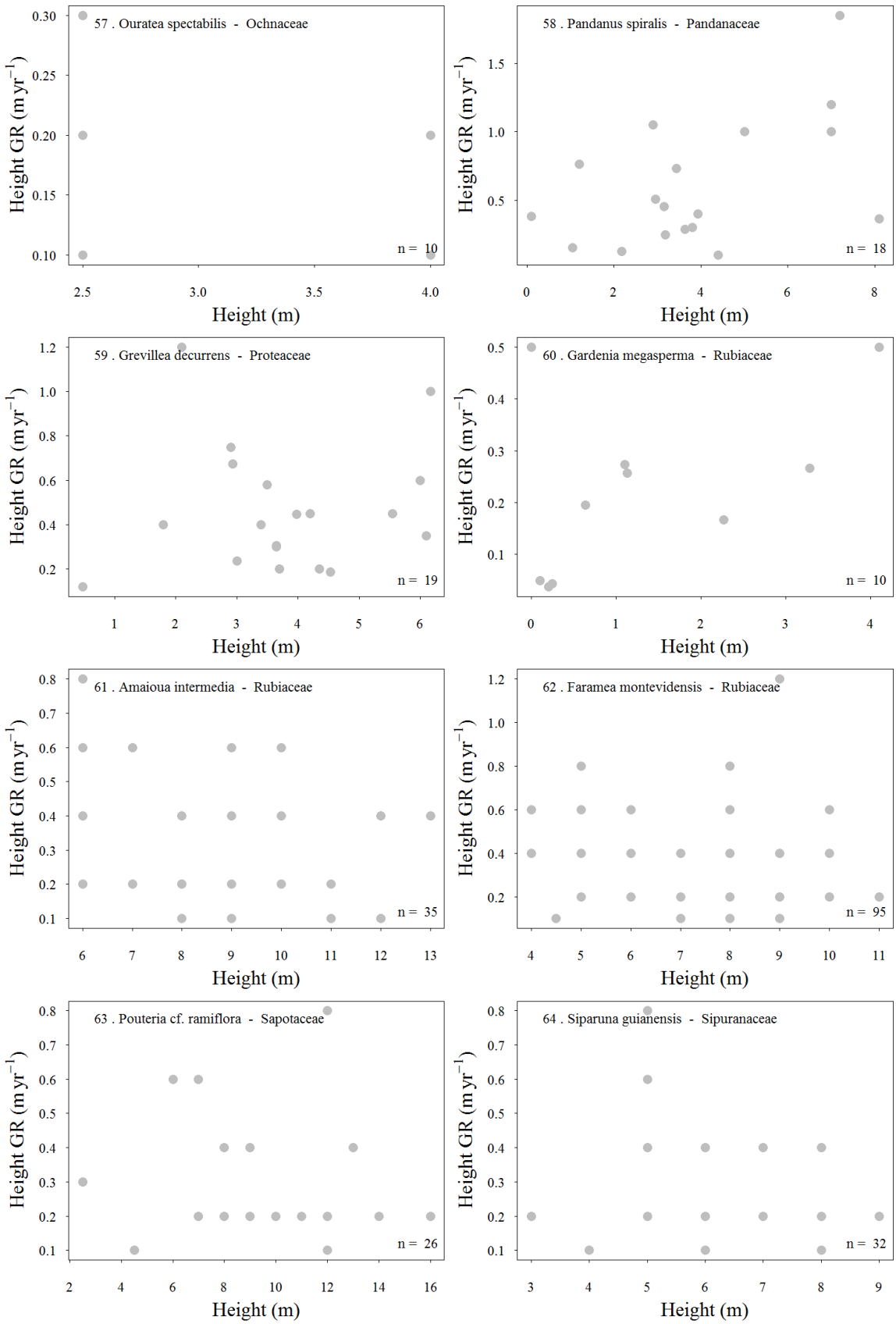



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

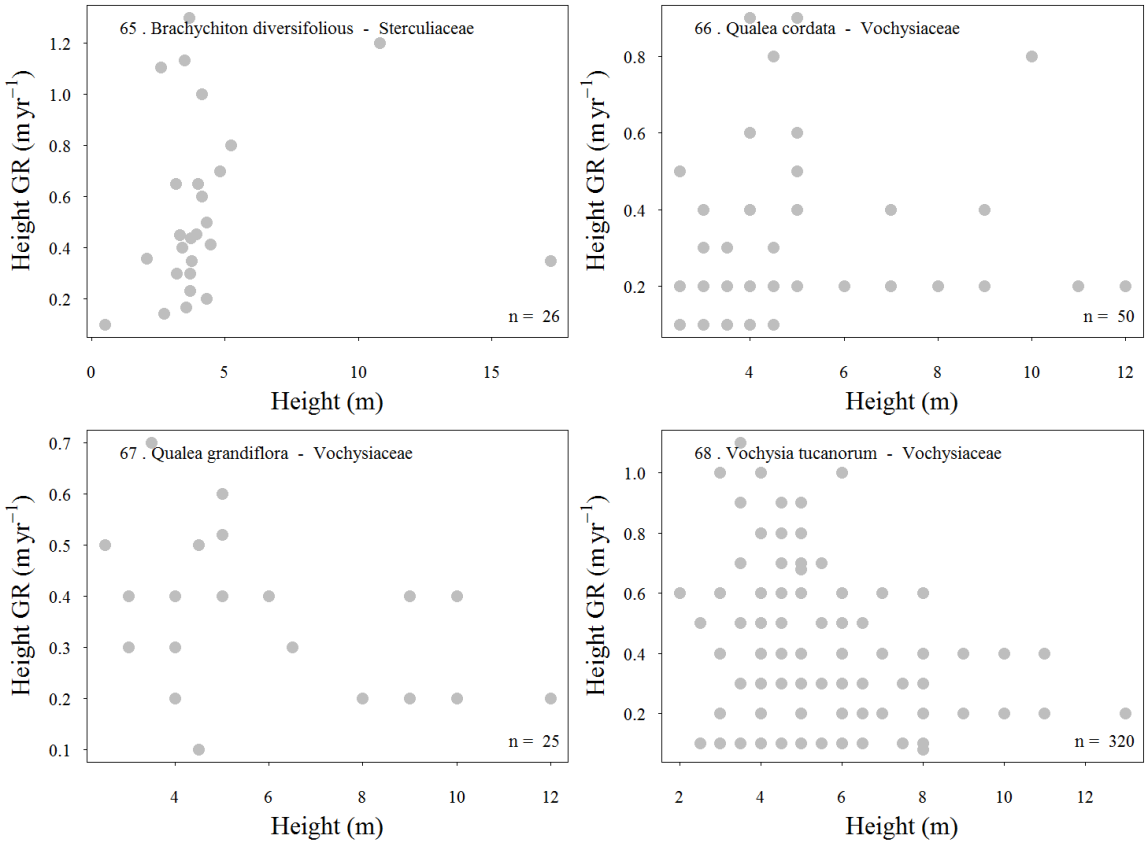



***Figure S4 cont.*** *Height size – height growth rate data spread for each sampled species. Each point is an individual.*

# Chapter 4

## Relative bark thickness is negatively related to tree growth rates across three biogeographically distinct savannas

# Abstract

The growth rates of woody plants and their ability to survive fire determines the rate of vegetation re-growth post disturbance, thereby impacting carbon storage and turnover. In frequently burnt systems such as savannas, thick bark is an important strategy for fire survival, but given finite carbon resources, it is assumed to be costly to growth. There has been minimal investigation into the relationship between tree growth rates and bark thickness, and here we examine interactions among growth rates, bark thickness and tree architecture in three savannas with variable regimes of disturbance by fire and herbivory.

We measured height and diameter growth rates, and trunk and canopy relative bark thickness on 58 species from a savanna site in each of Australia, Brazil and South Africa. We calculated a tree architecture metric (height at a standard diameter) of each species using height-diameter allometries. We compared stem diameter and height growth rates, relative bark thickness, and architecture across the three sites. We found evidence of a general trade-off between trunk relative bark thickness and growth rates across all species and sites. Within each site the strength of the trade-off varied, and was strongest in Australia where fires are most frequent. In South Africa, where fire return intervals are longer and herbivore densities highest, diameter growth rates were fastest, and less strongly related to bark thickness than in Australia. Thirdly, while there was no negative relationship between trunk bark thickness and growth in Brazil, these species (as well as those in Australia) provided support for our hypothesis that in frequent fire regimes canopy relative bark thickness should be negatively related to height growth rates. Lastly, tree architecture and relative bark thickness together explained over 60% of the variation in diameter growth rates, with taller species growing more slowly and having relatively thick bark.

This study represents the first evidence of a trade-off between relative bark thickness and growth rates across three savannas under distinct disturbance regimes. The strength of the relationship, and the relative influence of canopy and trunk bark on growth rates appears to be a function of site productivity, fire frequency, herbivory, and presumably also different evolutionary histories of the three savannas.

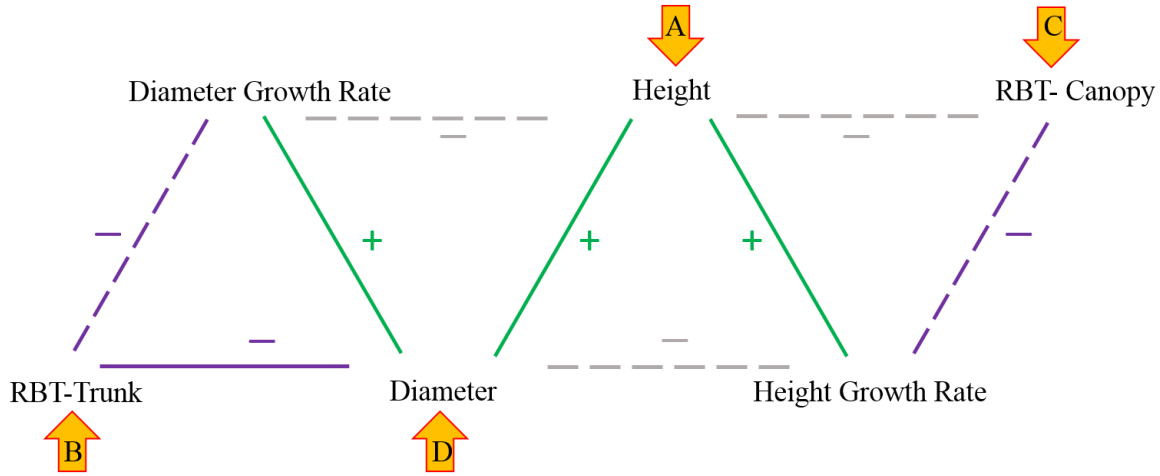
# Introduction

In frequently burnt systems such as savannas, many woody species use thick bark as protection from fire (Hoffmann & Franco 2003; Hoffmann et al. 2009; Keeley et al. 2011; Brando et al. 2012; Dantas & Pausas 2013; Dantas, Batalha, et al. 2013; Pausas 2015). Increased investment in bark should be resource costly and studies have suggested a negative relationship between bark thickness and tree growth rates (Midgley et al. 2010; Lawes, Adie, et al. 2011; Lawes et al. 2013; Pausas 2015), but this has not been widely tested (Gignoux et al. 1997). A trade-off between fire-resistance and growth rates would have important impacts on community assembly, and the resilience of ecosystems to state shifts (Pausas 2015; Pellegrini et al. 2016).

Trunk bark thickness is often expressed relative to stem diameter (i.e. relative bark thickness, Hempson et al. 2014; Pausas 2015), because bark thickness increases with size (Lawes et al. 2013; Hempson et al. 2014; Rosell 2016). Height-diameter allometries (a measure of tree architecture) in savannas have been linked to fire, rainfall and herbivory (Moncrieff et al. 2011; Dantas & Pausas 2013; Moncrieff et al. 2014). Species in savannas subject to frequent fires tend to invest in rapid height growth and thick bark, while those from savannas subject to less frequent fires but high herbivory invest more in lateral and branching growth (Archibald & Bond 2003; Lawes et al. 2013; Dantas & Pausas 2013). However, the relative importance of fire, rainfall and herbivory varies among regions and along productivity gradients (Lehmann et al 2014) to impact tree cover (Bond et al. 2005; Lehmann et al. 2014) and the limits of savanna globally (Bond et al. 2005; Lehmann et al. 2011; Staver et al. 2011; Hoffmann et al. 2012; Murphy & Bowman 2012; Archibald et al. 2013). All of these factors combine such that a relationship between tree growth and bark thickness could vary substantially among savanna regions as a result of differences in architecture and disturbance regimes.

Three ecological strategies to survive in frequently burnt systems are thought to be common in savanna tree species: (1) Construct relatively thick bark and thus rapidly acquire stem insulation; (2) Rapid height growth to enable escape from the flame zone (escape hypothesis; Higgins et al. 2000; Bond et al. 2012); and (3) Rapid diameter growth to enable accumulation of absolutely thick bark, although relative to total diameter it is still thin (Hoffmann et al. 2012; Dantas & Pausas 2013; Lawes et al. 2013). Adding to this, where fire is less frequent (a return time of 6 - 20 years) diameter growth is likely to be favoured due to herbivory or aridity, as shown by previous studies (Archibald & Bond

2003; Moncrieff et al. 2014). Additionally, higher relative bark thickness in canopy branches may be as important where fires are intense and heat is vented upwards through a canopy (Hoffmann et al. 2009; Dantas & Pausas 2013; Rosell et al. 2015). We expand on the above three strategies to consider a model that includes canopy bark thickness (Box 1).




***Box 1. The influence of fire on the relationships between relative bark thickness (RBT), growth rates and size.*** *Green lines indicate direct positive connections, purple lines indicate direct negative connections. Grey lines indicate indirect negative connections. Dashed lines indicate presumed connections. The slopes of each relationship are not necessarily equal to 1 (and may not even be linear), and should vary according to disturbance regime. Fires are represented by orange arrows and can influence the model at 4 points. The point of influence should be related to the prevailing fire regime. Frequent fires can drive selection for height (i.e. escape hypothesis) at point A, but unless they are very low intensity, they should also select for relatively thick trunk bark (point B). Very frequent or hotter fires may also select for thick canopy bark (point C), which would reduce the need to grow as tall to escape flame height (but equally, if a tree is tall there is no need to build thick canopy bark, so this relationship goes both ways). Less frequent fires allow longer periods of growth between fires. Here trees might invest in diameter (at point D) because absolute bark thickness is related to the diameter of a tree, and thus a relatively thin-barked species that is able to grow sufficiently large between fires will have thick enough bark to defend itself once a fire comes through.*

Based on the model in Box 1 we compare species in three savanna systems with differing site conditions (Table 1) to test if there is variability among savannas with respect to bark-growth-architecture strategies of fire survival. Our primary expectations are:

1. Growth rates will be negatively related to relative bark thickness. The strength of the relationship will vary relative to regimes of fire and herbivory, with canopy bark

thickness being more important in more frequent fire regimes. Diameter growth rates will be more tightly related to trunk relative bark thickness, while height growth rates will be more tightly related to canopy relative bark thickness.

2. Relative bark thickness (trunk or canopy) will be highest in savannas subject to most frequent fires.

3. Height growth rates will be fastest in savannas subject to frequent fire, while diameter growth rates will be fastest in the savanna site dominated by mega-herbivores (South Africa). Where fire is frequent, species will prioritise escape from the flame zone, and will therefore be tall even at small diameters. Height-diameter allometries should thus differ, and because bark thickness is a function of size, these differences may influence relative bark thickness.

4. Prediction 3 suggests importance of architecture, such that relative bark thickness and growth rates may be unrelated unless architecture is accounted for.

# Methods

We quantified species-level height and diameter growth rates, relative bark thickness and a measure of tree architecture using data from three savanna sites: one in Africa, one in Australia and one in South America.

**Table 1** Mean climate and fire conditions at each site (range across the degree squared encompassing the sites in brackets).

| | **MAP (mm)** | **Rainfall in driest quarter (mm)** | **MAT (°C)** | **Fire return interval (years)** |
|---|---|---|---|---|
| **Australia** | 1392 | 8 | 27.1 | 0.80 |
| | (1303 – 1569) | (6 – 12) | (26.2 – 27.4) | (0.57 – 1.01) |
| **Brazil** | 1268 | 133 | 21.8 | 1.40 |
| | (1199 – 1352) | (119 – 150) | (20.9 – 22.3) | (1.2 – 1.6) |
| **South Africa** | 625 | 24 | 21.3 | 5.98 |
| | (515 – 1050) | (17 – 44 ) | (15.2 – 22.0) | (4.9 – 7.5) |

These three sites varied in mean annual precipitation (MAP), rainfall seasonality, mean annual temperature (MAT) and fire return intervals (Table 1). Fire return intervals were extracted from Archibald et al. (2013). Rainfall and temperature indices for each site were

calculated using the bioclimatic variables in the Worldclim dataset (www.worldclim.org/bioclim). Both fire and climate datasets were in raster format, and we calculated a mean, minimum and maximum from the surrounding degree squared encompassing the tree measurement plots (i.e. 1 degree latitude x 1 degree longitude). MAP was highest in Australia but this site experienced the most rainfall seasonality. Mean annual rainfall was lowest in South Africa, while rainfall seasonality was lowest in Brazil. Fire return intervals were shortest in the Australian site and longest in the South African site.

**Growth and tree architecture**

Growth rates and tree architecture for 56 species were estimated using tree height and diameter measurements from repeat censuses in permanent tree measurement plots. Permanent plots in each study site were established independently of this study, and of each other, and so differ in plot size, extent, and time since establishment. Across all sites, individuals smaller than 1 cm in diameter or 0.5 m in height were excluded. We excluded a growth increment if it was negative, if the diameter increment was greater than 2.5 cm $yr^{-1}$, or if the height increment was greater than 2 m $yr^{-1}$. We excluded a species if it was represented by fewer than 10 individuals across all plots.

*Australia*

Data came from two sources, the Kapalga dataset (Andersen et al. 2003) and the Three Parks dataset (Murphy *et al.* 2010). Plots in the Kapalga dataset (Kakadu National Park, 12.8°S, 132.8°E) were established by CSIRO researchers, who measured both height and stem diameter at breast height of woody species as part of various experiments between the 1970s to the 1990s. The Three Parks dataset contains repeat census data for 163 plots spread across three National Parks in Northern Territory (Kakadu 86 plots, Litchfield 38 plots and Nitmiluk 39 plots). Diameters of all individuals with diameter at breast height greater than 5cm were measured between 1994 and 1997, and then twice more five years apart. We combined diameter measurements from the two datasets and removed obvious data entry errors. We used data from all sites except those that were recorded as experiencing severe and frequent fires. We calculated annual diameter increments from 2074 individuals of 15 species and annual height increments from 1709 individuals of 12 species.

*Brazil*

Thirty permanent plots were established by the Forestry Institute of Sao Paolo State at the Assis Research Station in 2006 (22.6°S, 50.4°W). Heights and diameters of all woody

plants greater than 5cm diameter at breast height were measured in 2006, and again in 2011. We calculated annual diameter increments for 2416 individuals of 25 species, and annual height increments for 1858 individuals of 25 species.

*South Africa*

Eighty four permanent plots were established in 2008 by the South African Environmental Observation Network, in the Phalaborwa region of the Kruger National Park, as well as adjacent private game reserves (all plots located between 23.6°S, 30.8°E and 24.6°S, 31.5°E). Heights and basal diameters of woody plants taller than 30cm were measured annually between 2008 and 2015. While fire was actively excluded in only 20% of plots, only six plots burnt over the course of the measurement period, and burnt trees were excluded from our growth rate estimates. We calculated annual diameter increments from 1295 individuals of 16 species, and annual height increments from 1204 individuals of 15 species.

*Growth rate and tree architecture calculation*

We calculated height and diameter annual increments for each individual using the formula $GR = (size_{y2} – size_{y1})/ (y2 – y1)$, where GR is annual absolute growth increment, and size is diameter or height of an individual at y1 and y2, which are the dates (in years) at which measurements were made. When multiple measurements existed for the same individual we took the mean of all positive annual increments for that individual. We then calculated the mean diameter growth rate (DGR) and height growth rate (HGR) of each species using the mean annual increment across all individuals of that species.

We calculated trunk diameter – height allometric relationships for each species. In the case of multi-stemmed trees only the largest diameter measurement was used, and the individual was treated as if it were single stemmed. We fitted ordinary least squares regression lines to the log-log relationships between trunk diameter and height for each species and used this to predict the height of each species at a standard stem diameters of 7.5 cm. We used 7.5 cm because this diameter fell within the measured range for most species (see supplementary Figure S1). Hereafter we refer to this species-level architectural traits as $H_{7.5}$. In order to determine the level of uncertainty surrounding this architectural trait, we employed a bootstrap resampling procedure using the R package *boot*.

**Bark thickness**

We sampled trunk bark thickness for at least five individuals of each species (see supplementary Table S1 for exact details of replicate numbers). We used a hammer and

chisel to remove a section of bark from the trunk (bark was considered as both inner and outer bark combined, to the depth of the sapwood layer) and measured the thickness of the removed piece. As far as possible sampling was done at 15 cm above ground level. The diameter at the point of sampling was measured. From the same individuals, we sampled an outer canopy branch approximately 1 cm in diameter. Bark thickness and density was measured by removing a small section of branch approximately 10 mm in diameter and 40 mm in length. The diameter including bark was measured, and then bark was removed and the sapwood diameter was measured. Canopy bark thickness was calculated by subtracting the sapwood diameter from total diameter, and dividing by two.

*Relative Bark Thickness*

Trunk and canopy relative bark thickness (RBT) was estimated following Rosell et al. (2014) who used the equation RBT = (2 × BT)/BD, where BT is bark thickness and BD is bole diameter (diameter without bark). Midgley & Lawes (2016) suggest estimating RBT using the equation RBT=BT/BD, which has the same effect.

**Data analysis**

All analyses were performed using R version 3.3.0 (R Development Core Team 2015), using the base R package unless otherwise stated. We used ANOVA to compare mean trunk-RBT, canopy-RBT, DGR, HGR and $H_{7.5}$ across the three savanna sites, and t-tests to compare means between site pairs. We used multiple linear regression to determine if the relationship between trunk- and canopy-RBT differed between sites.

We used multiple linear regression to fit site-specific RBT-GR relationships for both DGR and HGR, and both trunk-and canopy-RBT. We also tested for slope heterogeneity across these sites, and when they were found to be non-heterogeneous we tested whether the common slope across sites differed from zero. If slopes were found to be heterogeneous we tested whether a general relationship (ignoring site-membership) existed across all sites.

We then used a multiple linear regression to determine how much variation in growth rate was explained by RBT once we had accounted for architecture ($H_{7.5}$), excluding site from the model. Models were considered significant at $p <= 0.05$, but marginal significance at $0.05< p <= 0.1$ was also noted.

# Results

*Site related variation in bark thickness, growth rates and architecture*

Species mean and level of replication are reported in supplementary Table S1. Although both trunk- and canopy-RBT varied more widely within sites than between (87-95% variance within, versus 5-13% between) there were some significant differences in mean RBT between sites (Fig. 1a). Mean trunk-RBT was highest in Brazil (0.29 cm $cm^{-1}$) and lowest in South Africa (0.16 cm $cm^{-1}$), with significant differences between these sites ($p = 0.003$). Mean trunk-RBT of Australian species did not differ significantly from the other sites (0.24 cm $cm^{-1}$). Mean canopy-RBT was highest in Australia (0.47 mm $mm^{-1}$), and lowest in South Africa (0.32 mm $mm^{-1}$) with significant differences between these sites ($p = 0.05$). Brazilian species mean canopy-RBT (0.4 mm $mm^{-1}$) was not significantly different to other sites. Trunk and canopy-RBT were convincingly positively correlated in Brazil and South Africa ($R^2 = 0.65$ and $p < 0.0001$; $R^2 = 0.36$ and $p = 0.01$, respectively, Fig. 1b) but unrelated in Australia ($R^2 = 0.002$, $p = 0.89$). Across all species there was a strong general positive relationship between canopy-RBT and trunk-RBT ($R^2 = 0.36$, $p < 0.0001$).

Diameter growth rate (DGR) varied slightly more between sites than within sites, while height growth rate (HGR) varied more within sites (44% and 60% variance within site, respectively). Mean DGR differed significantly between sites ($p < 0.0001$), being highest in South Africa (0.63 cm $yr^{-1}$) intermediate in Australia (0.40 cm $yr^{-1}$) and lowest in Brazil (0.30 cm $yr^{-1}$, Fig 2a). Mean HGR of Australian species (0.48 m $yr^{-1}$) was significantly higher than those in Brazil and South Africa (both 0.32 m $yr^{-1}$, Fig. 2a).

Typical tree height at a standard diameter of 7.5 cm differed significantly between South Africa and the other two sites, with species in South Africa being much shorter (mean $H_{7.5}$ = 3.1 m, $p < 0.0001$, Fig. 2b), while Australian and Brazilian species did not differ significantly (mean $H_{7.5}$ = 6.1 m and 6.6 m respectively).

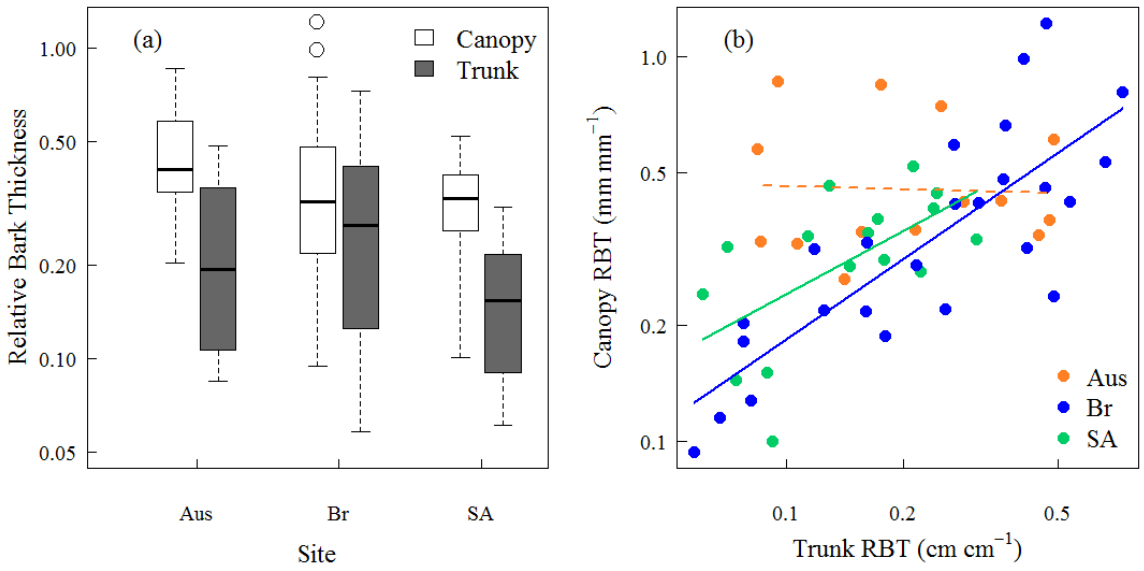



**Figure 1** a) Boxplot showing the variation in species mean relative bark thickness (canopy and trunk) in each site. Boxes indicate interquartile ranges, black bars indicate median, and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box ; b) Linear regression showing relationships between trunk and canopy relative bark thickness (RBT) for each site. Solid lines indicate slopes are significantly different from zero. Each data point is a species, and species names and sample sizes are provided in Table S1.

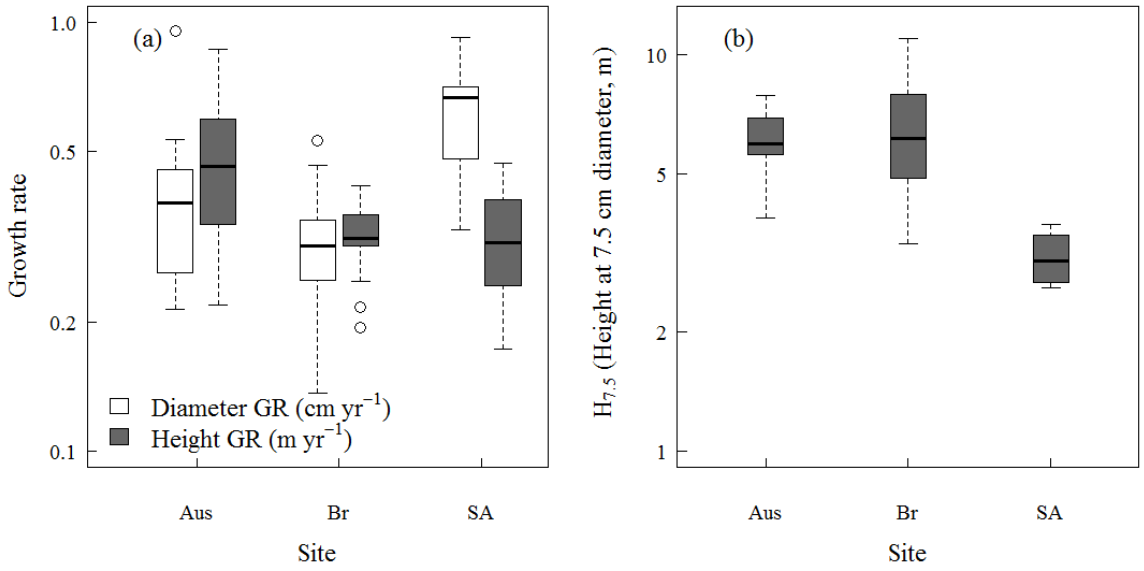



**Figure 2** a) Boxplots showing the variation in species mean diameter growth rates and height growth rates in each site; b) Boxplots showing the variation across sites in tree height at a standard diameter of 7.5 cm. Boxes indicate interquartile ranges, black bars indicate median, and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. Each data point is a species, and species names and sample sizes are provided in Table S1.

*Relationships between species relative bark thickness and growth rates*

Diameter growth rate and trunk-RBT were negatively related in Australia ($p = 0.05$) and South Africa (marginally significant, $p = 0.1$) but unrelated in Brazil (Fig. 3a, Table S2). Across all species (i.e., ignoring site membership), there was a general negative relationship between DGR and trunk-RBT ($p = 0.008$). DGR and canopy-RBT were unrelated across all sites, and within individual sites (all $p > 0.1$, Fig. 3b, Table S2).

Height growth rate and trunk-RBT were negatively related in Australia ($p = 0.02$) but elsewhere unrelated (both $p > 0.1$, Fig. 4a, Table S2). HGR and canopy-RBT were negatively related in Brazil ($p = 0.02$) and Australia (marginally significant $p = 0.09$), but unrelated in South Africa ($p = 0.35$). Ignoring site membership there was a general negative relationship between HGR and canopy-RBT ($p = 0.01$, Fig. 4b, Table S2). We note that at both high trunk-RBT and high canopy-RBT, no species had fast height or diameter growth rates (empty upper right corners in all Figs 3 and 4).

In summary, the only significant relationship between growth rates and relative bark thickness in South African species was between DGR and trunk-RBT. In Brazil, the only significant relationship was between HGR and canopy-RBT. In Australian species, the strongest relationship was between trunk-RBT and HGR, but there were also negative relationships between DGR and trunk-RBT, and HGR and canopy-RBT.

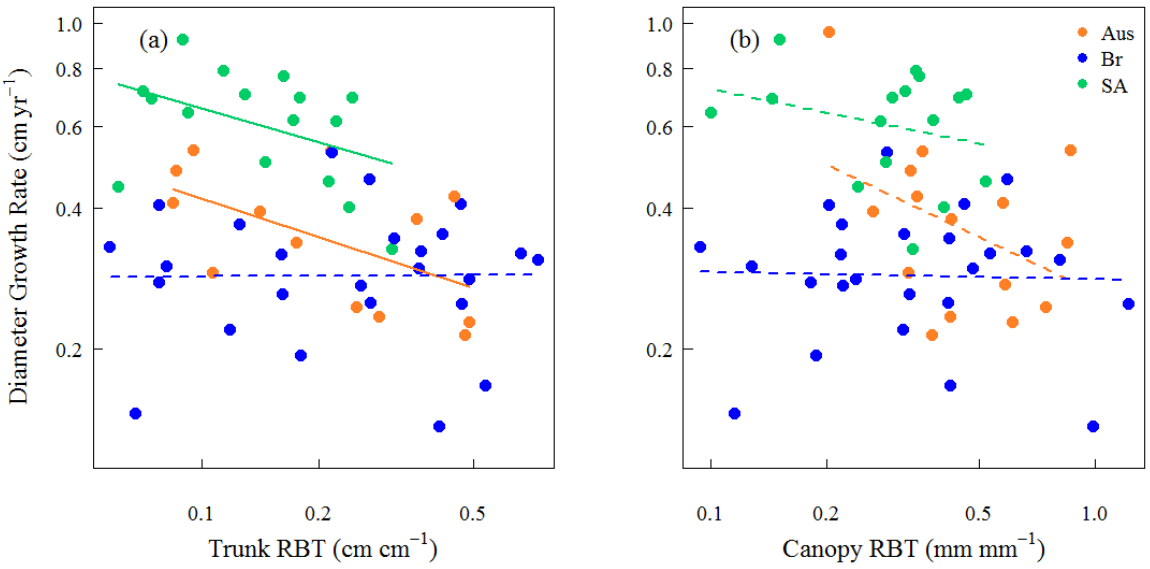



**Figure 3** Linear regressions of diameter growth rate as a function of a) relative bark thickness of the trunk; and b) relative bark thickness of a canopy branch in Australia (Aus), Brazil (Br) and South Africa (SA). Solid lines indicate relationships with $p < 0.1$. Each data point represents a species mean. Species names and sample sizes are provided in Table S1.

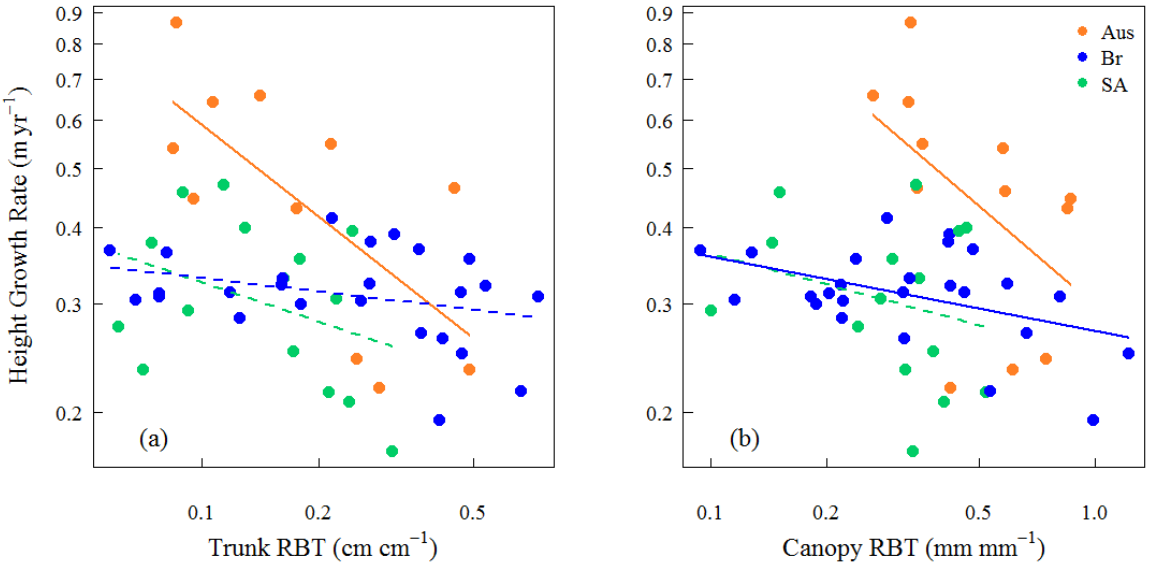



**Figure 4** Linear regressions of height growth rates as a function of a) trunk relative bark thickness, and b) canopy relative bark thickness in Australia (Aus), Brazil (Br) and South Africa (SA). Each data point represents a species mean. Solid lines indicate relationships with $p < 0.1$. Species names and sample sizes are provided in Table S1.

*Tree architecture, growth rates and relative bark thickness*

We expected growth rates to be linked to architecture, and indeed found that DGR was negatively related to $H_{7.5}$ across all sites ($R^2 = 0.39$, $p < 0.0001$, Fig. 5a). $H_{7.5}$ was positively related to HGR across all sites, though less strongly than in the case of DGR ($R^2 = 0.13$, $p = 0.01$, Fig. 5b). There was no relationship between trunk-RBT and the architecture metric (both $p= 0.6$), but because of the strong relationships between growth rate and architecture, of interest is whether growth rate variation was seen to be driven by variation in RBT once variation in architecture was accounted for.

Using linear regressions of growth rates to explore the relative importance of $H_{7.5}$, canopy-RBT and trunk-RBT as predictors, we found that canopy-RBT did not explain additional variation in HGR once variation in $H_{7.5}$ was accounted for, but it did explain signficant additional variation in DGR (Table 2). More strikingly, trunk-RBT explained significant additional variation in both DGR and HGR once $H_{7.5}$ was accounted for. Particularly in the case of DGR, once variation in $H_{7.5}$ was accounted for, trunk-RBT considerably increased the explanatory power of the regression model, and $H_{7.5}$ and trunk-RBT together explained 63% of the variation in DGR across all sites. This model explained more variation in DGR than a model including trunk-RBT and site as predictors ($R^2 = 0.58$, $p < 0.0001$).

**Table 2** Multiple linear regressions of diameter and height growth rates. F-values are represented by $F_{\beta 1}$, and the coefficient of each predictor is in brackets. When model includes two predictors the F-value of the second predictor is represented by $F_{\beta 2}$. Significance is indicated by stars (* p <= 0.05, ** p <= 0.01, *** p <= 0.001).

| **Response** | **Predictors** | **$F_{\beta 1}$** | **$F_{\beta 2}$** | **$R^2$** |
|---|---|---|---|---|
| DGR ~ | $H_{7.5}$ | 31.7 (-0.62)*** *** | | 0.39 |
| | Trunk-RBT | 7.7 (-0.23) ** | | 0.13 |
| | Canopy-RBT | 2.1 (-0.16) | | 0.04 |
| | $H_{7.5}$ + Trunk-RBT | 51.2 (-0.66) *** | 31.6 (-0.30) *** | 0.63 |
| | $H_{7.5}$ + Canopy-RBT | 38.4 (-0.70) *** | 11.6 (-0.27) ** | 0.51 |
| HGR ~ | $H_{7.5}$ | 6.9 (+0.27) * | | 0.13 |
| | Trunk-RBT | 6.8 (-0.16) * | | 0.12 |
| | Canopy-RBT | 0.9 (-0.08) | | 0.02 |
| | $H_{7.5}$ + Trunk-RBT | 7.3 (+0.24) ** | 4.9 (-0.14) * | 0.21 |
| | $H_{7.5}$ + Canopy-RBT | 6.7 (+0.27) * | 0.00 (-0.001) | 0.13 |

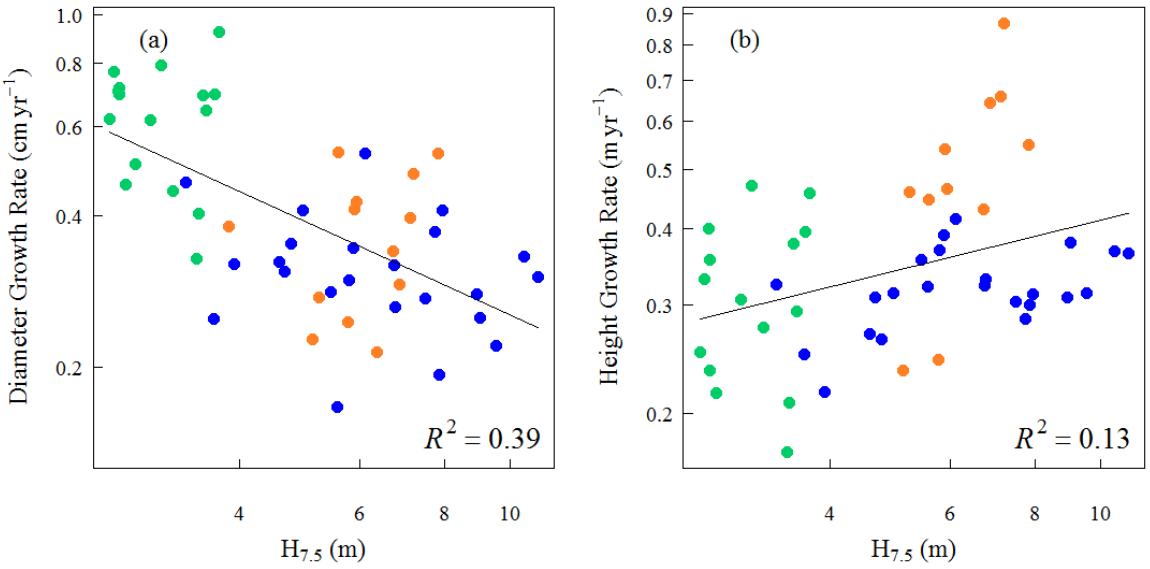



**Figure 5** Linear regressions between a tree architecture metric (height at a standard diameter of 10 cm, $H_{10}$) and (a) diameter growth rate; (b) height growth rate, across all sites. Each data point represents a species mean. Species names and sample sizes are provided in Table S1. Both relationships are significant ($p < 0.001$).

# Discussion

Our results provide some of the first evidence of an oft-hypothesised but little tested trade-off between growth rates and relative bark thickness (Hoffmann & Franco 2003; Midgley et al. 2010; Lawes, Adie, et al. 2011; Dantas & Pausas 2013) in three distinct savanna systems. Across all species, we found a general negative relationship between trunk relative bark thickness and both height and diameter growth rates. Further, relative bark thickness was highest in the sites that experience the most frequent fires (Australia and Brazil), but the relationships between relative bark thickness and growth rates differed between sites. Australian species exhibited the fastest height growth rates, and the strongest relationship in this site was between height growth rates and trunk relative bark thickness. Height growth rates of Brazilian species were negatively related to canopy relative bark thickness, but were no faster than those of South African species (despite more frequent fires in Brazil). Species in South Africa (where estimated fire return times are longest and herbivore pressure is highest) had the fastest diameter growth rates, and these were negatively related to trunk relative bark thickness. We were concerned that relative bark thickness and growth rates would be unrelated unless variation in architecture was accounted for, but this was clearly not the case. However, we did find that architecture was important, particularly regarding diameter growth rates.

*Australian savanna*

The strong trade-off between both height and diameter growth rates and relative bark thickness in Australia lends strong support to the hypothesis that species which have relatively thicker bark are not able to grow as rapidly (Midgley et al. 2010; Lawes, Adie, et al. 2011; Hoffmann et al. 2012; Pausas 2015). However, we did not find strong support for our expectation that there would be stronger links between canopy bark and height growth, than between trunk bark and height growth. Our hypothesis was based on the idea that if a species invested in thicker canopy bark (thus insulating their buds, Charles-Dominique et al. (2015)), they would not need to increase their height as rapidly to escape the flame zone (Dantas & Pausas 2013). While we found evidence of this trade-off between canopy bark and height growth, the relationship was weaker than that between height growth and trunk bark. In this site presumably trunk protection, rather than canopy protection, is paramount, and more costly to growth (Lawes et al. 2013).

*Brazilian savanna*

Species in Brazil had similar relative bark thickness to Australian species, with respect to

both trunk and canopy. However, their height growth rates were significantly lower than in Australia. This suggests that investing in relatively thick bark is sufficient to protect from fire, and investment in rapid height growth, as in Australia, is unnecessary. A similar finding was made in a study comparing Brazilian and African species (Dantas & Pausas 2013) which found that Brazilian species have comparatively thick bark enabling survival within the flame height. However they also found that Brazilian species were shorter on average, and we found they were as tall as Australian trees at a standard diameter (and in fact taller, at small sizes), and significantly taller than species in South Africa. Granted, the Dantas & Pausas study may have considered different species to ours, but the differences in natural disturbance regimes and productivity between the sites are similar. We suggest our estimates of architecture in Brazil are a result of anthropogenic changes to the fire regime. While the natural fire return interval in Brazilian savanna can be short (Hoffmann 1999; Archibald et al. 2013), currently there is a policy of fire exclusion in many Brazilian savanna protected areas (Durigan & Ratter 2016), including our study site. We suggest that this has allowed these trees to attain heights they would not have been able to under the natural fire regime, despite their slow growth rates, and thus our estimates of Brazilian species architecture are an anthropogenic artefact. The negative relationship we found between canopy bark thickness and height growth rates in Brazil lend support to the Dantas & Pausas theory that species in Brazil are generally adapted to being shorter and surviving within the flame height.

*South African savanna*

Results from the South African savanna suggest a strategy of rapid diameter growth. Lateral growth has been attributed to herbivory defence in this region (Archibald & Bond 2003), and is also likely related to the longer fire return intervals (Lawes et al. 2013). Absolute bark thickness is related to the diameter of a tree, and thus despite having relatively thin bark, these species are able to grow sufficiently large diameters between fires, such that they will have thick enough bark to defend themselves once a fire comes through (Hoffmann et al. 2012; Lawes et al. 2013). As expected, there was a trade-off between diameter growth rates and trunk relative bark thickness in this site, but it was relatively weak compared to Australia. This could be because when relative bark thickness is lower, the overall cost to growth is also relatively lower, and so the two are not as tightly coupled. Alternatively, higher allocation to below ground biomass in South African species (Tomlinson et al. 2012) may reduce the strength of the relationship between above ground traits from growth rates.

*Architecture, growth and relative bark thickness across savannas*

Our results suggest distinct bark-architecture-growth strategies at each site, which we attribute to regional differences in disturbance and productivity. However, it is important to note that the presence of distinct taxa and evolutionary histories in each of these regions may be equally important in determining differences in bark-architecture-growth strategies, as has been documented with respect to tree architecture in Australia and African savanna species (Moncrieff et al. 2014). It is unclear to what extent regional differences in phylogeny would impact our interpretation of site differences, and exploration of this would be a worthwhile future endeavour. Unfortunately, our sampling design was based entirely on available growth rate data, and we do not have sufficient replication within families to explore this topic here. Nevertheless, the bark-growth trade-off appears to be robust to differences in site conditions. Past studies have shown that tree architecture and growth rates vary across fire regimes and between continents (Hoffmann et al. 2003; Dantas & Pausas 2013; Moncrieff et al. 2014), and that bark thickness is related to size and fire regime (Lawes, Richards, et al. 2011; Brando et al. 2012; Hoffmann et al. 2012; Hempson et al. 2014; Rosell 2016). We were concerned that significant regional differences in architecture would limit our ability to detect a bark-growth trade-off across all our sites. In fact, we found the opposite. Although architecture explained significant variation in diameter growth rates across all sites, trunk relative bark thickness explained significant additional variation, such that together they explained more than 60% of the variation in diameter growth rates across all species and sites. While this link between tree architecture, bark thickness and growth was expected (Midgley et al. 2010), we are circumspect about the validity of these results, primarily due to the afore-mentioned potential artefact of anthropogenic fire suppression in Brazil.

## Conclusion

We found support for the expected trade-off between trunk relative bark thickness and growth rates across all of our sites (Gignoux et al. 1997; Midgley et al. 2010; Lawes, Adie, et al. 2011; Hoffmann et al. 2012; Lawes et al. 2013), although the relationship was weak in Brazil, possibly due to the generally lower growth rates in this site. We also found strong support for our hypothesis that canopy bark thickness has a significant negative relationship with growth in more frequent fire regimes (Hoffmann et al. 2009; Dantas & Pausas 2013; Rosell et al. 2015). However, we found little support for our expectation that height growth rate would be more tightly linked to canopy bark thickness than trunk bark thickness. Our study is the first examination of bark – growth relationships across multiple sites, that accounts for architectural variation and examines differences related to canopy versus trunk

bark thickness, and we conclusively demonstrate inter-relationships among bark, growth and architecture, contingent on the disturbance regime of a site.

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# Supplementary information

***Table S1.*** *Species mean diameter growth rate, height growth rate, and trunk and canopy relative bark thickness, with standard deviation and sample size shown in brackets. Species level estimates of predicted height at a standard diameter of 7.5 cm ($H_{7.5}$) are also given, with a 95% confidence interval in square brackets (estimated using a bootstrapping resampling technique).*

| Species | Family | Site | DGR (SD, n) cm $yr^{-1}$ | HGR (SD, n) m $yr^{-1}$ | RBT-Trunk (SD, n) cm $cm^{-1}$ | RBT-Canopy (SD, n) mm $mm^{-1}$ | $H_{7.5}$ [CI] m |
|---|---|---|---|---|---|---|---|
| *Buchanania obovata* | Anacardiaceae | Aus | 0.25 (0.23, 72) | 0.24 (0.21, 32) | 0.25 (0.07, 5) | 0.75 (0.25, 6) | 5.77 [4.5, 8.2] |
| *Lannea schweinfurthii* | Anacardiaceae | SA | 0.77 (0.47, 22) | 0.33 (0.28, 21) | 0.16 (0.08, 5) | 0.35 (0.15, 5) | 2.61 [2.5, 2.8] |
| *Sclerocarya birrea* | Anacardiaceae | SA | 0.71 (0.45, 48) | 0.40 (0.37, 43) | 0.13 (0.03, 5) | 0.46 (0.09, 5) | 2.65 [2.5, 3.0] |
| *Tapirira guianensis* | Anacardiaceae | Br | 0.41 (0.35, 44) | 0.31 (0.22, 23) | 0.08 (0.03, 5) | 0.20 (0.05, 5) | 7.96 [6.9, 9.2] |
| *Annona crassiflora* | Annonaceae | Br | 0.31 (0.17, 24) | 0.31 (0.21, 18) | 0.73 (0.09, 5) | 0.81 (0.17, 5) | 4.65 [4.0, 5.5] |
| *Xylopia aromatica* | Annonaceae | Br | 0.25 (0.16, 124) | 0.38 (0.19, 90) | 0.27 (0.15, 5) | 0.41 (0.07, 5) | 9.05 [8.6, 9.5] |
| *Gochnatia polymorpha* | Asteraceae | Br | 0.35 (0.20, 60) | 0.26 (0.16, 45) | 0.42 (0.22, 5) | 0.32 (0.10, 5) | 4.76 [4.3, 5.2] |
| *Cochlospermum fraseri* | Bixaceae | Aus | 0.38 (0.29, 18) | NA | 0.36 (0.08, 5) | 0.42 (0.02, 5) | 3.85 [2.4, 4.8] |
| *Eriotheca gracilipes* | Bombacaceae | Br | 0.25 (0.18, 54) | 0.25 (0.18, 54) | 0.46 (0.14, 5) | 1.19 (0.13, 5) | 3.66 [3.4, 4.0] |
| *Commiphora mollis* | Burseraceae | SA | 0.72 (0.62, 27) | 0.23 (0.29, 29) | 0.07 (0.02, 7) | 0.32 (0.02, 4) | 2.66 [2.4, 3.0] |
| *Erythrophloem chlorostachys* | Caesalpiniaceae | Aus | 0.53 (0.44, 114) | 0.45 (0.40, 268) | 0.09 (0.03, 5) | 0.86 (0.31, 5) | 5.58 [5.4, 5.7] |
| *Combretum apiculatum* | Combretaceae | SA | 0.64 (0.49, 177) | 0.29 (0.23, 165) | 0.09 (0.04, 5) | 0.10 (0.02, 5) | 3.57 [3.5, 3.7] |
| *Combretum hereroense* | Combretaceae | SA | 0.33 (0.26, 37) | 0.17 (0.17, 42) | 0.31 (0.06, 5) | 0.33 (0.14, 5) | 3.46 [3.3, 3.6] |
| *Terminalia glabrescens* | Combretaceae | Br | 0.22 (0.36, 22) | 0.31 (0.13, 14) | 0.12 (0.04, 4) | 0.35 (0.12, 2) | 9.6 [8.4,10.7] |
| *Terminalia sericea* | Combretaceae | SA | 0.70 (0.43, 50) | 0.40 (0.31, 48) | 0.24 (0.07, 5) | 0.44 (0.08, 5) | 3.67 [3.6, 3.8] |
| *Diosphyros mespiliformis* | Ebenaceae | SA | 0.92 (0.61, 23) | 0.46 (0.35, 24) | 0.09 (0.04, 5) | 0.15 (0.04, 5) | 3.73 [3.5, 4.0] |
| *Croton megalobotrys* | Euphorbiaceae | SA | 0.69 (0.64, 37) | 0.38 (0.23, 40) | 0.07 (0.01, 5) | 0.14 (0.11, 5) | 3.53 [3.3, 3.8] |
| *Mabea fistulifera* | Euphorbiaceae | Br | 0.33 (0.31, 60) | 0.37 (0.19, 37) | 0.06 (0.03, 5) | 0.09 (0.03, 5) | 10.5 [9.8, 11] |
| *Petalostigma pubescens* | Euphorbiaceae | Aus | 0.23 (0.15, 42) | 0.22 (0.23, 19) | 0.28 (0.13, 5) | 0.42 (0.06, 5) | NA |
| *Acacia difficilis* | Fabaceae | Aus | 0.96 (0.53, 16) | NA | NA | 0.20 (0.05, 5) | NA |
| *Acacia latescens* | Fabaceae | Aus | 0.53 (0.44, 64) | 0.55 (0.42, 60) | 0.21 (0.07, 5) | 0.35 (0.07, 6) | 7.85 [7.2, 8.5] |
| *Acacia mimula* | Fabaceae | Aus | 0.28 (0.19, 26) | 0.46 (0.66, 11) | NA | 0.58 (0.10, 5) | 5.23 [3.9, 7.6] |
| *Acosmium subelegans* | Fabaceae | Br | 0.14 (0.09, 25) | 0.19 (0.15, 18) | 0.41 (0.21, 5) | 0.99 (0.35, 5) | 3.39 [3.0, 3.7] |
| *Albiza harveyi* | Fabaceae | SA | 0.62 (0.45, 144) | 0.25 (0.20, 127) | 0.17 (0.04, 5) | 0.38 (0.11, 5) | 2.58 [2.5, 2.7] |
| *Anadenanthera falcata* | Fabaceae | Br | 0.41 (0.24, 70) | 0.31 (0.18, 56) | 0.46 (0.27, 5) | 0.46 (0.11, 5) | 4.95 [4.6, 5.5] |
| *Colophospermum mopane* | Fabaceae | SA | 0.46 (0.40, 158) | 0.22 (0.23, 147) | 0.21 (0.05, 5) | 0.52 (0.10, 7) | 2.72 [2.7, 2.8] |
| *Copaifera langsdorffii* | Fabaceae | Br | 0.27 (0.22, 412) | 0.30 (0.20, 303) | 0.26 (0.08, 5) | 0.22 (0.06, 5) | 7.50 [7.2, 7.8] |
| *Dalbergia melanoxylon* | Fabaceae | SA | 0.45 (0.32, 74) | 0.28 (0.19, 45) | 0.06 (0.06, 6) | 0.24 (0.05, 5) | 3.19 [3.0, 3.4] |

| Species | Family | Site | DGR (SD, n) cm $yr^{-1}$ | HGR (SD, n) m $yr^{-1}$ | RBT-Trunk (SD, n) cm $cm^{-1}$ | RBT-Canopy (SD, n) mm $mm^{-1}$ | $H_{7.5}$ [CI] m |
|---|---|---|---|---|---|---|---|
| *Dichrostachys cinerea* | Fabaceae | SA | 0.62 (0.49, 130) | 0.31 (0.26, 126) | 0.22 (0.17, 5) | 0.28 (0.06, 5) | 2.95 [2.8, 3.1] |
| *Dimorphandra mollis* | Fabaceae | Br | 0.46 (0.32, 31) | 0.32 (0.24, 25) | 0.27 (0.04, 5) | 0.59 (0.11, 5) | 3.33 [2.7, 3.9] |
| *Machaerium acutifolium* | Fabaceae | Br | 0.35 (0.25, 78) | 0.39 (0.19, 57) | 0.31 (0.11, 5) | 0.42 (0.13, 5) | 5.88 [5.2, 6.3] |
| *Philenoptera violacea* | Fabaceae | SA | 0.79 (0.53, 55) | 0.47 (0.42, 61) | 0.11 (0.05, 5) | 0.34 (0.06, 5) | 3.06 [2.9, 3.3] |
| *Platypodium elegans* | Fabaceae | Br | 0.28 (0.23, 11) | 0.36 (0.19, 18) | 0.49 (0.26, 5) | 0.24 (0.09, 5) | 5.45 [4.8, 6.1] |
| *Senegalia nigrescens* | Fabaceae | SA | 0.69 (0.45, 139) | 0.36 (0.26, 134) | 0.18 (0.06, 6) | 0.30 (0.06, 5) | 2.66 [2.6, 2.8] |
| *Stryphnodendron rotundifolium* | Fabaceae | Br | 0.32 (0.21, 103) | 0.27 (0.18, 104) | 0.37 (0.37, 5) | 0.66 (0.25, 5) | 4.58 [4.4, 4.8] |
| *Vachellia exuvialis* | Fabaceae | SA | 0.40 (0.32, 163) | 0.21 (0.18, 152) | 0.24 (0.06, 5) | 0.40 (0.10, 4) | 3.48 [3.0, 3.9] |
| *Nectandra cuspidata* | Lauraceae | Br | 0.30 (0.24, 67) | 0.37 (0.17, 52) | 0.08 (0.03, 5) | 0.13 (0.05, 5) | 11 [10.6,11.3] |
| *Ocotea corymbosa* | Lauraceae | Br | 0.32 (0.22, 427) | 0.32 (0.21, 323) | 0.16 (0.09, 5) | 0.22 (0.05, 5) | 6.75 [6.6, 6.9] |
| *Planchonia careya* | Lecythidaceae | Aus | 0.23 (0.23, 70) | 0.23 (0.19, 85) | 0.49 (0.27, 5) | 0.61 (0.06, 5) | 5.13 [4.5, 6.0] |
| *Byrsonima laxiflora* | Malpighiaceae | Br | 0.37 (0.33, 54) | 0.29 (0.14, 40) | 0.13 (0.03, 5) | 0.22 (0.07, 5) | 7.75 [6.9, 8.6] |
| *Rapanea umbellata* | Myrsinaceae | Br | 0.26 (0.18, 31) | 0.33 (0.19, 19) | 0.16 (0.08, 5) | 0.33 (0.06, 5) | 6.78 [6.2, 7.4] |
| *Corymbia bleeseri* | Myrtaceae | Aus | 0.29 (0.32, 100) | 0.64 (0.61, 16) | 0.11 (0.04, 5) | 0.33 (0.06, 5) | 6.88 [6.4, 7.4] |
| *Corymbia porrecta* | Myrtaceae | Aus | 0.41 (0.30, 203) | 0.54 (0.50, 263) | 0.08 (0.02, 5) | 0.57 (0.14, 5) | 5.90 [5.8, 6.0] |
| *Eucalyptus miniata* | Myrtaceae | Aus | 0.48 (0.36, 667) | 0.87 (0.51, 454) | 0.09 (0.01, 5) | 0.33 (0.10, 7) | 7.22 [7.1, 7.3] |
| *Eucalyptus tetrodonta* | Myrtaceae | Aus | 0.40 (0.34, 543) | 0.66 (0.55, 343) | 0.14 (0.03, 5) | 0.27 (0.12, 5) | 7.12 [7.0, 7.3] |
| *Myrcia bella* | Myrtaceae | Br | 0.32 (0.23, 19) | 0.22 (0.15, 18) | 0.66 (0.40, 5) | 0.53 (0.22, 5) | 3.92 [3.4, 4.6] |
| *Myrcia lingua* | Myrtaceae | Br | 0.15 (0.22, 38) | 0.31 (0.23, 19) | 0.07 (0.04, 5) | 0.12 (0.03, 5) | 4.54 [3.9, 5.2] |
| *Xanthostoemon paradoxus* | Myrtaceae | Aus | 0.34 (0.29, 92) | 0.43 (0.37, 139) | 0.17 (0.09, 5) | 0.84 (0.24, 5) | 6.73 [6.5, 6.9] |
| *Grevillea decurrens* | Proteaceae | Aus | 0.42 (0.25, 26) | 0.47 (0.28, 19) | 0.44 (0.08, 5) | 0.34 (0.04, 5) | 5.95 [5.6, 6.4] |
| *Persoonia falcata* | Proteaceae | Aus | 0.21 (0.18, 21) | NA | 0.47 (0.20, 5) | 0.38 (0.05, 4) | 6.37 [4.2, 9.0] |
| *Ziziphus mucronata* | Rhamnaceae | SA | 0.50 (0.52, 11) | NA | 0.15 (0.13, 5) | 0.29 (0.07, 5) | 2.81 [2.2, 3.3] |
| *Amaioua intermedia* | Rubiaceae | Br | 0.28 (0.33, 51) | 0.31 (0.17, 35) | 0.08 (0.07, 5) | 0.18 (0.11, 5) | 8.95 [8.4, 9.4] |
| *Faramea montevidensis* | Rubiaceae | Br | 0.19 (0.14, 142) | 0.30 (0.19, 95) | 0.18 (0.08, 5) | 0.19 (0.05, 5) | 7.88 [7.6, 8.2] |
| *Qualea cordata* | Vochysiaceae | Br | 0.17 (0.10, 63) | 0.32 (0.22, 50) | 0.54 (0.34, 5) | 0.42 (0.09, 5) | 5.57 [5.2, 6.0] |
| *Qualea grandiflora* | Vochysiaceae | Br | 0.30 (0.24, 26) | 0.37 (0.14, 25) | 0.36 (0.17, 5) | 0.48 (0.15, 5) | 5.80 [5.2, 6.4] |
| *Vochysia tucanorum* | Vochysiaceae | Br | 0.53 (0.34, 380) | 0.42 (0.22, 320) | 0.22 (0.06, 4) | 0.29 (0.04, 4) | 6.12 [5.9, 6.4] |

***Table S2*** *Linear regression results with height and diameter growth rates as response variables and relative bark thickness as predictor variables, first using the full dataset across all sites, and then data from each individual site. Significance is indicated by stars, marginal significance by † († p <= 0.1, * p <= 0.05, ** p <= 0.01, *** p <= 0.001)*

| **Response** | **Predictor** | **Site** | **slope** | **$R^2$** |
|---|---|---|---|---|
| Diameter Growth Rate | Trunk-RBT | All | -0.23 | 0.13 ** |
| | | Aus | -0.28 | 0.31 * |
| | | Br | 0.004 | 0.0001 |
| | | SA | -0.24 | 0.19 † |
| | Canopy-RBT | All | -0.16 | 0.04 |
| | | Aus | -0.39 | 0.17 |
| | | Br | -0.02 | 0.001 |
| | | SA | -0.17 | 0.07 |
| Height Growth Rate | Trunk-RBT | All | -0.16 | 0.12 ** |
| | | Aus | -0.50 | 0.48 * |
| | | Br | -0.07 | 0.1 |
| | | SA | -0.21 | 0.13 |
| | Canopy-RBT | All | -0.08 | 0.02 |
| | | Aus | -0.54 | 0.26 † |
| | | Br | -0.12 | 0.21 * |
| | | SA | -0.17 | 0.07 |

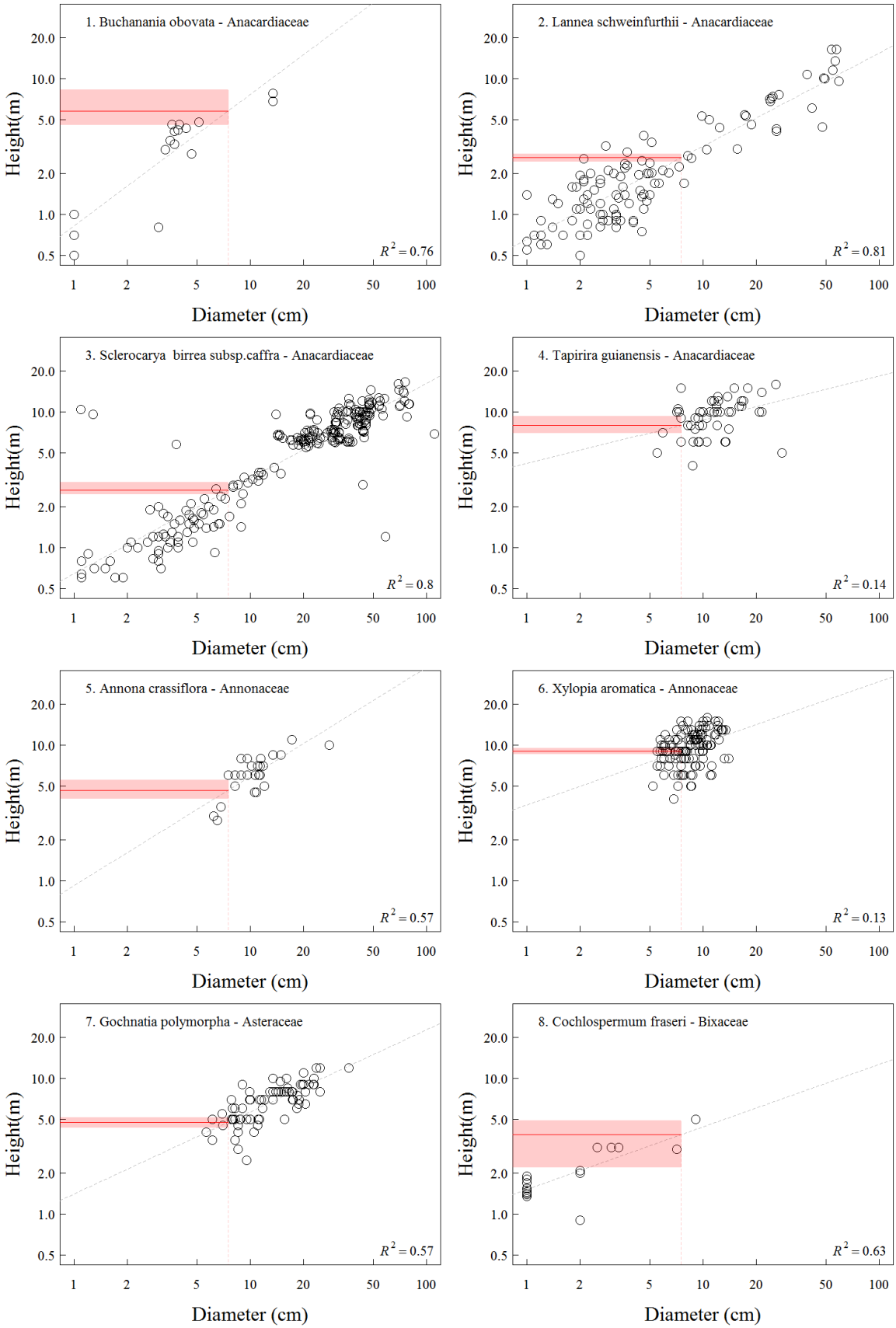


***Figure S1.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated during a bootstrap resampling procedure (2000 iterations)shown in light red. Associated $R^2$ for each allometry is also shown.*

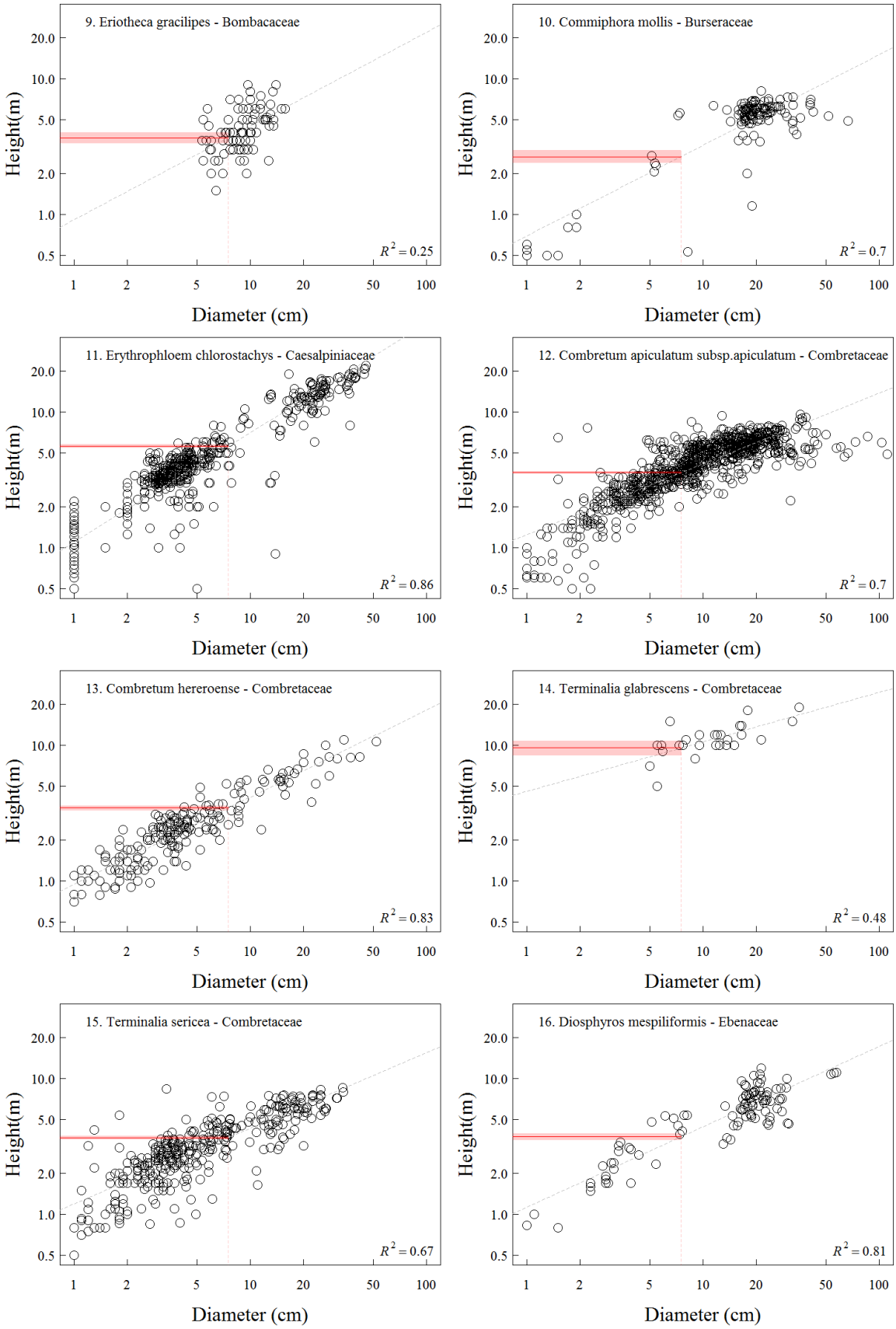


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

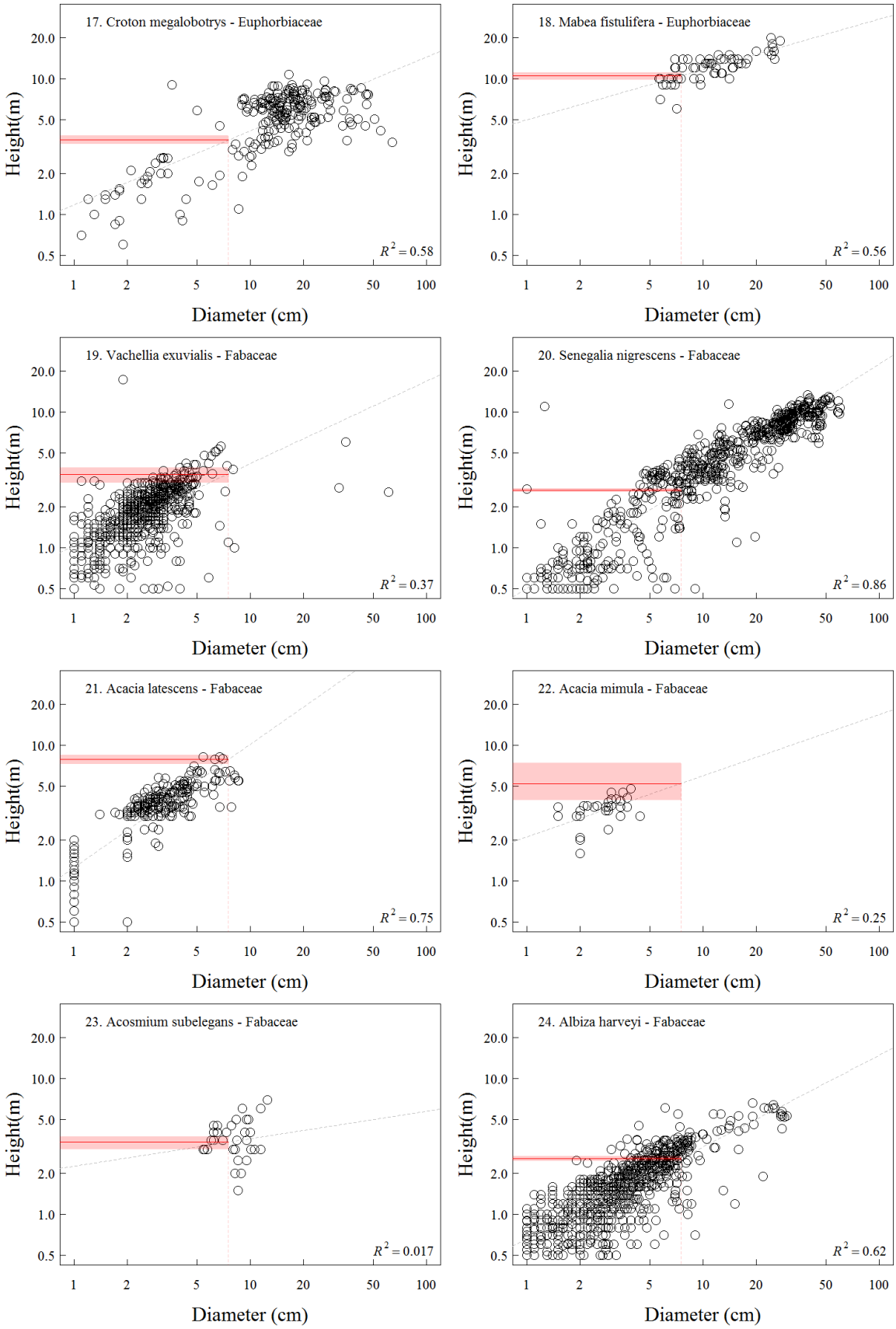


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

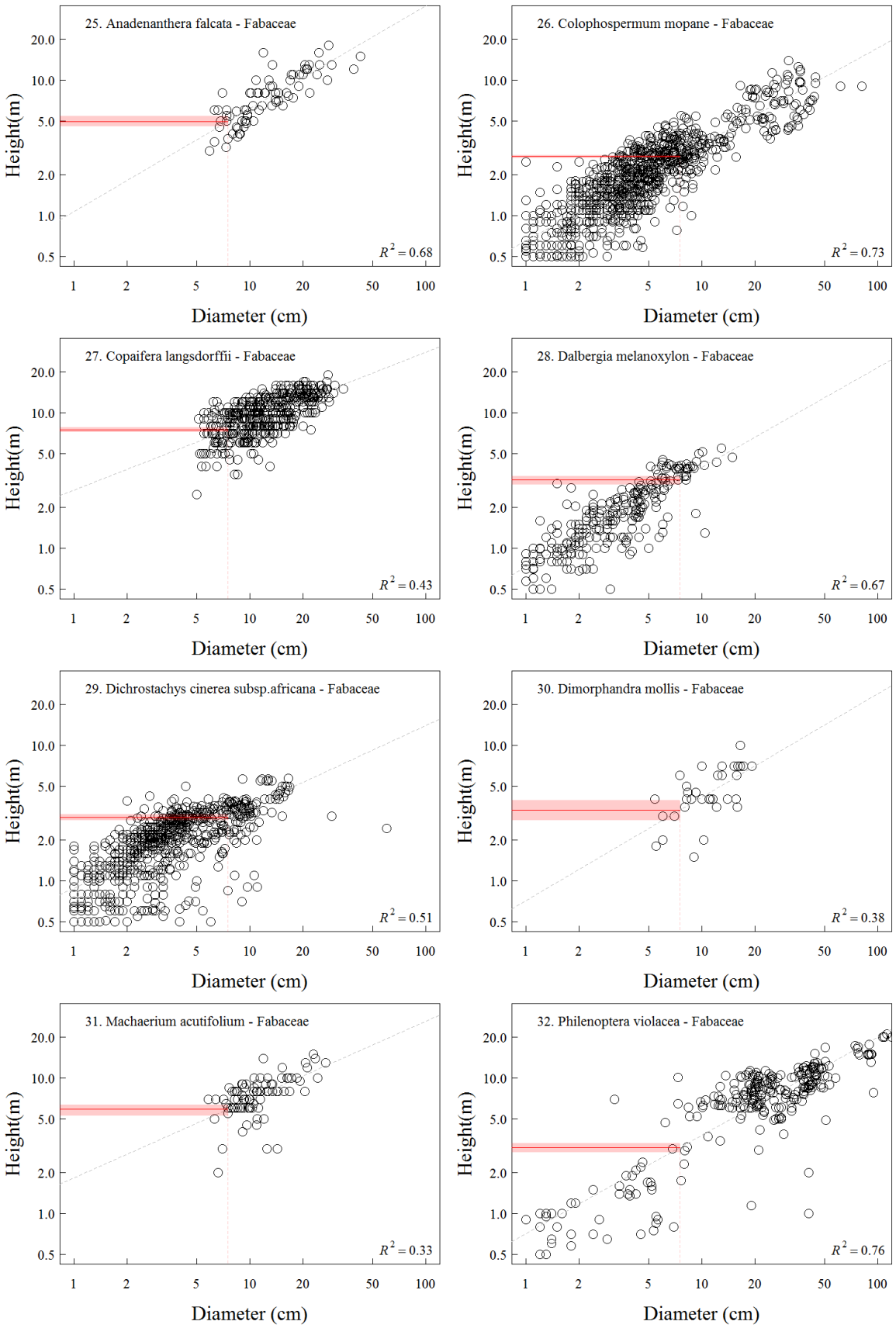


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

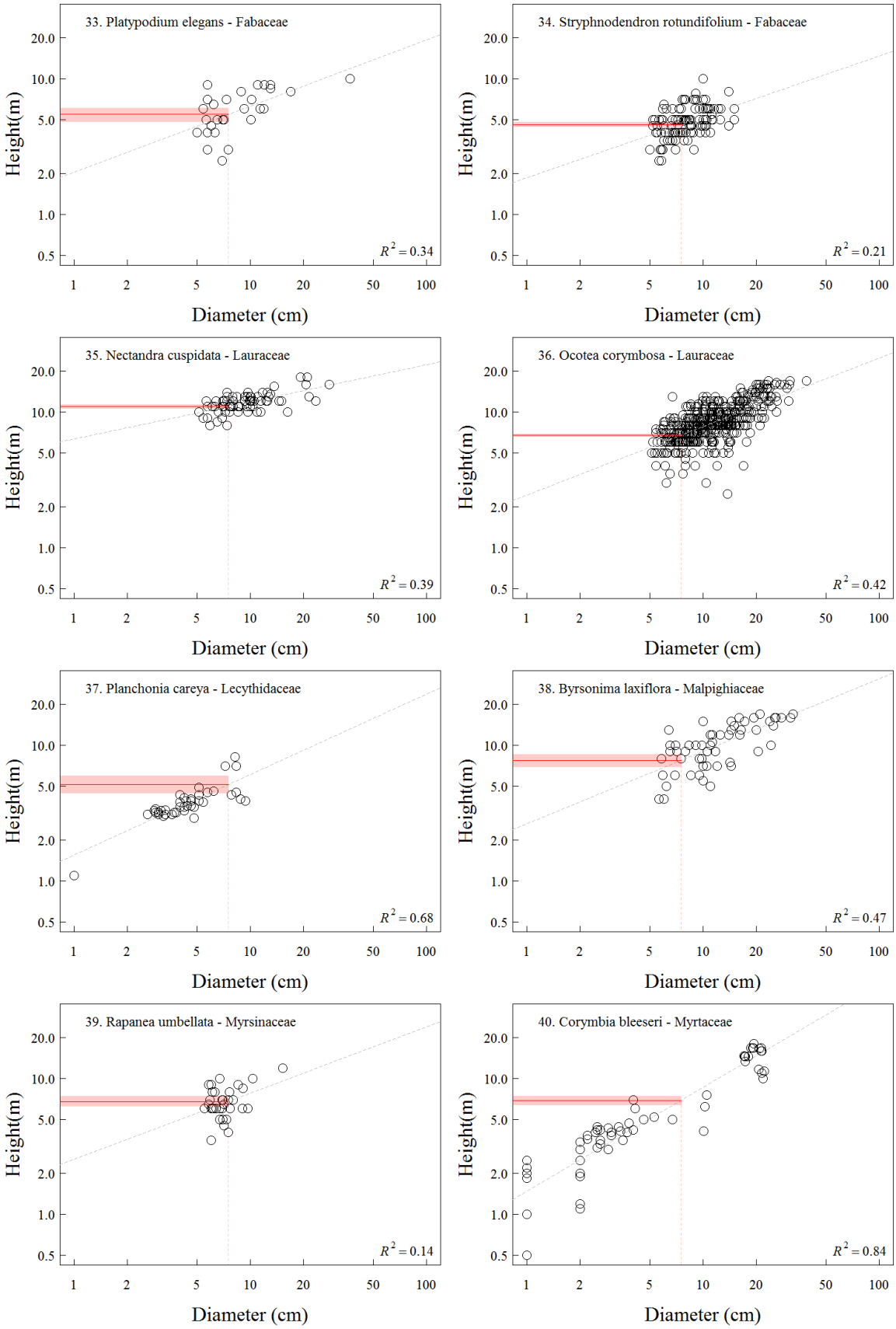


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

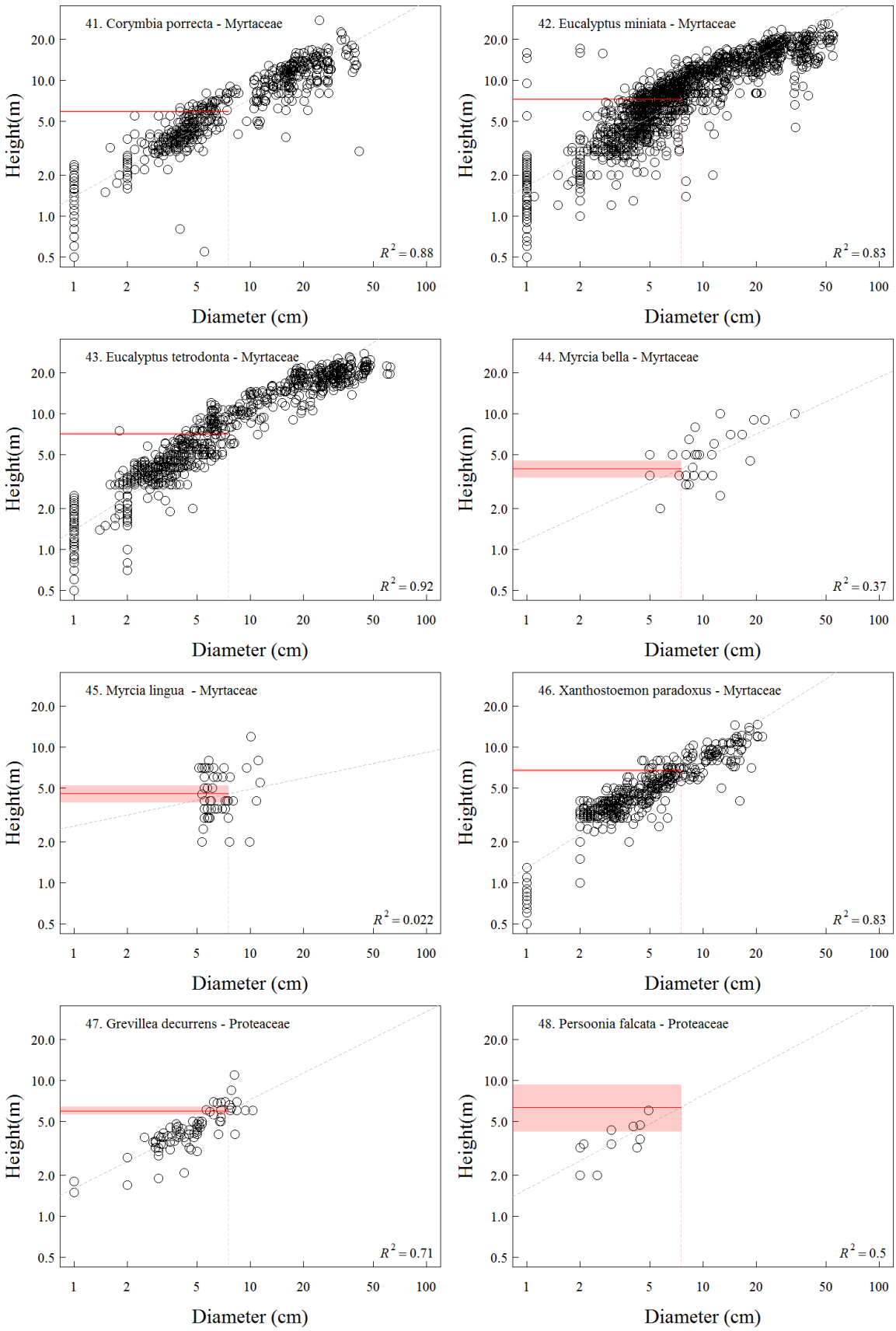


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

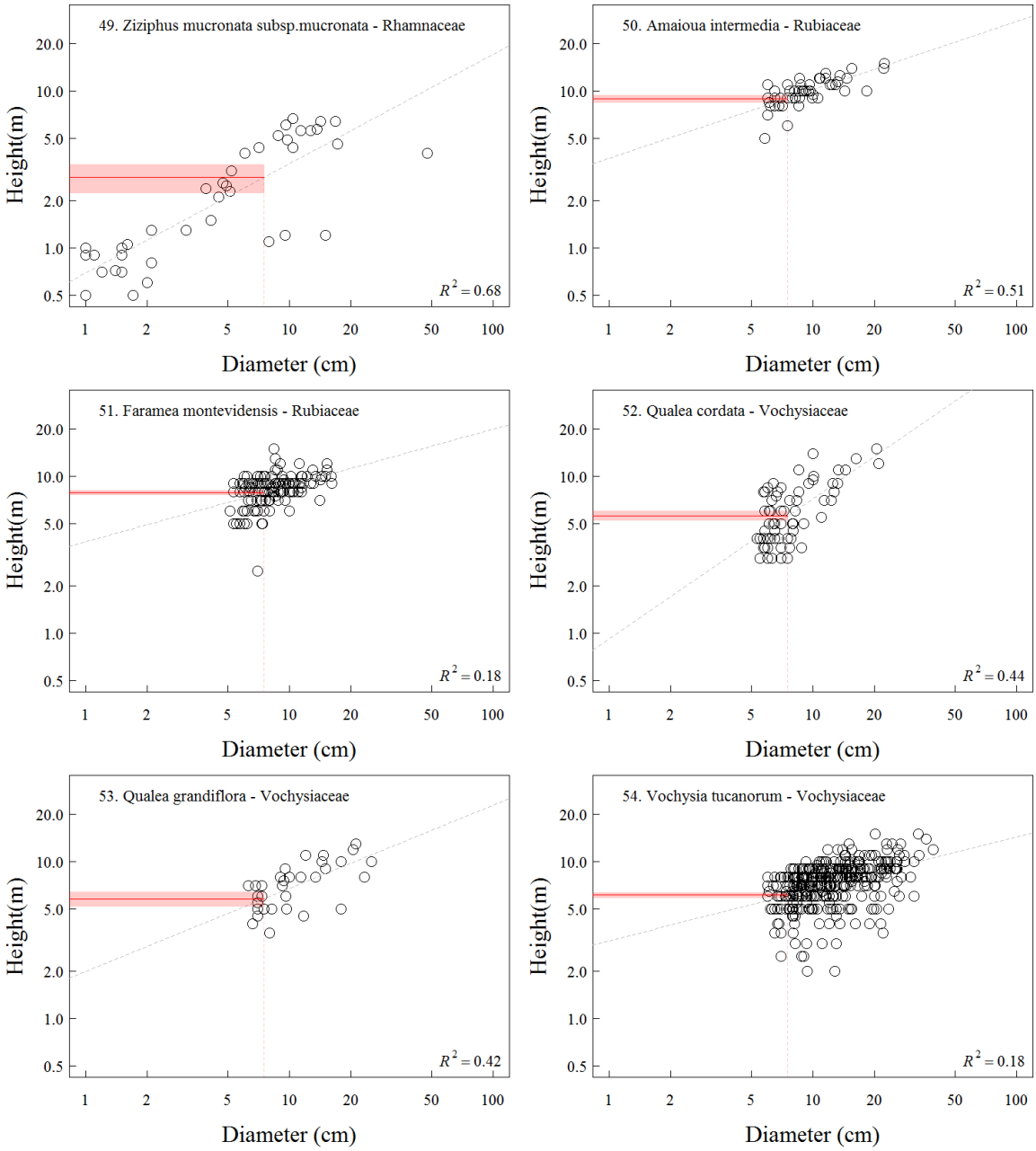


***Figure S1 cont.*** *Diameter-height allometries for each species. The predicted height at 7.5 cm diameter is shown in dark red, with the 95% confidence interval estimated through resampling shown in light red. Associated $R^2$ for each allometry is also shown.*

# Chapter 5

## Do all trees grow similarly? Describing and categorising species growth trajectories and their links to functional traits within a tropical rainforest

# Abstract

Growth rates influence the ecological strategies of tropical forest trees, but we currently lack a general understanding of how growth rates vary throughout ontogeny, and how traits might drive variation in growth trajectory shapes. Here we model the growth trajectories of 47 tropical tree species across their entire lifetime using three parameters: alpha (maximum growth rate), $D_{opt}$ (diameter at maximum growth rate), and K (ontogenetic variability in growth rate). We ask whether species can be objectively grouped into different shaped trajectories based on their modelled parameters. Traditional classifications of growth strategies (for example, pioneer vs climax, or canopy vs sub-canopy) rely heavily on expert knowledge, and are largely based on perceived light requirements, canopy position and successional strategies – factors which can be strongly subjective. Here we ask whether our modelled trajectory groups align with known expert classifications of species. We also ask whether trajectory groups are patterned with respect to seven plant functional traits.

Model-based cluster analysis identified three distinct trajectory groups. These were distinguished primarily by differences in alpha and $D_{opt}$ (group 1 was distinguished from groups 2 and 3 by its high alpha, group 2 was distinguished from group 3 by its high $D_{opt}$), but differences in K also contributed. Traits did not correlate with any individual trajectory parameter besides alpha, but trait means were significantly different between the three trajectory groups. Maximum height, leaf P and leaf N varied most strongly between trajectory groups, and were highest in group 1. Specific leaf area and wood density were highest in trajectory group 3 and lowest in trajectory group 1.

Overall the parameters of the fitted growth trajectories were distinguished more by traits than by expert groupings. Model-based clustering of species parameters allows for a nuanced grouping of growth trajectory strategies, and does not require prior knowledge. Growth trajectory strategies identified using this process were distinguished primarily by maximum growth rate and size at maximum growth rate, but the ontogenetic variability in growth rate also played a role. Wood density was the most informative trait for distinguishing growth trajectory shape, but maximum height, leaf chemistry and branch leaf:wood ratios were also influential.

# Introduction

Tree growth rates play an important role in determining the structure and composition of forests (Finegan et al. 1999). However, accurately predicting growth rates of trees is complicated by the fact that for many species they do not remain constant throughout ontogeny (Clark & Clark 1999; Hérault et al. 2011). How growth rates vary with plant size and age has been of interest to ecologists since at least the 1980s, with the recognition that all species do not exhibit the same growth trajectory shape (Lieberman et al. 1985). This started a drive to classify species into different growth trajectory shapes, because identification of a number of isolated trajectory shapes would suggest that species tend to conform to different growth strategies. Here we further consider this topic, but with an eye to linking a species' growth strategy to their functional traits. We take a two-step approach, first determining whether species can be classified into ecologically similar "growth strategies" through quantitative analysis of their trajectory shapes, and secondly asking whether these 'growth strategies' are driven by plant functional traits.

Life histories of a large majority of tropical tree species are unknown, because many of them remain undescribed (Wright et al. 2003). Understanding what drives species to exhibit different growth trajectories could help to generalise understanding of forest dynamics. This is not a new concept, but initial theory focused on external drivers such as light availability, forest gaps, and position in canopy (Denslow 1980; Vanclay 1991; Clark & Clark 1992; Condit et al. 1993). Lieberman et al. (1985) identified four main patterns of growth behaviour in tropical forest trees in Costa Rica, based primarily on vertical position in the canopy, growth rate and lifespan. These were: (1) Understorey species with slow maximum growth rates and short lifespans; (2) Shade-tolerant sub-canopy species with similarly slow maximum growth rates as understorey species but longer lifespans; (3) Canopy and sub-canopy species that are shade-tolerant but respond opportunistically to light, with long lifespans and fast maximum growth rates; and (4) Shade-intolerant canopy and sub-canopy species that are short-lived and have fast maximum growth rates.

This last category identified by Lieberman et al. is analogous to 'pioneer' species, a term coined by Swaine et al. (1988), who suggested that all tropical forest tree species could be divided into two categories, pioneer and non-pioneer (or climax), and that assignation to either group could be based arbitrarily on adult height. However, the prior work by Lieberman et al. (1985) and many studies since suggest that this does not capture the broad

range of life-history strategies of rainforest trees, particularly within the non-pioneer category. Clark and Clark (1992) recognised that pioneers were easy to characterise by high fecundity, small seeds, dependence on large gaps for germination/establishment, high growth rates, short lifespans and high mortality in shade, but that non-pioneers were more difficult to classify. They proposed a framework for classifying non-pioneer species which focused on long-term performance throughout ontogeny, with the expectation that species that were shade-tolerant would have a reduced capacity for rapid growth. They found no evidence for this trade-off, with most non-pioneer species exhibiting substantial growth rates. They suggested that the prevalent concepts of gap-dependence and shade-tolerance needed to be abandoned or refined to reflect the obvious complexity in tropical forest tree life-histories.

In response to the perceived subjectivity of these traditional classifications, Vanclay (1991) assigned species to trajectory groups based on the quantitative similarity of modelled growth trajectory curves. This was a major step forward with regards to developing an objective categorisation of trajectory types, but his method produced groupings that were too numerous to be ecologically meaningful. As a result, this data-driven approach to classifying growth strategies has not been widely adopted. Instead, more recent studies have moved away from trying to classify growth strategies, and instead have described growth using just one continuous parameter, such as species mean growth rate, or an upper percentile growth rate (as has been utilised in Chapters 2, 3 and 4 of this thesis). These more recent studies have considered strategies in a more continuous sense, linking single growth parameters to functional traits, to determine whether there are intrinsic functional constraints and trade-offs underlying a species investment in growth (Poorter et al. 2008; Wright et al. 2010; Paine et al. 2015; Gibert et al. 2016). While this approach has indeed enhanced our understanding of the functional drivers of growth rates, it fails to elicit any understanding of growth strategies throughout a species lifetime.

Hérault et al. (2011) aimed to address this gap by developing a trait-based model of growth throughout ontogeny. They described species growth trajectories with an individual growth model, and then replaced species information with trait information. They found that including trait information captured much of the variation in growth, and that wood traits and adult stature were most important for explaining interspecific differences in growth trajectories. While their approach was certainly an improvement on earlier trait-growth models, we believe their study would have benefited from consideration of growth trajectories in the light of ecological strategies. Essentially, their approach is just an

extension of the existing trait-growth studies, but instead of bivariate trait-growth relationships with one growth parameter, they investigate bivariate trait-growth relationships with three growth parameters. We propose that in addition to this, of interest is how traits shape the entire growth trajectory of a species. In other words, if the three growth parameters in combination can be considered an ecological strategy, can selection for a given strategy be predicted using traits? Hérault et al. (2011) used a growth model proposed by Canham et al. (2004), which they selected because it was the most parsimonious of the models they investigated. This model also has additional value in that it is easily interpretable from an ecological point of view. It has only three parameters, each related directly to a quantifiable aspect of growth dynamics. These three parameters are maximum growth rate (alpha), size at maximum growth rate ($D_{opt}$), and a kurtosis parameter (K) which can be interpreted as a species ability to modulate its growth rate throughout its lifetime (see Figure 1 for a graphical depiction of this model).

Because of the ecological interpretability of its parameters, we have also chosen to use the Canham model to describe growth trajectories, and combine the goals of Vanclay and Hérault et al., asking three questions. Firstly, based on modelled growth trajectory parameters, do the ontogenetic growth trajectories of tropical tree species fall naturally into similarly shaped clusters, which could be interpreted as being distinct ecological or growth 'strategies'. Secondly we ask whether these trajectory groups, and their parameters, are patterned with respect to seven plant functional traits which have been shown in past studies (and Chapter 2 of this thesis) to influence growth rates at some point in a plants ontogeny. Thirdly, we ask whether the trajectory groups align with previously introduced traditional concepts of growth strategies based on successional strategy, light requirements, and canopy position.

# Methods

### Growth data

Annual stem-increment data were derived from stem diameter records made at twenty 0.5 ha permanent plots located in tropical rainforest in northern Queensland, Australia. All trees greater than 10 cm diameter at breast height (dbh) were measured every two to five years for a period of up to 40 years between 1971 and 2012. Further details on these plots and the methods of data collection can be found in Bradford et al. (2014). While the full dataset is comprised of 481 species, for this study we focused on 47 species. We selected this subset because we had previously collected their associated trait data (See

Supplementary Tables S1 and S2 and Figure S1 for species information). In addition, most of these species were well replicated in the growth rate dataset, with at least 50 replicates, which gave us more confidence when fitting the growth trajectory models. We considered unreasonably low diameter measurements to be those where dbh had decreased by more than 5% between censuses, a common practise when cleaning permanent plot growth datasets (Condit et al. 1993). This resulted in deletion of 43 records from a total of 28066. Ten additional unreasonably high measurements were deleted as they were visually obvious outliers when the data were plotted. Our cleaned dataset was comprised of 28013 records of 3071 unique individuals of 47 species.

**Trait data**

For 44 species (Table S2) we collected specific leaf area (SLA), photosynthesis ($A_{area}$), nitrogen concentration per area ($N_{area}$), phosphorus concentration per area ($P_{area}$), trunk wood density (WD), branch leaf:wood mass ratio (LM:WM) and species maximum height ($H_{max}$). Trait data for all species were collected in or very near the permanent plots. All leaf measurements were made on outer-canopy leaves which were sampled from as high in the canopy as possible. For three to eight adult individuals of each species we measured $A_{area}$, individual leaf mass, individual leaf area and leaf N and P concentrations. Photosynthesis measurements were made under ambient $CO_2$ concentrations (approx. 400 ppm) and temperature (25–27°C), and high light (2000 μmol $m^{-2}$ $s^{-1}$), using a Li-Cor 6400XT portable infrared gas analyser (LICOR Inc., Lincoln, NE, USA). Three leaves from each individual were scanned and leaf area calculated using ImageJ software (U. S. National Institutes of Health, Bethesda, Maryland, USA). Leaves were oven dried at 60-70°C for at least five days and reweighed to determine dry mass. SLA was calculated by dividing leaf area by dry mass. Leaf nutrient analyses were performed at the Appleton Laboratory (University of Queensland). Leaf nitrogen concentration was determined by combustion using a LECO TruSpec CHN analyser. Leaf samples were digested in acid and total P concentration was determined by ICP-OES. Leaf $N_{area}$ and $P_{area}$ were calculated by multiplying N and P masses by SLA.

We measured branch scale leaf:wood mass ratios on terminal, outer-canopy, sunlit branches. Cumulative leaf mass and wood mass were measured at 100 cm from the branch tip, including biomass on any side branches, on a minimum of three individuals per species. Fruit and flowers were generally absent, but when present they were discarded to allow direct comparison of leaf and wood material. Samples were oven dried at 60-70°C until constant weight. We then calculated the ratio of dried branch leaf mass to dried wood mass

(LM:WM).

Trunk wood density for all species was sourced from published (Cause et al. 1989; Hyland 1989) and from unpublished data (M. Bradford, CSIRO, Atherton) collected from individuals within the study area. Species maximum height was estimated based on individuals within the study area and permanent plots (M. Bradford, CSIRO, Atherton).

## Data analysis

*Fitting growth trajectories*

We fitted hierarchical growth trajectory models to the dbh increments using an equation from Canham et al. (2004). This equation predicts how the growth rate of a species changes as a function of tree size and can be written as

$$\log(GR + 1) = \text{alpha} \times exp^{0.5\left[\frac{\log(\frac{DBH}{Dopt})}{K}\right]^2}$$

where alpha is the peak of the curve, $D_{opt}$ is the diameter at which alpha occurs, and K is the kurtosis of the function (see Figure 1). We chose to use this equation to model growth trajectories because in a comparison of six popular growth models, Hérault et al. (2011) found the Canham model to be the most appropriate model for two reasons; 1) It had the lowest AIC (Akaike Information Criterion) for most species, and 2) The parameters represent ecologically meaningful and interpretable concepts. Our model was hierarchical (mean and variance of each parameter was modelled assuming the normal distribution across species), used uninformative priors, and fitted in R 3.3.0 (R Core Team, 2016) using the package "rstan" 2.12.1 (Stan Development Team, 2016). It yielded unique alpha, $D_{opt}$ and K parameters for each of our 47 species. R code for the model can be found in Appendix 1 of the supplementary information.

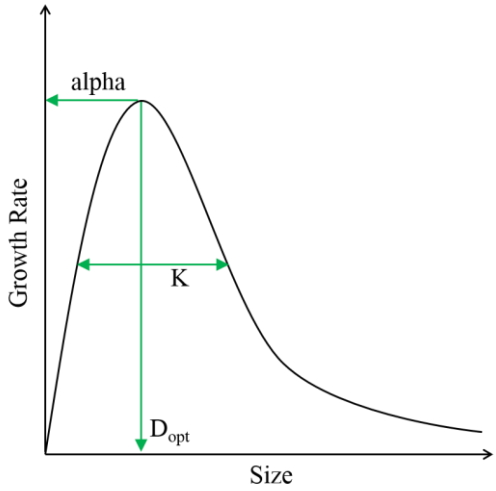


**Figure 1** Schematic depicting the Canham et al. (2004) model for growth trajectories of trees illustrating the parameters alpha (maximum growth rate), $D_{opt}$ (size at maximum growth rate), and K (ontogenetic variation in growth rate, or ability to modulate growth over a lifetime).

*Grouping growth trajectories*

We used model-based cluster analysis to group species based on their growth trajectory parameters using the R package "mclust". Model-based clustering is a method of categorisation, where each cluster is weighted by the probability that an observation belongs to that cluster (Fraley & Raftery 2002). These probability-based models are increasingly preferred in the literature over heuristic methods, where clusters are normally well separated, and the number of clusters is pre-defined. For model-based clusters, each cluster is centred at the parameter means, and the shape, volume and orientation of clusters are determined by a covariance matrix of the parameters. The available options are EII, VII, EEI, VEI, EVI, VVI, EEE, EEV, VEV and VVV. The first identifier refers to volume, the second to shape and the third to orientation, and E stands for "equal", V for "variable" and I for "coordinate axes". Model-based clustering allows for overlapping clusters, producing a probabilistic clustering that quantifies the uncertainty of observations belonging to clusters (Fraley & Raftery 2002; Mun et al. 2008). We henceforth refer to the groups identified using model-based cluster analysis as "trajectory groups".

*Traits and growth trajectories*

We used ANOVA to determine whether the seven traits differed significantly between trajectory groups. We also considered bivariate relationships between all traits and trajectory parameters. We were also interested in multi-trait models, and used backward stepwise regression (using the 'leaps' R package) to identify the best models (i.e. most influential traits) of each of the three trajectory parameters. These stepwise reduced models were compared to full models using Akaike's Information Criterion (AIC). A lower AIC

implies the model is a better fit, and penalises a model for additional parameters (Hooten & Hobbs 2015).

*Expert-classification*

In addition to model-based clustering, we categorised species through expert knowledge (M. Bradford, CSIRO, Atherton) according to three categories: 1) Whether species are light-demanding or shade-tolerant (a reference to their requirements in early ontogeny); 2) whether species are canopy or sub-canopy (a reference to their vertical positions in the canopy as adults); and 3) Whether species are pioneer, intermediate, or climax (a subjective categorisation of their successional strategy). Successional strategy category is henceforth referred to as "successional group". We combined the information on light requirements and canopy positions of species to place each into one of four categories (light-demanding canopy, light-demanding sub-canopy, shade-tolerant canopy, shade-tolerant sub-canopy), and henceforth refer to this category as "light-canopy group". We used chi-squared tests to test whether the trajectory groups that we identified were correlated with the expert-identified groups. In addition, we used ANOVA to determine whether the modelled growth trajectory parameters alpha, $D_{opt}$ and K differed between expert-identified groups.

# Results

*Growth trajectory parameters*

Growth trajectories fitted using the Canham model (Canham et al. 2004) are illustrated in supplementary Figure S1; the raw data for each species are also shown. The model parameter alpha is an estimate of the maximum growth rate, and ranged across species from 0.08 to 0.47 cm $yr^{-1}$, with a mean of 0.22 cm $yr^{-1}$ across all species. $D_{opt}$ is the stem diameter of the plant when it is at its maximum growth rate and, although this ranged widely from 4.3 to 142.1 cm, all but one species fell between 4.3 and 69.5 cm. This high-$D_{opt}$ species was *Flindersia brayleyana* (Rutaceae) and supplementary Figure S1.44 confirms it has high growth rates at large sizes. The mean $D_{opt}$ across species was 41.0 cm. K estimates the ontogenetic variation in growth rate of a species (i.e. the kurtosis of the curve) and ranged from 0.56 to 2.09, with a mean of 1.33 for all species. Parameter estimates for each species can be found in Table S1.

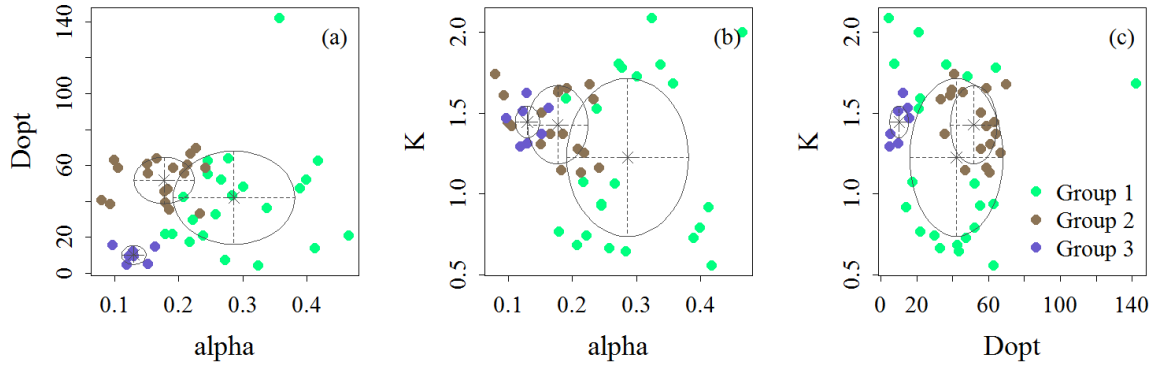


**Figure 2** Model parameters for 47 species grouped using model-based cluster analysis. Three groups were identified, with some overlap in all parameters between groups. Group 1 = green, Group 2 = brown, Group 3 = blue.

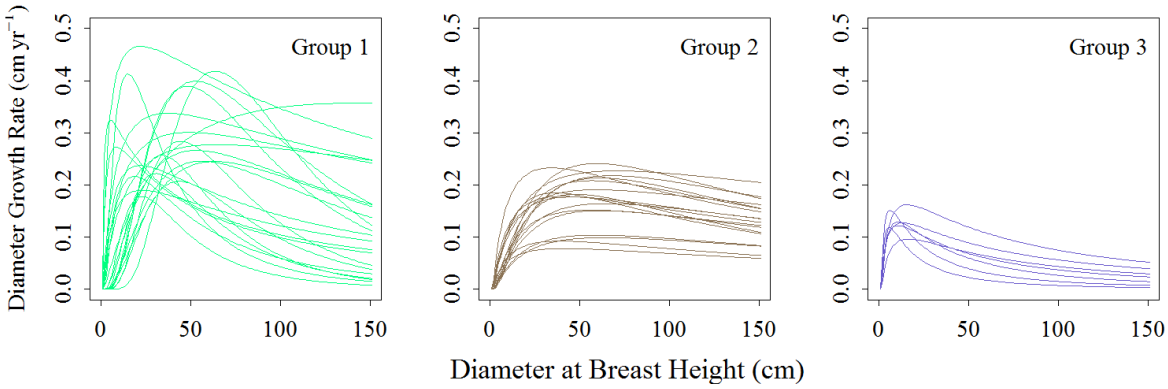


**Figure 3** Modelled rainforest species growth trajectories, separated into trajectory groups, Group 1 (22 species), Group 2 (18 species) and Group 3 (7 species). Trajectory groups were identified using model-based cluster analysis (illustrated in Figure 2). Probabilities of group membership are in supplementary Table S1.

*Trajectory Groups*

Model-based cluster analysis identified three clusters which had variable volumes and equal shapes, and clusters were orientated according to coordinate axes (Figure 2). Trajectory group 1 contained 22 species, group 2 contained 18 species, and group 3 only contained 7 species, with the mean posterior probability for cluster membership (the probability that a given species would belong to a cluster) being 0.49, 0.365 and 0.145 respectively. The mean and standard deviations of trajectory parameters of each group are in Table 1.

**Table 1** Mean and standard deviation for parameters in each trajectory group, identified through model-based cluster analysis of species parameters.

| | **Group 1** | **Group 2** | **Group 3** | **Units** |
|---|---|---|---|---|
| **n species** | 22 | 18 | 7 | - |
| **alpha (± sd)** | 0.29 (0.095) | 0.18 (0.047) | 0.13 (0.019) | cm $yr^{-1}$ |
| **$D_{opt}$ (± sd)** | 42.2 (25.94) | 51.7 (12.89) | 10.24 (5.23) | cm |
| **K (± sd)** | 1.23 (0.489) | 1.43 (0.243) | 1.45 (0.099) | - |

Pairwise occupancy of the three-parameter space is shown in Figure 2. These plots help to illustrate that trajectory group 1 differed from trajectory groups 2 and 3 most notably in terms of alpha; whereas groups 2 and 3 were distinguished most strongly in terms of $D_{opt}$. The modelled probabilities of trajectory group occupancy for each species can be found in supplementary information Table S1. Species were assigned to a group if the probability of occupancy in that group was higher than 0.5. Modelled growth trajectories of study species, separated into trajectory groups, are displayed in Figure 3. The three groups had distinct trajectory shapes. Species in trajectory group 1 tended to have high maximum growth rates (alpha), which they reached at intermediate diameters (see Table 1). Growth rates of trajectory group 1 species generally dropped off rapidly once they reached maximum growth rate, as a result of K being lower than in other groups. On average, species in trajectory group 2 had higher $D_{opt}$ values than species in trajectory group 1 (Table 1), but their growth rates at a given $D_{opt}$ tended to be lower (Figure 2). They had higher K values than trajectory group 1, suggesting less variation in growth rate throughout ontogeny. Mean alpha and $D_{opt}$ values in trajectory group 3 were lower than those for either of the other groups (Table 1). Trajectory group 3 species were distinguished from trajectory group 1 primarily on alpha values, and from trajectory group 2 primarily on $D_{opt}$ values.

*Traits and growth trajectories*

Species with higher alpha typically had higher photosynthetic rate ($A_{area}$), leaf nitrogen per

area ($N_{area}$), leaf phosphorus per area ($P_{area}$), and maximum height ($H_{max}$), but lower specific leaf area (SLA) and wood density (WD). Branch-scale leaf:wood mass ratio (LM:WM) was unrelated to alpha (Table 2, see supplementay table S2 for species trait information). Stepwise regression identified a combination of SLA, $H_{max}$, WD and $P_{area}$ as the best model of alpha, which captured 56% of the variation in alpha. $D_{opt}$ was not significantly related to any individual traits. Stepwise regression identified a combination of SLA and $A_{area}$ as the best model to capture variation in Dopt, though this model only had an $R^2$ of 0.11, and was only marginally significant (p = 0.09, Table 2). Variation in K was best captured by $P_{area}$, though this trait only explained 7% of the variation in K and was only marginally significant (p = 0.08, Table 2). A combination of $P_{area}$ and SLA explained 12% of the variation in K, but this model was also only marginally significant (p = 0.07). Interestingly, all traits except WD were negatively related to K, whereas they were generally positively related to alpha. SLA was the only trait for which the slope was negative for alpha, $D_{opt}$ and K.

**Table 2.** Regression statistics for linear regressions between trajectory parameters (alpha, $D_{opt}$, K) and traits ($P_{area}$, $N_{area}$, $A_{area}$, SLA, wood density, LM:WM, $H_{max}$) for 44 rainforest species. Stepwise regression was also used to determine which traits in combination best explained variation in trajectory parameters. Best models are highlighted in bold.

| **Model** | **$R^2$** | **p** | **slope** |
|---|---|---|---|
| alpha ~ $A_{area}$ | 0.13 | 0.02 | 0.02 |
| alpha ~ WD | 0.16 | 0.007 | -0.52 |
| alpha ~ $H_{max}$ | 0.28 | 0.0002 | 0.01 |
| alpha ~ SLA | 0.19 | 0.003 | -0.61 |
| alpha ~ LM:WM | 0.04 | 0.18 | 0.17 |
| alpha ~ $P_{area}$ | 0.27 | 0.0004 | 0.57 |
| alpha ~ $N_{area}$ | 0.22 | 0.002 | 0.70 |
| **alpha~ $P_{area}$ +$H_{max}$+ SLA+ WD** | **0.56** | **< 0.0001** | **0.35; 0.01; -0.42;-0.36** |
| $D_{opt}$ ~ $A_{area}$ | 0.06 | 0.10 | -0.03 |
| $D_{opt}$ ~ WD | 0.01 | 0.52 | -0.23 |
| $D_{opt}$ ~ $H_{max}$ | 0.01 | 0.64 | 0.003 |
| $D_{opt}$ ~ SLA | 0.01 | 0.49 | -0.27 |
| $D_{opt}$ ~ LM:WM | 0.001 | 0.84 | 0.05 |
| $D_{opt}$ ~ $P_{area}$ | 0.0001 | 0.94 | -0.02 |
| $D_{opt}$ ~ $N_{area}$ | 0.03 | 0.22 | -0.51 |
| **$D_{opt}$ ~ SLA+$A_{area}$** | **0.11** | **0.09** | **-0.60; -0.04** |
| K ~ $A_{area}$ | 0.01 | 0.46 | -0.01 |
| K ~ WD | 0.05 | 0.15 | 0.22 |
| K ~ $H_{max}$ | 0.03 | 0.23 | -0.003 |
| K ~ SLA | 0.02 | 0.36 | -0.16 |
| K ~ LM:WM | 0.0004 | 0.90 | -0.01 |
| K ~ $P_{area}$ | 0.07 | 0.08 | -0.23 |
| K ~ $N_{area}$ | 0.04 | 0.20 | -0.24 |
| **K ~ $P_{area}$ + SLA** | **0.12** | **0.07** | **-0.29; -0.26** |

We also quantified relationships between traits and trajectory group membership. All traits except photosynthetic rate ($A_{area}$) showed some significant differences between trajectory groups (Figure 4, Table 3). Wood density (WD) was most strongly related to trajectory group ($R^2 = 0.27$). SLA was only significantly different between trajectory group 1 and 3, with trajectory group 2 having intermediate SLA ($R^2 = 0.1$). While no traits were significantly different between all groups there was definite patterning with respect to traits. $N_{area}$, $P_{area}$, LM:WM and $H_{max}$ decreased from trajectory group 1 to 3, while SLA and wood density increased (Table 3, Figure 4).

**Table 3** ANOVA output comparing variation in trait values for 44 species across trajectory groups. Mean trait values for each trajectory group are shown, and significant differences and similarities between groups are indicated by symbols †§. Bold indicates significant models (at $p < 0.05$).

| | $A_{area}$ | **$N_{area}$** | **$P_{area}$** | SLA | **WD** | **LM:WM** | **$H_{max}$** |
|---|---|---|---|---|---|---|---|
| | μmol $m^2$ $s^{-1}$ | g $cm^{-2}$ | g $cm^{-2}$ | $cm^2$ $g^{-1}$ | g $cm^{-3}$ | g $g^{-1}$ | m |
| Group 1 | 9.0 § | 0.023 § | 0.0014 § | 86.4 § | 0.51 § | 1.51 § | 37.2 § |
| Group 2 | 7.7 § | 0.018 † | 0.0010 † | 92.8 §† | 0.61 † | 1.33 § | 30.1 † |
| Group 3 | 8.6 § | 0.018 † | 0.0009 † | 113.1 † | 0.72 † | 0.79 † | 28.8 † |
| **$R^2$** | 0.05 | **0.22** | **0.22** | 0.1 | **0.27** | **0.18** | **0.22** |
| **p** | 0.37 | **0.007** | **0.006** | 0.1 | **0.002** | **0.02** | **0.006** |
| **F (df)** | 1.1 $_{(2,41)}$ | **5.7 $_{(2,41)}$** | **5.8 $_{(2,41)}$** | 2.3 $_{(2,41)}$ | **7.4 $_{(2,41)}$** | **4.3 $_{(2,41)}$** | **5.8 $_{(2,41)}$** |

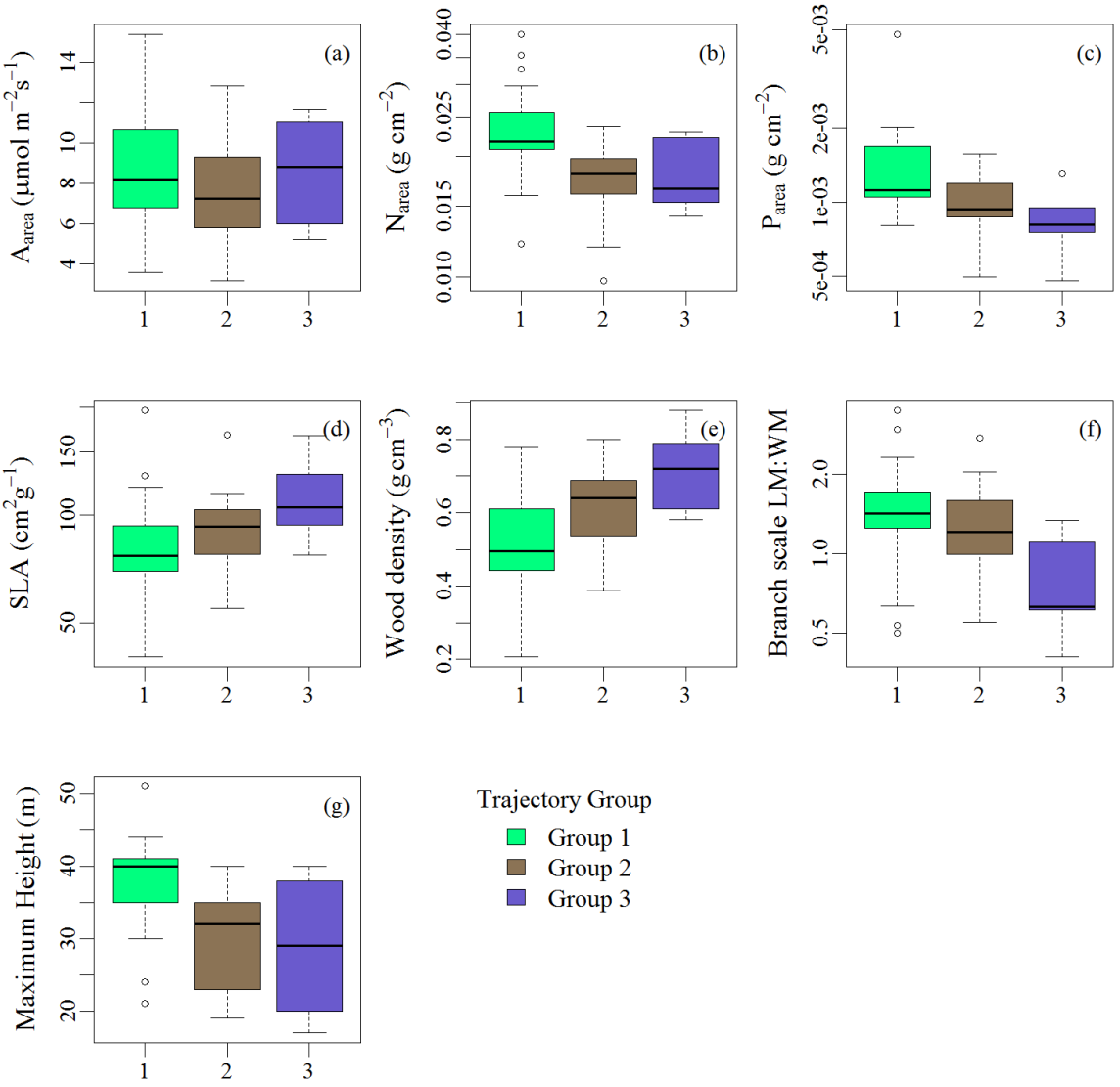


**Figure 4** Boxplots showing species mean trait values as a function of trajectory groups identified using model-based cluster analysis for 44 rainforest species (See Table S2). The seven traits were (a) Light-saturated photosynthetic rate ($A_{area}$), (b) Leaf nitrogen per area ($N_{area}$), (c) Leaf phosphorus per area ($P_{area}$), (d) Specific leaf area (SLA), (e) wood density, (f) branch scale leaf mass to wood mass ratio (LM:WM) and (g) maximum height of a species. ANOVA statistical output in supplementary Table 3. Boxes indicate interquartile ranges, black bars indicate median, and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box

*Alignment of trajectory groups with expert-classification*

If we were to describe trajectory groups according to the traditional succession-based paradigm of gap-dependence and shade-tolerance, species from trajectory group 1 could be considered as "large, pioneer, gap-dependant canopy species", those from trajectory group 2 as "large, climax, shade-tolerant canopy species", and those from trajectory group 3 as "small, shade-tolerant sub-canopy species". But do these definitions align with traditional expert classification of the species? Table S3 reports the light-canopy and successional groups (see methods for definitions) that species and families were assigned to according to expert knowledge. Anecdotally, there was no obvious effect of family on any groupings; in cases where families were represented by more than one species, they did not restrict themselves to either individual trajectory groups, light-canopy groups or successional groups. However, this study was not designed to test this explicitly.

We performed Pearson's Chi-squared tests of independence between expert groups and our trajectory groups. The correlation between light-canopy groups and our trajectory groups yielded a chi-squared value of 10.61 ($p = 0.1$, $df = 6$), that is, there was little concordance between our trajectory groups and the groups based on canopy position and light requirement. Similarly, a Pearson's chi-squared test of independence between successional group and trajectory groups yielded a chi-squared value of 2.26 ($p = 0.69$, $df = 4$), suggesting that expert grouping of species based on their assumed successional strategy (pioneer, intermediate or climax) also did not align well with our modelled trajectory groups.

The variation in trajectory parameters across light-canopy groups is shown in Figure 5. Alpha showed significant differences, though these were largely between canopy and sub-canopy, and irrespective of light. Canopy species generally had higher alpha values than sub-canopy species ($F = 7.78$, $R^2 = 0.35$, $p = 0.0002$). Neither $D_{opt}$ ($F = 1.04$, $R^2 = 0.07$, $p = 0.39$) nor K ($F = 0.96$, $R^2 = 0.06$, $p = 0.42$) varied predictably or significantly between light-canopy groups. None of the trajectory parameters varied significantly among successional groups (all $R^2 < 0.1$ and all $p > 0.1$, Figure 6). Overall these results suggest that, for the 47 species sampled, traditional categorisations largely reflect differences in maximum growth rates, with little influence from other aspects of a species growth trajectory.

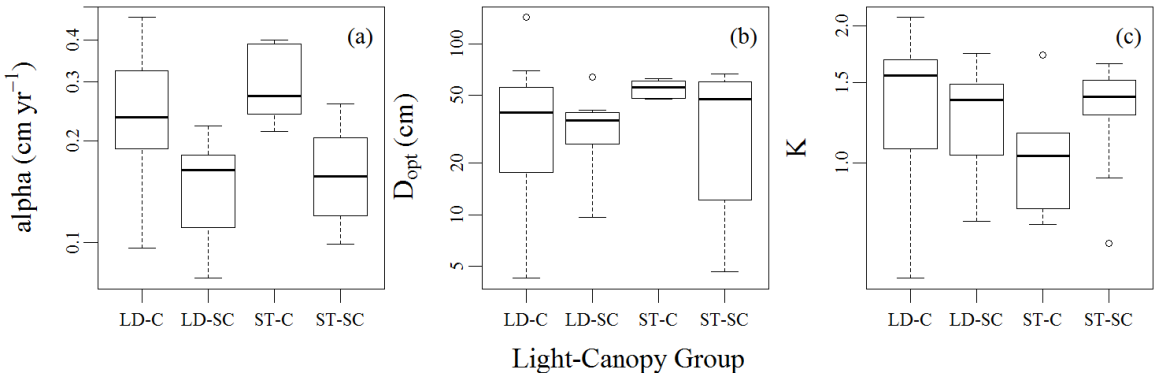


**Figure 5** Boxplots of 47 rainforest species trajectory parameters (a) maximum growth rate (alpha), (b) Size at maximum growth rate ($D_{opt}$) and (c) ontogenetic variation in growth rates (K) as a function of expert-identified groups based on juvenile light requirements and adult canopy positions. Groups were: light-demanding canopy (LD-C, 22 species), light-demanding sub-canopy (LD-SC, 7 species), shade-tolerant canopy (ST-C, 6 species) and shade-tolerant sub-canopy (ST-SC, 12 species). Boxes indicate interquartile ranges, black bars indicate median, and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box

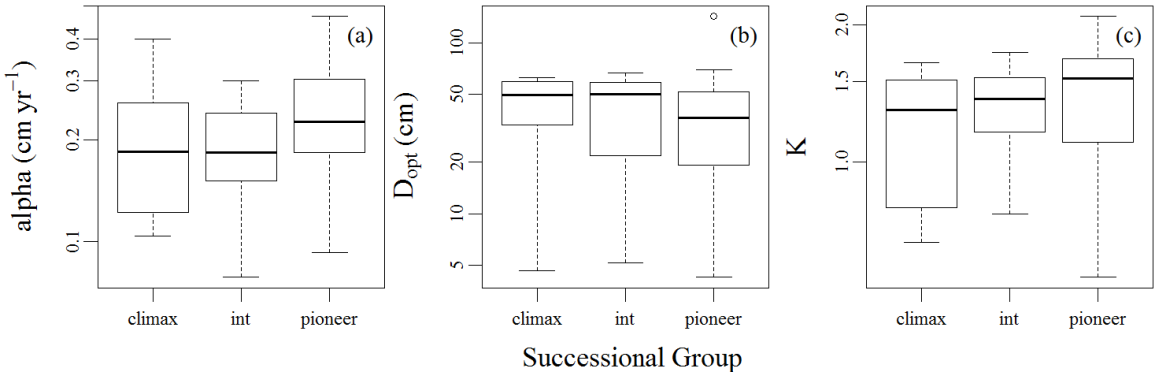


**Figure 6** Boxplot of 47 rainforest species trajectory parameters (a) maximum growth rate (alpha), (b) Size at maximum growth rate ($D_{opt}$) and (c) ontogenetic variation in growth rates (K) as a function of expert-identified groups based on successional strategy; climax (10 species), intermediate (14 species) or pioneer (23 species). Boxes indicate interquartile ranges, black bars indicate median, and whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box

# Discussion

This study had three aims. Firstly, to fit growth trajectory models as a function of size for each species, and identify whether species cluster into distinguishable and ecologically meaningful trajectory groups. Secondly, to quantify patterning between several plant traits and trajectory groups and parameters, to determine whether traits varied predictably among trajectory groups. Finally, to determine if modelled trajectory groups were comparable to expert-identified groups based on traditional concepts of species classification, namely successional strategies, light-dependence and adult stature (Lieberman et al. 1985; Swaine et al. 1988; Clark & Clark 1992). We identified three distinct groups based on trajectory parameters. While individual parameters were largely unrelated to traits, there was clear patterning of traits by trajectory group membership. Trajectory groups did not align well with existing groupings based on expert knowledge.

*Growth trajectory groups*

We used a model of individual growth developed by Canham et al. (2004), which requires only diameter growth measurements over time as input. It has the added advantage of having just three parameters which translate into meaningful aspects of growth that are easy to interpret. We found that our study species grouped into three distinct trajectory shapes (see Figures 2 and 3). Groups were distinguished primarily by differences in alpha (maximum growth rate) and $D_{opt}$ (size at maximum growth rate), and much less by K (ontogenetic variability in growth rate). Trajectory group 1 species were most distinguishable from the other groups by their high maximum growth rates. They were the tallest trees on average, fast-growing, and reached their maximum growth rate at about 40 cm diameter. They had slightly lower K on average than other groups, suggesting they are able to modulate their growth rate more than other groups throughout their life, and their growth rates dropped off rapidly once they had peaked. Based on their maximum height, their canopy would be exposed to sun at maturity. Trajectory group 2 species were most distinguishable by their large size at maximum growth rate. They grew more slowly than group 1 species, but reached their maximum growth rate at larger diameters, after which point their growth rates did not drop off significantly. This allowed them to grow almost as tall as trajectory group 1 species (Figure 4) just more slowly. They are likely to be more shade-tolerant by necessity. Trajectory group 3 species were small and slow growing throughout their life time, reaching their peak growth rates at very small sizes. Their maximum height was significantly lower than other groups. They could be considered as

shade-tolerant sub-canopy species. Trajectory group 3 was comparatively poorly represented – only 7 out of 47 species were assigned to this group. However, sub-canopy species are often comparatively rare, and not present in high numbers (Wright 2002). Further, their small maximum size makes them less likely to be tagged in a survey restricted to stems above 10 cm dbh, as this one was. Our results suggest that model-based clustering can be a useful tool for identifying ecologically interpretable groups from modelled growth trajectories.

*Traits and growth trajectories*

Despite expectations to the contrary, traits have often been uninformative when considering growth rates in larger plants (Wright et al. 2010; Paine et al. 2015). Potentially contributing to this is that growth rates are most commonly reduced to one value per species, and it varies from study to study whether that value is a mean across a life time, a mean within a restricted size range (Iida, Kohyama, et al. 2014), a higher percentile (Wright et al. 2010), or a relative growth rate expressed as a function of size (Prado-Junior et al. 2016). By considering growth patterns across the entire life span of a species, and describing them with more than one parameter, we hoped to understand more explicitly what aspects of a trajectory might be influenced by traits. In a similar study using the same growth trajectory model, Hérault et al. (2011) found that individual parameters were well predicted by four traits. They found that alpha correlated most strongly with maximum dbh (positive), maximum height (negatively), wood density (negatively) and leaf stable carbon isotope ratio ($\delta_{13}C$, an indicator of leaf-level water-use efficiency). In their study, K was best predicted by wood density (positively); a lower wood density and therefore lower K suggested a stronger ability to modulate growth in response to external factors. Specific leaf area was not related to any parameters in their study. Our study found considerably different results. In our study, alpha was the only parameter related to any of the traits. Of course our study did not include all the same traits as Hérault, and so it is not exactly comparable, but of the traits that were common to both studies, the only similarity was a negative relationship between alpha and wood density. Describing parameters using multi-trait models did no better than the bivariate models in helping us to understand the drivers of growth. The best model of alpha included almost all traits (suggesting that alpha is driven by a number of variables), while variation in the other parameters was not significantly described by any combination of traits, just as with the bivariate relationships. If we had stopped here we would be forced to admit that considering ontogenetic growth trajectories is no more informative than traditional trait-growth models which consider only

single parameter growth rates.

But we were more interested in whether traits were related to the growth trajectory shapes, rather than individual growth parameters, and we were rewarded in this regard. We observed clear patterning of most traits according to trajectory 'strategies' (Figure 4). $A_{area}$ was the *only* trait not to show clear patterning with respect to trajectory group. Maximum height differed most significantly between trajectory groups. In the past, assignation to pioneer or climax strategy has been arbitrarily based on height (Swaine et al. 1988), and our results suggest height is also important here. However it was not the only trait of importance. In particular, leaf chemistry ($P_{area}$ and $N_{area}$) had high explanatory power with respect to trajectory group membership. Species with relatively higher leaf mass than wood mass tended to be in trajectory group 1, the fastest growing, largest species. Wood density was lowest in trajectory group 1, the group that had lowest K on average, which supports the theory of Hérault et al. (2011) that lower wood density should result in a greater ability to modulate growth rates throughout ontogeny. Historically, researchers have expected species at the 'fast' end of the trait spectrum to exhibit fast growth rates (Freschet et al. 2010; Reich 2014), which was well supported by our results concerning leaf chemistry and wood density. In trajectory group 1 leaf and wood traits tended towards the 'fast' end of the trait spectrum (higher $P_{area}$ and $N_{area}$, and lower wood density), while species in trajectory group 3 (small-stature, slow growing species) tended towards the slow end of the spectrum (low $P_{area}$ and $N_{area}$, and higher wood density). Species in group 2 had intermediate trait values. The exception in this pattern was specific leaf area, where trajectory group 3 had the highest SLA on average, and high SLA is considered a fast trait. In explaining this odd pattern of SLA, we need to consider that these three trajectory groups were distinguished strongly on their maximum height, which means that as adults they would experience very different light conditions. While shade-tolerant, sub-canopy species (trajectory group 3 in this study) have generally been shown to have lower SLA as seedlings (Kitajima 1994), our results suggest they have higher SLA as adults. Lusk (2004) suggests this is because while canopy species (exposed to high light as adults) start off with higher SLA as seedlings, they maintain a relatively constant SLA throughout ontogeny. Shade-tolerant species on the other hand increase their SLA as they grow, in order to maintain a positive carbon balance in low light. As a result, as adults they can end up with higher SLA than canopy species, as we observed in our study.

*Alignment of trajectory groups with expert classification*

In using model-based cluster analysis we hoped to classify species into growth trajectory

strategies objectively, based on quantitative measures, rather than using prior knowledge of life histories (which does not always exist). The paradigm within ecology is often still focused on gap-dependence and shade-tolerance, with species trajectory types categorised *a priori* into groups such as pioneer and climax (Baker et al. 2004; van Gelder et al. 2006; Aiba & Nakashizuka 2009; Fayolle et al. 2012), or by position in canopy (Clark & Clark 1999; Finegan et al. 1999). While this does capture some of the variability in growth trajectories present within a complex forest, we found our modelled trajectories provided additional information not captured by traditional classification. At least to some extent, our trajectory groups aligned with the shade-tolerance gap-dependent paradigm – alpha values were significantly different between canopy and sub-canopy species. However, perceived light requirements appeared to have no impact on alpha values (see Figure 5). Further, $D_{opt}$ and K parameters did not vary significantly between any of the expert-classified groupings. In addition, there was no correlation between expert classified groupings and modelled trajectory group membership. Our results suggest that traditional classifications can largely be captured by just the alpha parameter of our trajectories. In contrast, our modelled trajectory parameters provide additional information on size and modulation of growth rate across a species lifetime.

**Conclusion**

This study represents a first exploration into the topic of growth trajectories, and what determines them. Most notably, it would benefit from the inclusion of a much greater number of species, rather than just those for which trait values were known. This would allow us to establish whether this method of growth trajectory modelling and categorisation could be generally applicable and useful for understanding forest dynamics more broadly. Particularly, it would provide us with a more general understanding of the role of traits in determining growth trajectories.In addition, while our results suggest anecdotally that there is no phylogenetic patterning with respect to growth trajectory strategies, future studies could usefully explore this more formally. Despite the shortcomings of this study, our approach of trajectory strategies holds potential for better understanding the role of functional traits in ecological strategies. Using the parameters of modelled species growth trajectories based only on diameter increment data, we identified three distinct trajectory groups present within our sample species. These groupings pointed to contrasting growth strategies, which were ecologically interpretable. They were also patterned with respect to traits, with ‘fast’ traits generally linked to fast-growing species. The exception was SLA, which we suggest is because species in the sub-canopy have to increase their SLA as they grow, to maintain a positive carbon balance. Overall, groupings based on modelled growth

trajectories aligned more closely with traits than with groupings based on expert knowledge. Expert groupings were found to be distinguished primarily by differences in modelled maximum growth rate. The trajectory based groupings include additional, ecologically descriptive information such as a species size at maximum growth rate, and their ability to modulate their growth. Further research into this topic holds significant potential.

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# Supplementary Information

***Appendix 1*** *R code for fitting growth trajectory models*

```
#‘data’ is a dataframe with species (spp), individual (ind), diameter at
#time 1 (dbh1), diameter at time 2 (dbh 2) and change in time (dt)

library (plyr)
library (dplyr)
library(rstan)
library(parallel)

fit_canham_model <- function(data) {

  model="
  data {
      int<lower=1> n_obs;
      int<lower=1> n_spp;
      int<lower=1> n_inds;
      int<lower=1> spp[n_obs];
      int<lower=1> ind[n_obs];
      real dbh1[n_obs];
      real dbh2[n_obs];
      real dt[n_obs];
    }

  parameters { # Declare parameters the models must estimate
    real<lower=0> sigma_obs;

    real<lower=0> alpha[n_spp];
    real<lower=0> mu_alpha;
    real<lower=0> sigma_alpha;

    real<lower=0> Dopt[n_spp];
    real<lower=0> mu_Dopt;
    real<lower=0> sigma_Dopt;

    real<lower=0> K[n_spp];
    real<lower=0> mu_K;
    real<lower=0> sigma_K;

  }

  model { # Define priors and likelihood

    real G;
    real a;
    real log_dk;
    real log_canham;
    real dbh2_hat;

    # Species random effects
    alpha ~ normal(mu_alpha, sigma_alpha);
    Dopt ~ normal(mu_Dopt, sigma_Dopt);
    K ~ normal(mu_K, sigma_K);

    for (i in 1:n_obs) {
      # Estimate individual rate
      a <- alpha[spp[i]];
      log_dk <- log(dbh1[i] / Dopt[spp[i]]) / K[spp[i]];
      log_canham <- a * exp(-0.5 * pow(log_dk,2));
      dbh2_hat <- dbh1[i] + (exp(log_canham)-1)*dt[i];

      # Likelihood
      dbh2[i] ~ normal(dbh2_hat, sigma_obs)T[0,];
    }
```

```
# Priors
    mu_alpha ~ normal(0,10)T[0,];
    sigma_alpha ~ cauchy(0,10);
    sigma_obs ~ cauchy(0,10);

    mu_Dopt ~ normal(10,100)T[0,];
    sigma_Dopt ~ cauchy(0,50);

    mu_K ~ normal(1,10)T[0,];
    sigma_K ~ cauchy(0,10);

  }"

  fit_model(data, model, pars =
c("mu_alpha","sigma_alpha","sigma_obs","alpha",

"mu_Dopt","sigma_Dopt","sigma_obs","Dopt",
                                      "mu_K","sigma_K","sigma_obs","K"))
}
```

***Table S1*** *Species trajectory parameters, the probability that a species will fall into a given trajectory group, given its trajectory parameters, as determined via model-based cluster analysis, and the group a species was assigned to based on these probabilities.*

| Species | **Family** | alpha | $D_{opt}$ | K | P (Gr 1) | P (Gr 2) | P (Gr 3) | Group |
|---|---|---|---|---|---|---|---|---|
| *Alstonia muelleriana* | Apocynaceae | 0.13 | 12.4 | 1.63 | 0.02 | 0 | 0.98 | 3 |
| *Alstonia scholaris* | Apocynaceae | 0.42 | 62.8 | 0.56 | 1 | 0 | 0 | 1 |
| *Polyscias australiana* | Araliaceae | 0.09 | 38.6 | 1.61 | 0.14 | 0.86 | 0 | 2 |
| *Agathis robusta* | Araucariaceae | 0.3 | 48.1 | 1.73 | 0.87 | 0.14 | 0 | 1 |
| *Gillbeea adenopetala* | Cunoniaceae | 0.19 | 22.1 | 1.59 | 0.5 | 0.49 | 0.01 | 1 |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 0.1 | 15.6 | 1.47 | 0.02 | 0.01 | 0.98 | 3 |
| *Pullea stutzeri* | Cunoniaceae | 0.18 | 45.5 | 1.63 | 0.09 | 0.91 | 0 | 2 |
| *Elaeocarpus grandis* | Elaeocarpaceae | 0.23 | 33.2 | 1.59 | 0.42 | 0.58 | 0 | 2 |
| *Aleurites rockinghamensis* | Euphorbiaceae | 0.28 | 43.6 | 0.65 | 0.99 | 0 | 0 | 1 |
| *Cleistanthus myrianthus* | Euphorbiaceae | 0.25 | 55.3 | 0.93 | 0.74 | 0.26 | 0 | 1 |
| *Cleistanthus semiopacus* | Euphorbiaceae | 0.12 | 9.7 | 1.51 | 0 | 0 | 0.99 | 3 |
| *Croton insularis* | Euphorbiaceae | 0.16 | 14.8 | 1.53 | 0.05 | 0.02 | 0.93 | 3 |
| *Rockinghamia angustifolia* | Euphorbiaceae | 0.1 | 58.9 | 1.42 | 0.07 | 0.93 | 0 | 2 |
| *Castanospermum australe* | Fabaceae | 0.32 | 4.3 | 2.09 | 1 | 0 | 0 | 1 |
| *Homalium circumpinnatum* | Flacourtiaceae | 0.26 | 32.9 | 0.66 | 0.99 | 0.01 | 0 | 1 |
| *Apodytes brachystylis* | Icacinaceae | 0.15 | 5.2 | 1.37 | 0.01 | 0 | 0.99 | 3 |
| *Citronella smythii* | Icacinaceae | 0.1 | 63.2 | 1.45 | 0.08 | 0.92 | 0 | 2 |
| *Beilschmiedia bancroftii* | Lauraceae | 0.27 | 52.2 | 1.06 | 0.72 | 0.28 | 0 | 1 |
| *Cinnamomum laubatii* | Lauraceae | 0.24 | 58.7 | 1.16 | 0.39 | 0.61 | 0 | 2 |
| *Cryptocarya mackinnoniana* | Lauraceae | 0.15 | 55.8 | 1.5 | 0.05 | 0.94 | 0 | 2 |
| *Cryptocarya murrayi* | Lauraceae | 0.22 | 66.7 | 1.26 | 0.23 | 0.77 | 0 | 2 |
| *Endiandra leptodendron* | Lauraceae | 0.16 | 64 | 1.37 | 0.08 | 0.92 | 0 | 2 |
| *Endiandra monothyra* | Lauraceae | 0.21 | 55.7 | 1.28 | 0.14 | 0.86 | 0 | 2 |
| *Litsea leefeana* | Lauraceae | 0.27 | 7.6 | 1.8 | 0.99 | 0 | 0 | 1 |
| *Neolitsea dealbata* | Lauraceae | 0.18 | 35.6 | 1.37 | 0.17 | 0.83 | 0 | 2 |
| *Dysoxylum pettigrewianum* | Meliaceae | 0.39 | 47.2 | 0.73 | 1 | 0 | 0 | 1 |
| *Acacia celsa* | Mimosaceae | 0.47 | 21.2 | 2 | 1 | 0 | 0 | 1 |
| *Daphnandra repandula* | Monimiaceae | 0.13 | 9.6 | 1.32 | 0.01 | 0 | 0.99 | 3 |
| *Tetrasynandra laxiflora* | Monimiaceae | 0.08 | 40.9 | 1.74 | 0.2 | 0.8 | 0 | 2 |
| *Myristica insipida* | Myristicaceae | 0.18 | 21.9 | 0.77 | 0.96 | 0.04 | 0 | 1 |
| *Gossia hillii* | Myrtaceae | 0.18 | 39.5 | 1.64 | 0.12 | 0.88 | 0 | 2 |
| *Syzygium sayeri* | Myrtaceae | 0.24 | 62.6 | 0.94 | 0.74 | 0.26 | 0 | 1 |
| *Cardwellia sublimis* | Proteaceae | 0.24 | 21 | 1.53 | 0.79 | 0.22 | 0 | 1 |
| *Darlingia darlingiana* | Proteaceae | 0.18 | 47 | 1.15 | 0.16 | 0.84 | 0 | 2 |
| *Alphitonia petriei* | Rhamnaceae | 0.41 | 14 | 0.92 | 1 | 0 | 0 | 1 |
| *Alphitonia whitei* | Rhamnaceae | 0.22 | 17.6 | 1.07 | 0.91 | 0.09 | 0 | 1 |
| *Acronychia acidula* | Rutaceae | 0.22 | 29.7 | 0.74 | 0.96 | 0.04 | 0 | 1 |
| *Acronychia laevis* | Rutaceae | 0.15 | 60.9 | 1.31 | 0.07 | 0.93 | 0 | 2 |
| *Brombya platynema* | Rutaceae | 0.12 | 4.7 | 1.29 | 0.01 | 0 | 0.99 | 3 |
| *Dinosperma erythrococcum* | Rutaceae | 0.19 | 58.7 | 1.65 | 0.09 | 0.91 | 0 | 2 |
| *Flindersia bourjotiana* | Rutaceae | 0.28 | 64 | 1.78 | 0.73 | 0.27 | 0 | 1 |
| *Flindersia brayleyana* | Rutaceae | 0.36 | 142.1 | 1.69 | 1 | 0 | 0 | 1 |
| *Flindersia pimenteliana* | Rutaceae | 0.34 | 36.3 | 1.8 | 0.99 | 0.01 | 0 | 1 |
| *Castanospora alphandii* | Sapindaceae | 0.21 | 60.5 | 1.13 | 0.25 | 0.75 | 0 | 2 |
| *Argyrodendron peralatum* | Sterculiaceae | 0.4 | 52 | 0.79 | 1 | 0 | 0 | 1 |
| *Franciscodendron laurifolium* | Sterculiaceae | 0.23 | 69.5 | 1.68 | 0.29 | 0.72 | 0 | 2 |
| *Dendrocnide photinophylla* | Urticaceae | 0.21 | 42.7 | 0.68 | 0.92 | 0.08 | 0 | 1 |

*Table S2 Trait values for 44 rainforest species, with standard deviation and sample sizes provided in brackets. Wood density (WD) and maximum height ($H_{max}$) were obtained from literature and unpublished data and so have no associated standard deviation and sample size.*

| Species | Family | $A_{area}$ (SD, n) | $N_{area}$ (SD, n) | $P_{area}$ (SD, n) | SLA (SD, n) | LM:WM (SD, n) | WD | $H_{max}$ |
|---|---|---|---|---|---|---|---|---|
| | | µmol $m^{-2}$ $s^{-1}$ | g $cm^{-2}$ | g $cm^{-2}$ | $cm^2$ $g^{-1}$ | g $g^{-1}$ | g $cm^{-3}$ | m |
| *Alstonia muelleriana* | Apocynaceae | 11.04 (2.74, 7) | 0.017 (0.0009, 5) | 0.0008 (0.00009, 5) | 129.95 (46.23, 7) | 0.61 (0.22,7) | 0.68 | 38 |
| *Alstonia scholaris* | Apocynaceae | 13.64 (1.28, 4) | 0.027 (0.0012, 5) | 0.0012 (0.00012, 5) | 93.34 (3.97, 3) | 1.08 (0.26, 3) | 0.34 | 41 |
| *Polyscias australiana* | Araliaceae | 6.83 (3.09, 7) | 0.02 (0.0005, 5) | 0.01 (0.0002, 5) | 90.27 (7.31, 4) | 2.75 (0.50, 4) | 0.50 | 19 |
| *Agathis robusta* | Araucariaceae | 6.63 (3.49, 13) | 0.023 (0.0021, 5) | 0.0017 (0.00030, 5) | 54.69 (9.18, 7) | 0.63 (0.25, 7) | 0.40 | 40 |
| *Daphnandra repandula* | Atherospermataceae | 5.99 (0.85, 6) | 0.016 (0.0005, 5) | 0.0008 (0.00013, 5) | 166.35 (14.11, 6) | 1.12 (0.51, 6) | 0.58 | 30 |
| *Gillbeea adenopetala* | Cunoniaceae | 6.77 (1.11, 5) | 0.016 (0.0018, 5) | 0.0008 (0.00009, 5) | 75.98 (13.42, 3) | 1.75 (0.69, 3) | 0.46 | 31 |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | 5.23 (1.65, 6) | 0.014 (0.0009, 5) | 0.0005 (0.00014, 5) | 77.35 (8.78, 6) | 0.41 (0.17, 6) | 0.76 | 40 |
| *Pullea stutzeri* | Cunoniaceae | 3.17 (1.88, 6) | 0.010 (0.0004, 5) | 0.0005 (0.00008, 5) | 104.76 (12.24, 6) | 1.35 (0.58, 6) | 0.64 | 39 |
| *Elaeocarpus grandis* | Elaeocarpacee | 10.18 (2.46, 5) | 0.022 (0.0016, 5) | 0.001 (0.0001, 5) | 83.32 (12.39, 3) | 0.99 (0.18, 3) | 0.41 | 40 |
| *Aleurites rockinghamensis* | Euphorbiaceae | 10.11 (3.01, 6) | 0.022 (0.0016, 5) | 0.0015 (0.00016, 5) | 88.93 (6.88, 3) | 3.51 (1.60, 3) | 0.39 | 51 |
| *Cleistanthus myrianthus* | Euphorbiaceae | 7.81 (2.03, 5) | 0.018 (0.0013, 5) | 0.0010 (0.00010, 5) | 128.88 (13.71, 3) | 1.31 (0.30, 3) | 0.62 | 21 |
| *Cleistanthus semiopacus* | Euphorbiaceae | 6.99 (1.29, 8) | 0.015 (0.0005, 5) | 0.0008 (0.00007, 5) | 108.13 (6.07, 6) | 0.64 (0.31, 6) | 0.88 | 28 |
| *Croton insularis* | Euphorbiaceae | 11.67 (1.91, 6) | 0.022 (0.0008, 5) | 0.0013 (0.00009, 5) | 102.64 (9.19, 6) | 0.62 (0.10, 6) | 0.79 | 17 |
| *Rockinghamia angustifolia* | Euphorbiaceae | 5.78 (3.30, 5) | 0.018 (0.0007, 4) | 0.0009 (0.00016, 4) | 92.99 (8.82, 3) | 1.59 (0.12, 3) | 0.69 | 26 |
| *Acacia celsa* | Fabaceae | 12.90 (1.34, 5) | 0.040 (0.0032, 5) | 0.0020 (0.00051, 5) | 68.96 (4.13, 3) | 1.47 (0.22, 3) | 0.49 | 31 |
| *Castanospermum austral* | Fabaceae | 11.81 (5.28, 5) | 0.036 (0.0020, 5) | 0.0020 (0.00026, 5) | 72.88 (11.71, 3) | 2.96 (1.60, 3) | 0.63 | 40 |
| *Homalium circumpinnatum* | Flacourtiaceae | 7.29 (2.78, 6) | 0.021 (0.0013, 5) | 0.0010 (0.00010, 5) | 76.51 (15.32, 6) | 0.54 (0.13, 6) | 0.64 | 24 |
| *Beilschmiedia bancroftii* | Lauraceae | 6.08 (1.20, 4) | 0.026 (0.001, 4) | 0.0012 (0.0002, 4) | 99.17 (35.96, 4) | 1.72 (0.40, 4) | 0.56 | 41 |
| *Cinnamomum laubatii* | Lauraceae | 7.35 (1.75, 4) | 0.016 (0.0005, 4) | 0.0009 (0.00012, 4) | 115.10 (6.90, 4) | 1.21 (0.29, 4) | 0.41 | 36 |
| *Cryptocarya mackinnoniana* | Lauraceae | 12.22 (3.30, 6) | 0.020 (0.0018, 5) | 0.0016 (0.00033, 5) | 54.87 (11.54, 4) | 2.05 (0.15, 4) | 0.73 | 32 |
| *Cryptocarya murrayi* | Lauraceae | 12.82 (2.46, 5) | 0.019 (0.0022, 4) | 0.0014 (0.00024, 4) | 64.74 (1.02, 3) | 1.81 (1.11, 3) | 0.68 | 33 |

| Species | Family | $A_{area}$ (SD, n) μmol $m^{-2}$ $s^{-1}$ | $N_{area}$ (SD, n) g $cm^{-2}$ | $P_{area}$ (SD, n) g $cm^{-2}$ | SLA (SD, n) $cm^2$ $g^{-1}$ | LM:WM (SD, n) g $g^{-1}$ | WD g $cm^{-3}$ | $H_{max}$ m |
|---|---|---|---|---|---|---|---|---|
| *Endiandra leptodendron* | Lauraceae | 8.59 (3.02, 5) | 0.022 (0.0009, 5) | 0.0012 (0.00007, 5) | 94.54 (8.87, 3) | 1.03 (0.58, 3) | 0.75 | 28 |
| *Endiandra monothyra* | Lauraceae | 4.80 (3.10, 5) | 0.016 (0.0006, 5) | 0.0009 (0.00013, 5) | 100.62 (12.62, 6) | 1.39 (0.65,6) | 0.80 | 35 |
| *Litsea leefeana* | Lauraceae | 11.48 (1.70, 60 | 0.023 (0.0008, 5) | 0.0011 (0.00022, 5) | 77.54 (7.63, 3) | 1.42 (0.45, 3) | 0.42 | 36 |
| *Neolitsea dealbata* | Lauraceae | 6.49 (1.87, 7) | 0.015 (0.0009, 5) | 0.0009 (0.00022, 5) | 107.75 (3.82, 3) | 1.19 (0.22, 3) | 0.65 | 22 |
| *Argyrodendron peralatum* | Malvaceae | 10.57 (2.69, 5) | 0.033 (0.0019, 5) | 0.0018 (0.00037, 5) | 40.22 (6.22, 3) | 1.45 (0.51, 3) | 0.65 | 44 |
| *Franciscodendron laurifolium* | Malvaceae | 5.00 (1.92, 5) | 0.012 (0.0013, 5) | 0.0008 (0.00003, 5) | 96.17 (10.84, 5) | 0.92 (0.55, 5) | 0.39 | 35 |
| *Tetrasynandra laxiflora* | Monimiaceae | 6.65 (1.72, 6) | 0.017 (0.0006, 5) | 0.0008 (0.00014, 5) | 167.62 (16.43, 6) | 1.31 (0.16, 6) | 0.55 | 27 |
| *Myristica insipida* | Myristicaceae | 6.62 (2.90, 8) | 0.017 (0.0015, 5) | 0.0011 (0.00012, 5) | 92.80 (11.21, 8) | 1.25 (0.19, 8) | 0.48 | 37 |
| *Gossia hillii* | Myrtaceae | 9.31 (2.46, 6) | 0.020 (0.0014, 5) | 0.0009 (0.00012, 5) | 61.61 (11.54, 6) | 0.55 (0.16, 6) | 0.63 | 20 |
| *Syzygium sayeri* | Myrtaceae | 9.25 (3.12, 5) | 0.021 (0.0008, 5) | 0.0010 (0.00008, 5) | 77.03 (7.40, 3) | 1.44 (0.16, 3) | 0.78 | 36 |
| *Cardwellia sublimis* | Proteaceae | 10.65 (3.77, 5) | 0.021 (0.0013, 5) | 0.0010 (0.00011, 5) | 69.82 (7.07, 3) | 2.33 (0.76, 3) | 0.48 | 38 |
| *Darlingia darlingiana* | Proteaceae | 12.50 (3.90, 6) | 0.013 (0.0014, 5) | 0.0010 (0.00028, 5) | 74.95 (11.79, 6) | 1.80 (0.51, 6) | 0.65 | 40 |
| *Alphitonia petriei* | Rhamnaceae | 15.38 (3.86, 5) | 0.030 (0.0021, 5) | 0.0019 (0.00032, 5) | 67.29 (4.29, 3) | 1.69 (0.22, 3) | 0.44 | 42 |
| *Alphitonia whitei* | Rhamnaceae | 7.60 (2.57, 7) | 0.021 (0.0017, 5) | 0.0011 (0.00013, 5) | 81.25 (13.51, 7) | 1.34 (0.36, 7) | 0.61 | 41 |
| *Acronychia acidula* | Rutaceae | 6.78 (1.75, 6) | 0.022 (0.0010, 5) | 0.0048 (0.00130, 5) | 119.31 (16.86, 3) | 1.36 (0.25, 3) | 0.55 | 35 |
| *Acronychia laevis* | Rutaceae | 7.28 (1.46, 6) | 0.019 (0.0027, 5) | 0.0009 (0.00017, 5) | 103.77 (28.04, 6) | 0.75 (0.40, 6) | 0.54 | 22 |
| *Brombya platynema* | Rutaceae | 10.53 (2.38, 5) | 0.023 (0.0008, 5) | 0.0009 (0.00009, 5) | 94.02 (2.99, 3) | 1.34 (0.23, 3) | 0.61 | 20 |
| *Dinosperma erythrococcum* | Rutaceae | 7.25 (2.98, 5) | 0.018 (0.0008, 5) | 0.0010 (0.00007, 5) | 77.82 (2.99, 4) | 0.71 (0.12, 6) | 0.79 | 23 |
| *Flindersia bourjotiana* | Rutaceae | 8.85 (2.96, 7) | 0.019 (0.0025, 5) | 0.0009 (0.00014, 5) | 64.78 (4.80, 6) | 1.31 (0.38, 6) | 0.52 | 41 |
| *Flindersia brayleyana* | Rutaceae | 8.17 (4.16, 7) | 0.021 (0.0025, 5) | 0.0011 (0.00010, 5) | 73.55 (14.35, 7) | 1.83 (0.52, 7) | 0.48 | 40 |
| *Flindersia pimenteliana* | Rutaceae | 3.58 (1.33, 5) | 0.012 (0.0014, 5) | 0.0011 (0.00037, 5) | 95.64 (29.47, 5) | 0.74 (0.37, 5) | 0.53 | 41 |
| *Castanospora alphandii* | Sapindaceae | 4.29 (2.62, 6) | 0.022 (0.0008, 5) | 0.0014 (0.00013, 5) | 86.81 (7.59, 6) | 1.16 (0.27, 6) | 0.59 | 34 |
| *Dendrocnide photinophylla* | Urticaceae | 7.84 (2.70, 7) | 0.025 (0.0034, 5) | 0.0011 (0.00010, 5) | 196.23 (22.71, 7) | 0.50 (0.10, 7) | 0.21 | 30 |

***Table S3*** *Expert classifications of species and families into canopy groups and successional groups. Canopy group categories are light-dependant canopy (LD-C), shade-tolerant canopy (ST-C), light-dependant sub-canopy (LD-SC) and shade-tolerant sub-canopy (ST-SC). Successional group categories are pioneer, climax and intermediate.*

| **Species** | **Family** | **Canopy group** | **Successional group** |
|---|---|---|---|
| *Alstonia muelleriana* | Apocynaceae | LD-C | pioneer |
| *Alstonia scholaris* | Apocynaceae | LD-C | pioneer |
| *Polyscias australiana* | Araliaceae | LD-SC | pioneer |
| *Agathis robusta* | Araucariaceae | ST-C | intermediate |
| *Gillbeea adenopetala* | Cunoniaceae | LD-C | intermediate |
| *Pseudoweinmannia lachnocarpa* | Cunoniaceae | LD-C | intermediate |
| *Pullea stutzeri* | Cunoniaceae | LD-C | pioneer |
| *Elaeocarpus grandis* | Elaeocarpaceae | LD-C | pioneer |
| *Aleurites rockinghamensis* | Euphorbiaceae | LD-C | pioneer |
| *Cleistanthus myrianthus* | Euphorbiaceae | ST-SC | intermediate |
| *Cleistanthus semiopacus* | Euphorbiaceae | ST-SC | climax |
| *Croton insularis* | Euphorbiaceae | ST-SC | intermediate |
| *Rockinghamia angustifolia* | Euphorbiaceae | ST-SC | climax |
| *Castanospermum australe* | Fabaceae | LD-C | pioneer |
| *Homalium circumpinnatum* | Flacourtiaceae | ST-SC | climax |
| *Apodytes brachystylis* | Icacinaceae | ST-SC | intermediate |
| *Citronella smythii* | Icacinaceae | ST-SC | intermediate |
| *Beilschmiedia bancroftii* | Lauraceae | LD-C | intermediate |
| *Cinnamomum laubatii* | Lauraceae | ST-C | intermediate |
| *Cryptocarya mackinnoniana* | Lauraceae | LD-C | pioneer |
| *Cryptocarya murrayi* | Lauraceae | ST-SC | intermediate |
| *Endiandra leptodendron* | Lauraceae | LD-SC | intermediate |
| *Endiandra monothyra* | Lauraceae | LD-C | intermediate |
| *Litsea leefeana* | Lauraceae | LD-C | pioneer |
| *Neolitsea dealbata* | Lauraceae | LD-SC | pioneer |
| *Dysoxylum pettigrewianum* | Meliaceae | ST-C | climax |
| *Acacia celsa* | Mimosaceae | LD-C | pioneer |
| *Daphnandra repandula* | Monimiaceae | LD-SC | pioneer |
| *Tetrasynandra laxiflora* | Monimiaceae | LD-SC | intermediate |
| *Myristica insipida* | Myristicaceae | LD-SC | intermediate |
| *Gossia hillii* | Myrtaceae | ST-SC | climax |
| *Syzygium sayeri* | Myrtaceae | ST-C | climax |
| *Cardwellia sublimis* | Proteaceae | LD-C | pioneer |
| *Darlingia darlingiana* | Proteaceae | LD-C | pioneer |
| *Alphitonia petriei* | Rhamnaceae | LD-C | pioneer |
| *Alphitonia whitei* | Rhamnaceae | LD-C | pioneer |
| *Acronychia acidula* | Rutaceae | LD-SC | pioneer |
| *Acronychia laevis* | Rutaceae | ST-SC | climax |
| *Brombya platynema* | Rutaceae | ST-SC | climax |
| *Dinosperma erythrococcum* | Rutaceae | ST-SC | climax |
| *Flindersia bourjotiana* | Rutaceae | LD-C | pioneer |
| *Flindersia brayleyana* | Rutaceae | LD-C | pioneer |
| *Flindersia pimenteliana* | Rutaceae | LD-C | pioneer |
| *Castanospora alphandii* | Sapindaceae | ST-C | pioneer |
| *Argyrodendron peralatum* | Sterculiaceae | ST-C | climax |
| *Franciscodendron laurifolium* | Sterculiaceae | LD-C | pioneer |
| *Dendrocnide photinophylla* | Urticaceae | LD-C | pioneer |

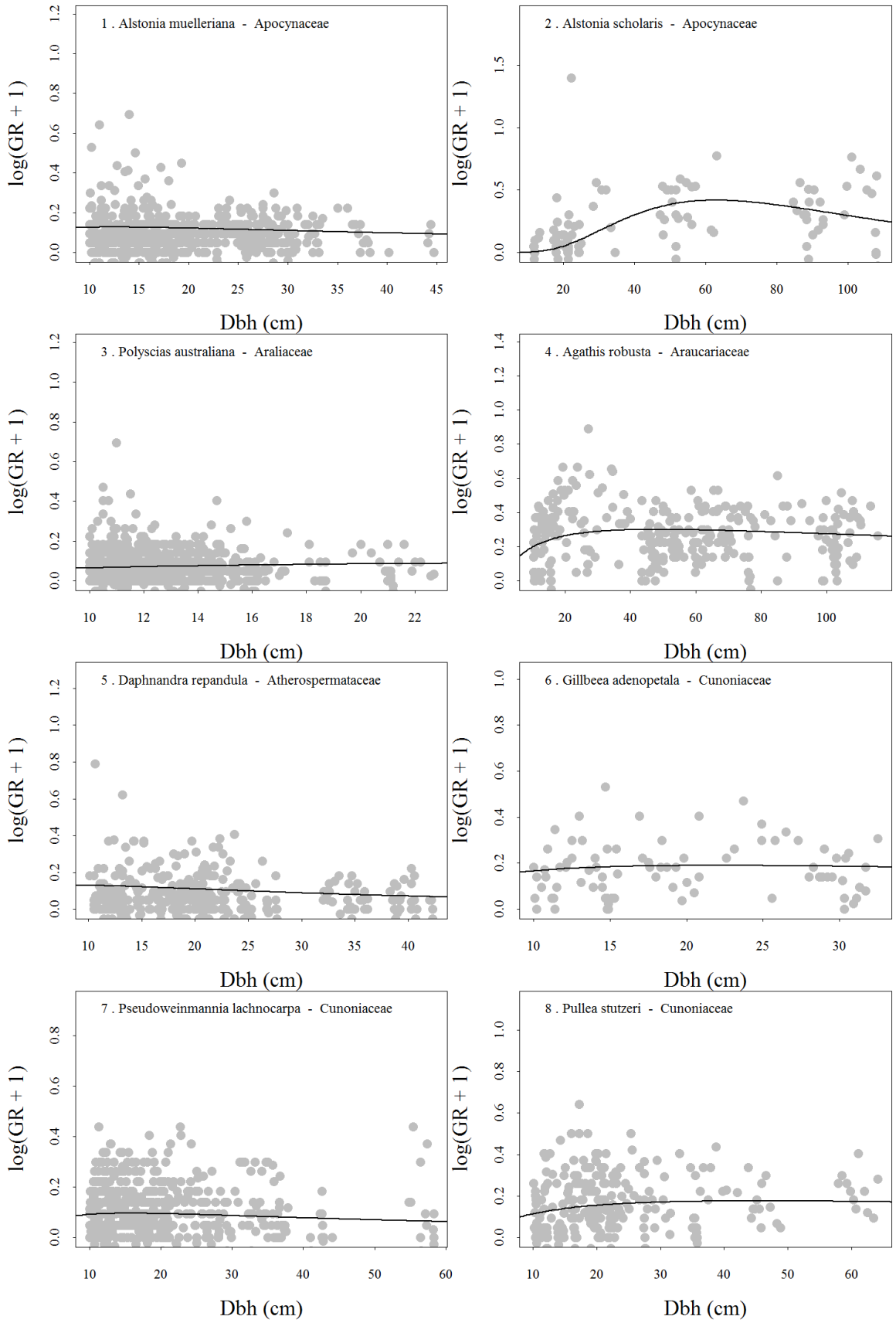


***Figure S1*** *Modelled growth trajectories and raw data of all species.*

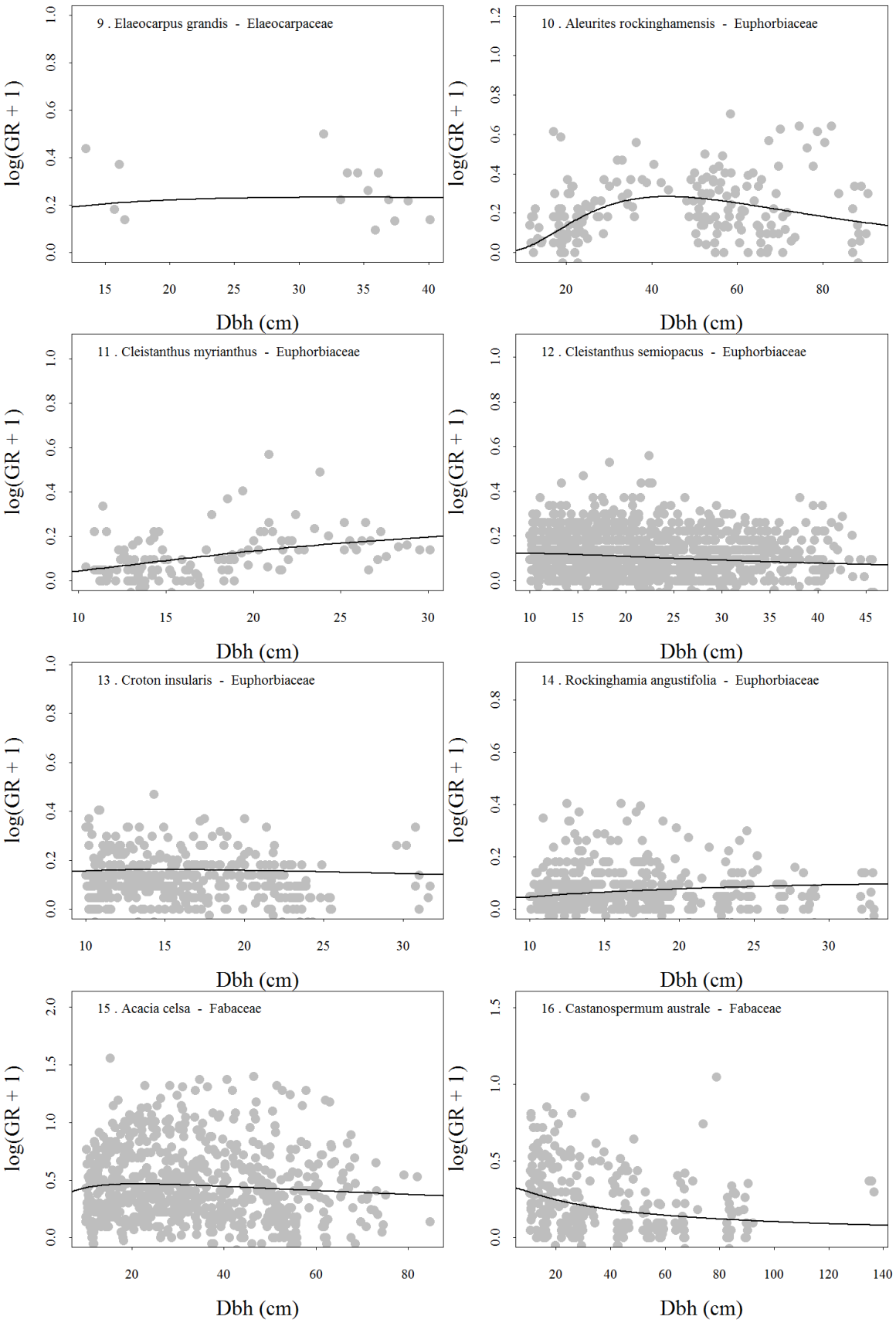


**Figure S1 cont.** Modelled growth trajectories and raw data of all species

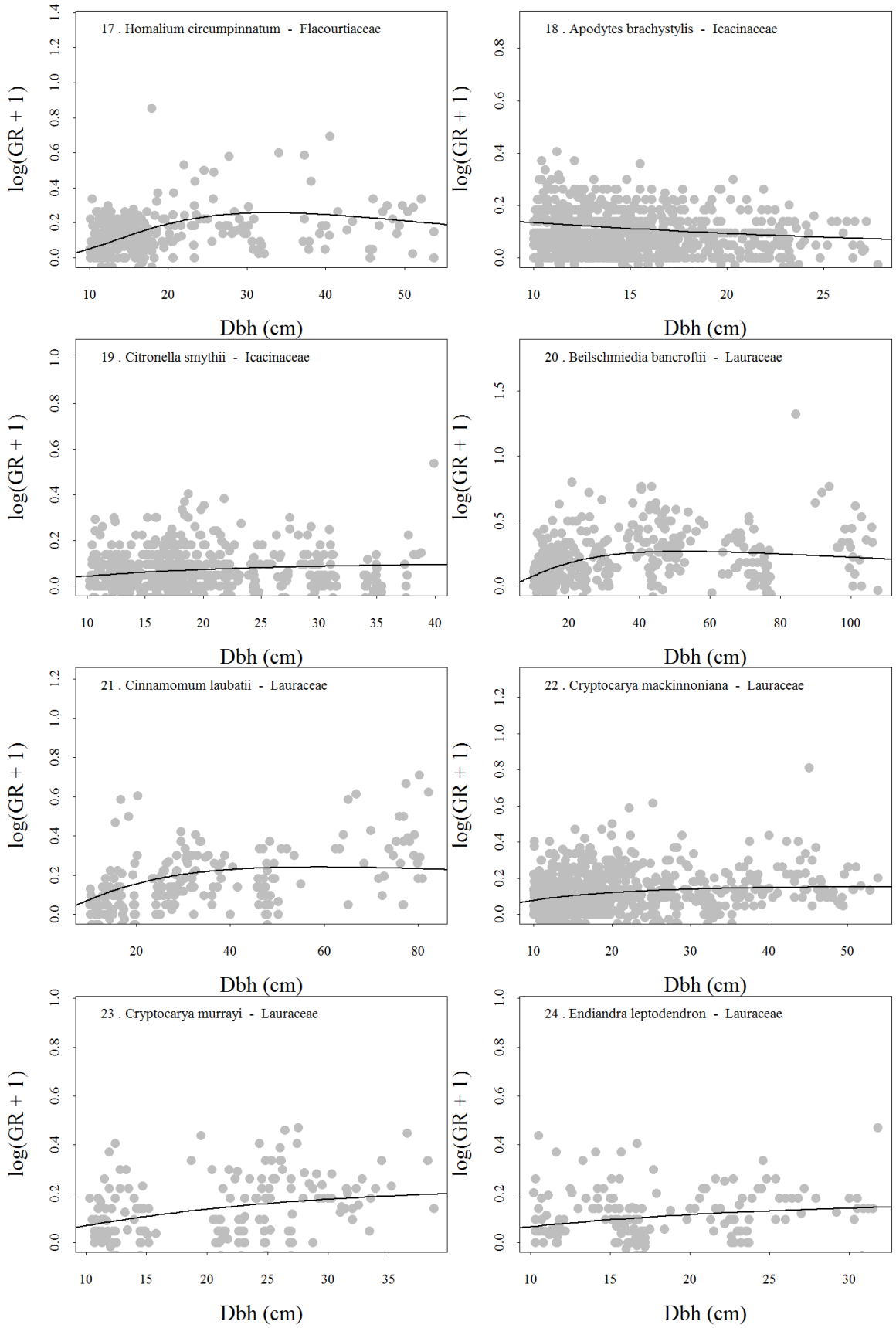


**Figure S1 cont.** Modelled growth trajectories and raw data of all species

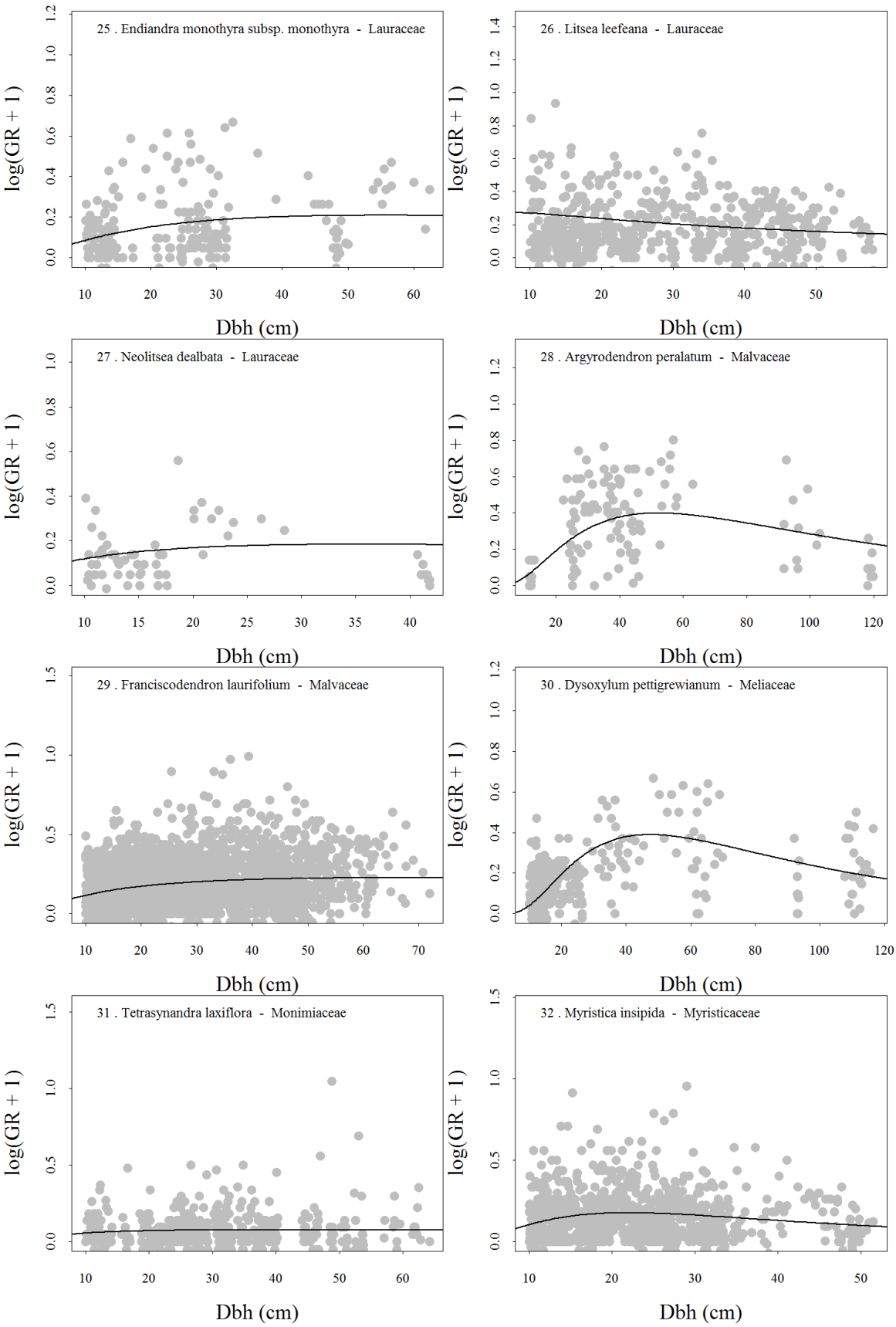


**Figure S1 cont.** Modelled growth trajectories and raw data of all species

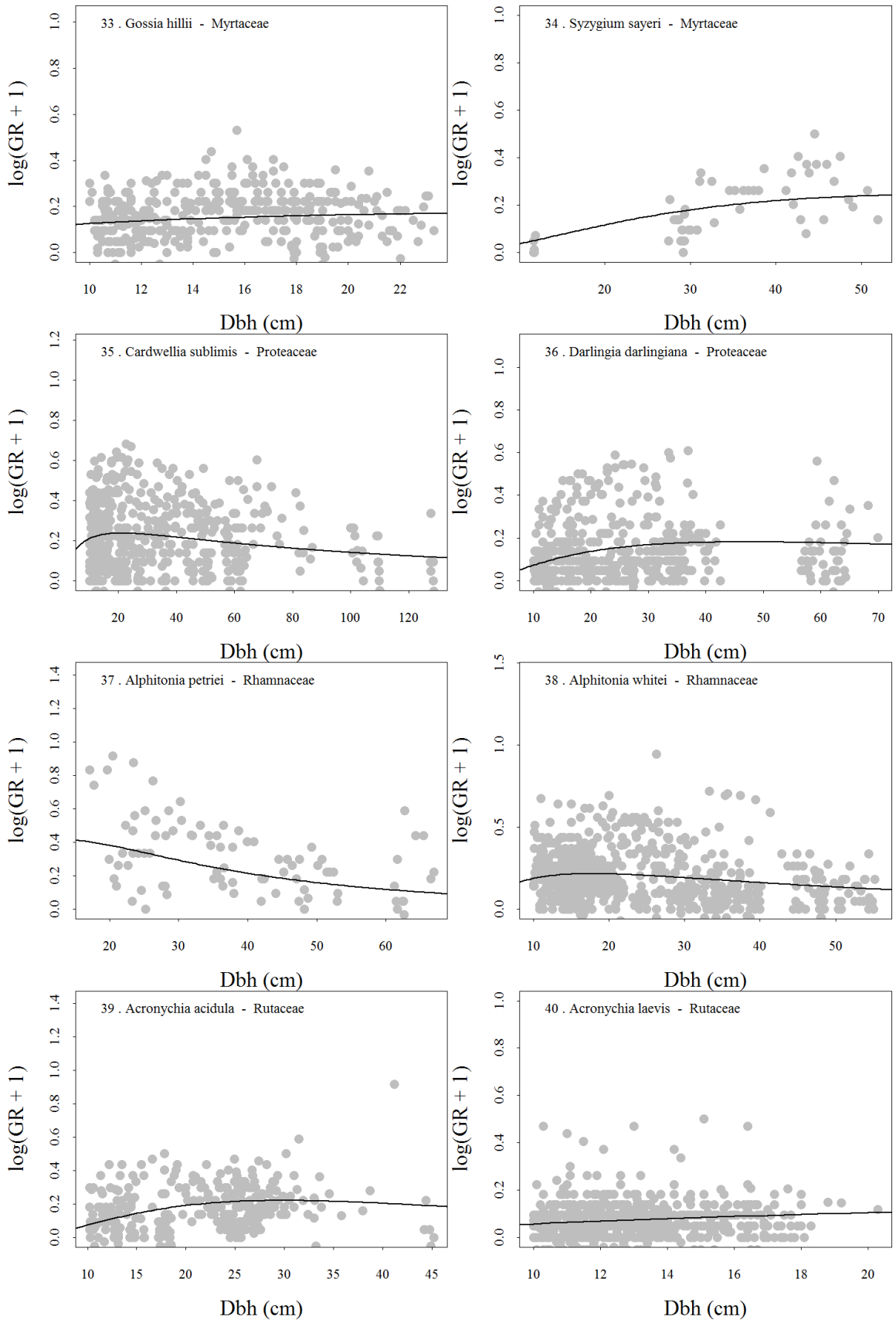


**Figure S1 cont.** Modelled growth trajectories and raw data of all species

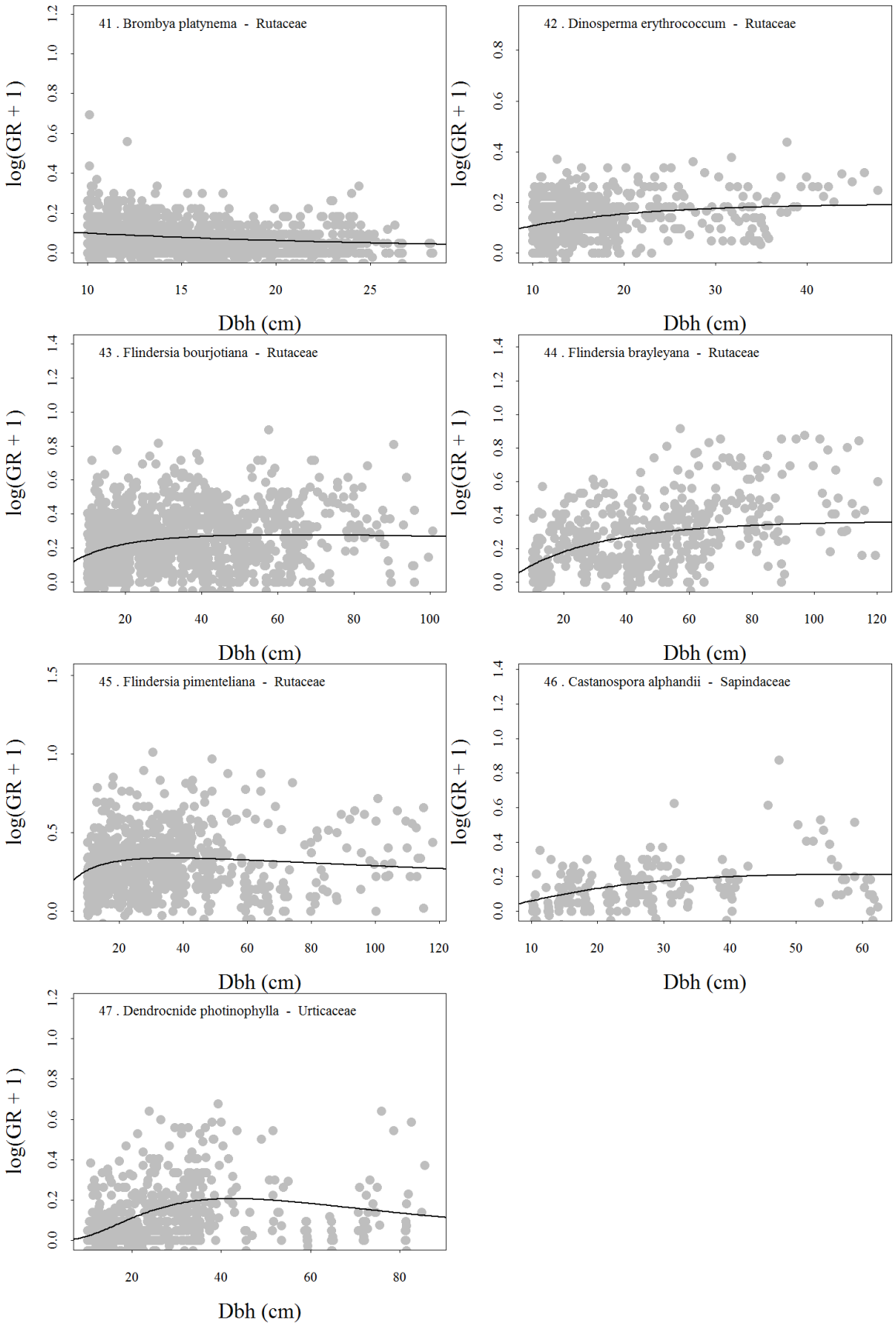


**Figure S1 cont.** Modelled growth trajectories and raw data of all species

# Chapter 6

General Discussion

# General Discussion

In this thesis I set out to better understand how functional traits drive variability in plant species growth rates, and my findings can be separated into two particular themes; (1) The consistency of trait-growth relationships throughout ontogeny in tropical forests; and (2) The consistency of trait-growth relationships in tropical savannas. While interactions between plant growth rates and plant functional traits have been much researched over the last three decades (e.g. Poorter & Remkes 1990; Poorter & Lambers 1991; Lambers & Poorter 1992; Walters et al. 1993; Wright & Westoby 1999; Shipley 2006), the vast majority of studies have considered only seedling growth experiments (Gibert et al. 2016). It is only in the last five to ten years that attention has turned to adult plants, and field-based measurements, and studies have considered that because growth rates change over the lifetime of a plant, the relative importance of different functional traits is likely to shift (Poorter et al. 2008; Wright et al. 2010; Hérault et al. 2011; Ruger et al. 2012; Iida, Poorter, et al. 2014; Paine et al. 2015; Gibert et al. 2016; Prado-Junior et al. 2016; Visser et al. 2016). Most evidence for the effect of traits on field-measured growth rates has been accumulated in closed forest systems (see Gibert et al. 2016 for a meta-analysis of past studies), and while tropical forest-based literature has been crucial in developing our understanding of trait-growth relationships, a large portion of the world is not tropical forest (Schimper 1903; Woodward et al. 2004). Tropical forests, being closed canopy environments, have characteristics peculiar to them, making generalisations of our understanding of plant growth to other biomes potentially problematic. In tropical forests, light availability can be extremely low, and is highly variable, both spatially and temporally (Canham et al. 1990; Chazdon et al. 1996; Nicotra et al. 1999), while rainfall is generally high and relatively aseasonal (Bazzaz 1991), and disturbance by fire a rarity (Cochrane 2003). If we aim to develop a more general understanding of trait-growth relationships, it is essential to consider patterns in high light, seasonally dry and disturbed environments. Considering this background, four main points of novelty in this thesis stand out. Firstly, all measurements were made on plants growing in the wild, rather than in greenhouses. Secondly, I considered patterns in savanna systems as well as tropical forests. Thirdly, I measured traits that have previously not been measured in conjunction with growth rates, such as branch biomass, and relative bark thickness. Finally, I considered growth rates both as a single parameter, and by modelling multi-parameter growth trajectories across ontogeny. These novel approaches to long-standing questions have elicited some interesting findings, which I summarise and integrate here.

**Tropical forests**

In considering how trait-growth relationships in tropical forests vary with plant size, I asked two questions. Firstly, when considering only adult plants, are patterns similar to those observed for seedlings, and if they are not, are there mechanistic explanations for why this is so? Secondly, is it better to consider growth variation throughout ontogeny using more than one parameter, such that we can describe lifetime trajectories, which may be better linked to traits, and overall plant strategies, than just one estimate of growth?

*Adult trait – growth relationships*

Using maximum potential growth rate estimates, in Chapter 2 I tested mechanistic predictions of how traits and growth rates should be related in these species. Most of the predictions, as well as the findings, did not differ from what is expected in seedlings. I found positive relationships between growth rates and area-based estimates of leaf nitrogen, phosphorus, and photosynthetic rates (Cornelissen et al. 1997; Poorter & Bongers 2006; Gibert et al. 2016), and I found a negative relationship between growth rate and wood density (King et al. 2005; Roque & Fo 2007; Poorter et al. 2010; Wright et al. 2010; Ruger et al. 2012). However, two traits provided significant novelty in this chapter. The first was specific leaf area (SLA), which departed from the expectation that there would be no relationship, and exhibited a negative relationship with growth rate, a result previously predicted by Gibert et al. (2016). This trait provides talking points throughout the thesis, and so I return to it later. The second was the ratio of branch leaf mass to sapwood mass (LM:SM). The relationship between LM:SM and growth has never been empirically tested but the importance was alluded to in Pickup et al. (2005). Here, LM:SM exhibited a strong positive relationship with growth rates (and was similarly positively related to growth rates in savanna species; Chapters 3 and 4). Concerning adults in tropical forests, I could convincingly demonstrate that trait-growth relationships follow predictable patterns, and that trait-growth relationships can differ from those observed in seedlings (particularly in the case of SLA). In Chapter 2, it was also worth noting that in this Australian tropical forest ecosystem, while individual traits explained significant variation in growth rates, the combination of wood density, specific leaf area, and LM:SM together explained over 50% of interspecific variation in growth rates. In other words, growth was well explained by the combined information provided by basic leaf and wood traits, together with an estimate of the relative allocation of these tissue types on a branch.

*Ontogenetic variability in growth rates, and the role of traits*

It is unlikely that one mean or upper percentile estimate of growth rate can fully inform us

of the growth strategy of a species throughout its lifetime, as we lack an understanding of the size and age at which maximum growth rates occur, as well as the ability of a species to modulate its growth throughout its lifetime. In Chapter 5 I had two primary goals: 1) to model growth trajectories of species using ecologically meaningful parameters, and determine whether species could be grouped into similar shaped, distinguishable, and ecologically meaningful trajectory groups; and, 2) Determine whether these parameters, or the resultant groups, could be linked to functional traits. The high diversity of tropical forests has invited much research seeking to generalise understanding of forest tree growth and dynamics, and indeed, tropical forest ecologists have grappled with the classification of species into ecologically similar groups for decades (Lieberman et al. 1985; Swaine et al. 1988; Oldeman & Van Dijk 1991; Clark & Clark 1992).

I modelled species growth trajectories using three parameters: maximum growth rate, size at maximum growth rate, and ontogenetic variability in growth rate. I found that species clustered into three distinct groups, which were distinguished primarily based on their maximum growth rates and size at maximum growth rates, though their ability to modulate their growth across their lifetime also played a role. The first group could be described as large, fast growing species with high ontogenetic variation in growth rates. The second group were large, slow growing species that reached their maximum growth rate at a large size, and the third group were small, sub-canopy species that were slow growing. In contrast to a similar study by Hérault et al. (2011), I did not find that different functional traits were important for different parameters. Hérault et al. (2011) found that, for example, species with low wood density had more variability in growth rates across their lifetime. What I found was that with respect to individual parameters of the trajectories, traits were only strongly related to maximum growth rates. In other words, when considering bivariate trait-growth relationships, describing the entire growth trajectory was no more informative than Chapter 2, in which we considered just the maximum potential growth rates.

A more interesting result from Chapter 5 was that species trajectories clustered into three distinct shapes, and that these were patterned with respect to traits. Large, fast growing species were linked to ‘fast’ traits, and small, slow growing species were largely linked to ‘slow’ traits (Reich 2014). The exception was SLA, which was generally higher (i.e. at the “fast end” of the leaf economic spectrum) in the slow growing, small, sub-canopy species. This contrasted with studies that have identified shade-tolerant species as usually having slower foliage turnover (and lower SLA) than light-demanding species (Williams et al. 1989; Kitajima 1994). However, these were seedling studies, and in considering larger

plants, Lusk (2004) suggests that while light-demanding species maintain a relatively constant SLA throughout ontogeny, shade-tolerant species increase their SLA with age, in order to maintain a positive carbon balance, such that as adults they have the higher SLA. This could explain why in my study sub-canopy species had higher SLA than canopy species.

Chapter 5 highlights that, at least within tropical forests, species appear to conform to a discrete number of trajectory shapes, and these trajectory shapes are patterned with respect to traits. But of equal importance, this chapter highlights that while understanding trajectories throughout a species lifetime is undoubtedly of interest, the maximum adult growth rate captures much of the between-species variation in trajectory shapes, and is the only growth parameter that had strong bivariate relationships with traits. In other words, rather than negating past studies (and the earlier chapters of this thesis), this chapter reconfirms that considering growth as a single parameter has value when considering how traits influence species growth strategies.

**Trait-growth relationships in savanna systems**

Forest and savanna are the two dominant biomes across the tropics (Woodward et al. 2004), yet different processes govern the dynamics of vegetation in each biome, and the boundaries between the two are commonly abrupt (Bond & Parr 2010). In tropical forests with closed canopies, tree densities can be high, and, hence ecological strategies are commonly associated with overcoming competition for light (Oldeman & Van Dijk 1991; Canham et al. 2004). On the other hand, tropical savannas have a discontinuous tree cover, and are faced with little light limitation, but chronic disturbance via fire, mammalian herbivory or both (Ratnam et al. 2011). In savannas, competition is commonly considered as being between trees and grasses during establishment (Scholes & Archer 1997; Sankaran et al. 2004), while demographic bottlenecks as a result of fire and herbivory limit tree growth and accession of trees to larger size classes (Higgins et al. 2000; Wakeling et al. 2011). Because of these differences, I was interested in whether trait-growth relationships in savannas operate in a functionally similar manner to those I observed in tropical forests.

While three studies have considered trait-growth relationships within a single savanna ecosystem (Hoffmann & Franco 2003; Prior et al. 2004; Rossatto et al. 2009), and an experimental study has considered trait-growth relationships across multiple savannas (Tomlinson et al. 2012; Tomlinson et al. 2014), Chapter 3 represents the first study I know of testing the generality of adult trait – growth relationships across savanna ecosystems

that are biogeographically distinct. I found some evidence that trait-growth relationships in savannas are consistent with those in forests; there was a general positive relationship between photosynthetic rates and height growth rates across all species, a common negative slope between wood density and diameter growth rates in all sites, and a common positive slope between branch leaf mass to wood mass ratios (LM:WM) and height growth rates in all sites. SLA was generally unrelated to growth rate. However, it was apparent that growth rates in each of the three savanna ecosystems were linked to different traits (i.e. wood versus leaf traits) and with variable strength. While leaf traits were most strongly linked to growth in Australian savanna (where evergreen species are common), wood density was more strongly linked to growth rates in South Africa and Brazil. I attributed the differences in the strength of the relationships to the nature of disturbance regimes and site conditions.

With respect to SLA, in general, my thesis results have highlighted how the nature of the SLA-growth relationship is dependent on many factors. For example in Chapter 2, in large forest trees, the relative cost of regular leaf replacement in species with high SLA appeared to outweigh the initial cost of leaf construction in species with low SLA leaves, such that in this particular forest site, SLA was negatively related to growth rate. In Chapter 5, the light environment of species when they are adults was highlighted as important. I found that high SLA species tended also to be small-stature (shaded as adults), and slow growing throughout their lifetime, while low SLA species were generally taller (exposed to sun as adults) and faster growing, with a greater ability to modulate their growth across their lifetime. Chapter 5 highlighted our need to further explore how SLA is linked to growth across the whole of ontogeny, not just when growth is at a maximum. Finally, Chapter 3 highlighted the importance of understanding leaf seasonality with respect to SLA and growth. Having low SLA appeared to drive fast growth where evergreen species were more common (Australian savanna), while SLA had no influence in sites dominated by deciduous species (Brazil and South Africa). This makes intuitive sense, when one considers that the growth benefit of low SLA leaves is because trees can retain their leaves for longer, which is not an option in deciduous species. A comparative study based on greenhouse-grown species from savanna regions found the opposite – high SLA was linked to fast growth in deciduous species, but not in evergreen species (Tomlinson et al. 2014). However, as emphasised by results in Chapter 2, as well as by Gibert et al. (2016), patterns observed in juveniles in greenhouses are not always representative of patterns in the field.

Two important points emerge from Chapter 3. First, many consistencies between tropical forest and savanna trait-growth relationships would not have been apparent if only one of

diameter growth rate or height growth rate had been considered. Second, differences in prevailing disturbance regimes likely drive stark differences in the strength of trait-growth relationships due to the nature of the dominant environmental filter. For example, in South Africa the presence of mega herbivores and the higher aridity quite likely selects for rapid diameter growth and increased wood density (Archibald & Bond 2003; Hemborg & Bond 2006), generating a strong correlation between these two variables. In Brazil, traits appear largely decoupled from measured growth rates, for which I identified two potential reasons. First, a long standing policy of fire exclusion in Brazilian savannas in general, and particularly at this site (Durigan & Ratter 2016), has resulted in higher canopy cover than would otherwise be expected with a natural fire regime (Fig. 1, Chapter 3). Consequently, height growth rates of species may be suppressed as savanna species are adapted to high light conditions (Hoffmann et al. 2012). Evidence for this stems from the comparative independence of height versus diameter growth rates at this site. In Australia and South Africa, where canopy cover was lower, height growth rate was more tightly coupled to diameter growth rates, and the slope of the relationship was closer to 1. The second potential reason for the observed decoupling of traits from growth was that particularly in Brazilian savannas, species have been found to invest heavily in bark as insulation from fire (Dantas & Pausas 2013). Bark thickness is an important fire protection trait in savannas generally (Pausas 2015), expected to be negatively related to growth rates (Gignoux et al. 1997; Midgley et al. 2010; Lawes et al. 2013), and I investigated this further in Chapter 4.

*Bark thickness and its relation to growth rates*

Based on my findings from Chapter 3, in Chapter 4, I sought to test the expectation that bark thickness-growth relationships will be consistently negative across these same three savannas (Gignoux et al. 1997; Midgley et al. 2010; Lawes, Adie, et al. 2011; Hoffmann et al. 2012; Lawes et al. 2013). I found strong support for this expectation, but just as with the leaf and wood traits examined in Chapter 3, the relationship was weakest in Brazil. This was a surprising result, considering the often assumed importance of bark in protecting stems from fire in Brazilian savannas (Hoffmann et al. 2012; Dantas & Pausas 2013). To understand this, I returned to the influence of anthropogenic fire suppression, which has allowed trees in this Brazilian savanna site to potentially grow taller than they naturally would. It is assumed that there is a link between bark, growth rates, and tree height (Midgley et al. 2010), so environmental perturbations impacting growth and tree size are likely to weaken these interactions. Perhaps in a site with a more natural fire regime (i.e. as found in Australia), the relationship would have been stronger. However, despite the peculiar relationships in Brazil, evidence supported my hypotheses in Chapter 4: (i) relative

bark thickness had a negative relationship with growth rates (both diameter and height); (ii) canopy bark thickness was negatively related to height growth rates in sites subject to frequent fire; and (iii) architecture of trees interacted with relative bark thickness, to further strengthen the trade-off with diameter growth; specifically, shorter trees had faster diameter growth rates and relatively thin bark. The variability in trait-growth and bark-growth relationships observed among savanna sites in Chapters 3 and 4 highlighted the importance of further understanding regional differences in ecology, evolutionary history and disturbance regimes across savannas (Lehmann et al. 2014; Moncrieff et al. 2014).

**Comparability and shortcomings of growth datasets**

The datasets used to calculate growth rates in tropical forests and savannas were quite different in nature. For Chapter 2 and 5 I used tree measurements from tropical forest plots in Far North Queensland, Australia, where only trees larger than 10 cm in diameter at breast height were measured. This is common in tropical forests, as tree density is high such that measuring all trees below 10 cm would be exceedingly time consuming, and add little to overall estimates of woody biomass and change (Condit et al. 1993). In contrast, trees of 10 cm diameter can be some of the largest present in a savanna, and tree densities are often low. As such, savanna tree measurement plots often contain fewer individuals with a smaller maximum size, than in tropical forests. Both types of datasets have their limitations. In tropical forests plots, the obvious is that no trees less than 10 cm in diameter are sampled, thus we have to infer growth behaviour below this size using models. Another is that the sub-canopy of tropical forests sees many individuals with suppressed growth rates due to the exceedingly low light conditions. Hence, robust measures of growth rates require many individuals and can be skewed. To combat this I considered the maximum potential growth rate of a species to be the $95^{th}$ percentile annual growth increment across all individuals of a species (as has been done in the past, see Clark & Clark 1999; Wright et al. 2010). In contrast, in the savanna-focused analyses, I used the mean rather than upper percentiles of growth rates, as the far lower sample size due to low stem densities in plots could also skew growth rates. Where most forest species were represented by hundreds of individuals, some savanna species were represented by as few as ten individuals. I concluded the mean to be a more robust estimate of a species growth rate tendency in savanna. This was unavoidable but it must be noted that just as competition for light suppresses the growth of many individuals in tropical forests, so demographic bottlenecks due to disturbance suppress many individuals in savannas (Wakeling et al. 2011). Just as in tropical forests, the higher percentile growth rate is likely a better estimate of a species potential growth rates (Wakeling et al. 2011), and thus potentially more tightly related to

traits (Wright et al. 2010). On a positive note, the savanna datasets did provide one advantage which is not common in forest plots: height measurements. As such, I undertook the first comparison of diameter and height growth rates across savannas, and this elicited an important and novel understanding of these ecosystems that would otherwise have gone undetected.

**Future investigations**

This thesis addresses two distinct knowledge gaps in the literature, with some degree of success. Firstly, it quantifies trait-growth relationships in adults, and throughout ontogeny, and secondly it considers the role of traits in savanna systems. Here I highlight its shortcomings, and consider further avenues of interest.

*Phylogeny*

A recurring theme within this thesis is the lack of consideration of phylogenetic relatedness. For example, while disturbance regimes clearly play a role in driving distinct trait-growth patterns in savanna regions, there are also likely to be regional differences resulting from distinct evolutionary histories (Moncrieff et al. 2014). For example, in Australian savannas proportionally more species are evergreen (Bowman & Prior 2005), which appears to promote the influence of leaf traits on growth, while in South Africa and Brazil, species tend to allocate more resources below ground (Tomlinson et al. 2012), which may act to reduce the relative influence of leaf traits. Future studies could very usefully explore whether certain lineages are more likely to retain a given trait than others. In addition to the ecological reasons for considering phylogenetic relatedness, there are statistical concerns. Throughout this thesis, I have considered species as statistically independent entities, and historically there has been some debate on whether this is appropriate, if they are closely related (Felsenstein 1985). As such, comparative studies often account for phylogenetic similarity by employing phylogenetic comparative methods such as phylogenetically independent contrasts (Felsenstein 1985; Grafen 1989; Pagel & Harvey 1989). Other studies argue that even if a significant component of trait variation within a community is associated with phylogeny, this is irrelevant because it just reflects the likelihood that species with similar traits (which are often closely related) will also tend to occupy similar niches. In other words, observed patterns of trait variation across species reflect the ecological environment, and the fact that species are closely related is irrelevant (Westoby et al. 1995). That is not to say that questions of evolutionary relatedness are not important or interesting, but rather that the use of statistical methods to account for these differences is only relevant with respect to certain questions. My questions were concerned primarily

with whether species traits are at all linked to growth rates, and thus evolutionary relatedness was not of direct relevance. However, future studies could further explore different questions, such as whether certain families are more likely to exhibit a given trait, or be faster growing, than other families, regardless of their environment. Particularly with respect to questions spanning multiple biogeographic regions (such as Chapters 3 and 4), of interest is whether closely related taxa have diverged in their ecological strategies, or whether they maintain similar strategies despite experiencing contrasting environmental conditions.

*Environmental gradients*

Chapters 3 and 4 of this thesis aimed to address our lack of knowledge surrounding trait-growth relationships in savannas. This thesis was limited to three sites, primarily because these are some of the only long term savanna tree measurement data in existence. While valuable in disentangling the effects on trait-growth relationships of coarse grain differences in fire, herbivory and rainfall, noticeably lacking is a contribution to our understanding of how these relationships operate across continuous environmental gradients. The reason for our inability to disentangle trait-growth relationships across broad environmental gradients, is the current lack of permanent tree measurement plots. The majority of long-term ecological research plots are based in tropical forests, and those that are not often do not systematically remeasure individual trees. Future researchers would be well-served by the establishment of long-term tree measurement plots along broad environmental gradients, and collaboration across continents to achieve this goal is required.

*Growth trajectories in savannas*

Chapter 5 highlights the value and interest in describing growth trajectories of species across their entire lifetime. Future growth trajectory investigations using this approach would do well to consider a larger pool of species, and a broader range of size classes, as the species in Chapter 5 were restricted to those that obtained an adult size of 10 cm or greater, thus potentially excluding smaller stature species. However, this is of course limited by the data available. Future studies could also usefully explore whether similarly distinct trajectory shapes are observed in savanna species as in forest species. However, this approach is also limited by the data available for savanna species. Many species in the savanna dataset were represented by too few individuals to model a reliable growth trajectory, further highlighting the need to establish more savanna tree-measurement plots.

## Conclusion

In this thesis, I showed that adult growth rates are related to traits in both tropical forests and savannas. In general, photosynthetic rate was positively related to growth rate, wood density was negatively related, branch scale leaf:wood mass ratios were positively related, and specific leaf area was unrelated to growth, except in sites with very large trees. In tropical forests, I demonstrated that the relative influence of specific leaf area on adult growth rates differs predictably from that observed for seedlings. Future investigations could usefully consider how specific leaf area is related to growth rates in habitats that differ in the maximum size of canopy trees, to further empirically test the effect of proportional total biomass allocation to sapwood on growth rates. I also showed that the entire growth trajectory of a tropical forest species appears to be linked to functional traits. A point of novelty in this thesis was the usefulness of branch leaf:wood mass ratios in predicting growth rates. Across all four forest and savanna sites used in my thesis, and with respect to both stem diameter and height growth rates, leaf:wood mass ratios (at the branch scale) were positively related to growth, and this has never been tested across such a broad range of species. In savanna sites, I found a general negative relationship between relative bark thickness and growth rates, which had been previously assumed, but never broadly tested. While there were some general consistencies across savanna and forests sites there were important differences. In savannas, regional differences in fire, herbivory and climate underpinned variation in traits, growth rates and architecture, which influenced trait-growth relationships. These disturbance and climatic processes are already changing at regional and global scales due to human activities (Moncrieff et al. 2016), and tropical forests are equally vulnerable, due to deforestation and climate change (Malhi et al. 2008). Better understanding of trait-growth relationships in different regions provides us with insight into how species are adapted to their current environments, and thus how they are likely to respond to predicted changes.

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