Growth races in The Mallee: Height growth in woody plants examined with a trait-based model

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Abstract

1. Plant height and growth are fundamental to the understanding of species ecological strategies, to the description and prediction of ecosystem dynamics and to vegetation management, such as plant species’ fire responses. However, a convenient way to characterise the height growth strategies for multiple species has been elusive.

2. We examine the height growth trajectories in 18 woody plant species in a light-saturated, fire-prone, semi-arid environment as well as the influence of functional traits on those trajectories. We test trait-growth relationships by examining the influence of specific leaf area, woody density, seed size and leaf nitrogen content on three aspects of plant growth; maximum relative growth rate, age at maximum growth and asymptotic height.

3. Woody plant species in the semi-arid mallee exhibit fast growth trajectories. Small seeded species were likely to be the fastest to reach maximum height, while large-seeded species with high leaf nitrogen were likely the slowest. Tall species had low stem densities and tended to have low specific leaf area.

Synthesis: We modeled plant growth using a hierarchical multi-species model that formally incorporates plant functional traits as species-level predictors of growth, which provides a method for predicting species height growth strategies as a function of their traits. We extend this approach by using the modeled relationships from our trait-growth model to predict: growth trajectories of species with limited data; real species with only trait data and; hypothetical species based only on trait coordination. We hope this highlights the potential to use trait
information for ecological inference and to generate predictions that could be
used for management.

Keywords: height-growth, functional traits, mallee, prediction, woody plants
Introduction

Plants compete for sunlight. The tallest plant in a community will have the greatest access to light and consequently will experience a more productive environment relative to shorter plants (Givnish 1988; Monsi & Saeki 2005; Craine & Dybzinski 2013). Competition for light can be thought of as the partitioning of height dominance and is divided along two gradients. The vertical gradient reflects direct competition for light between individuals, whereby plants can gain dominance of available light by growing the fastest and tallest. By contrast, temporal gradients reflect light competition through time, whereby individuals may dominate time in the sun for some period before being overtopped (Kobe 1999; Falster & Westoby 2003; 2005b). Light competition can be studied by measuring plant height through time, which can also provide measures of vegetation structure and change. Plant height is also a commonly used plant functional trait associated with competitive vigour, whole plant fecundity, and is an important indicator of community disturbance intervals and environmental tolerances (Westoby et al. 2002; Cornellissen et al. 2003). In fire-prone ecosystems, measurements of plant height are often used to reflect vegetation structure and habitat redevelopment after disturbance. Height can be used as an indicator of habitat provision and tolerable fire intervals (Haslem et al. 2010; Muir, Vesk & Hepworth 2014) although quantitative estimates of growth trajectories for this purpose remain scarce (but see Muir, Vesk & Hepworth 2014).

Despite the importance of plant height to these various branches of ecology, a general model of cross species variation in height growth is lacking. Developing functional trait-
based models of growth has become an important research goal for plant ecologists in an
effort to generalize trait-growth relationships. Traits have been linked to species growth
rates in several field studies (Kobe 1999; Reich *et al.* 1999; Falster & Westoby 2005a;
Falster & Westoby 2005b; King *et al.* 2005; Poorter *et al.* 2008; Adler *et al.* 2014), but
the influence traits have on aspects of plant growth can seem inconsistent or ambiguous.
Seed mass has previously been variously reported as a positive predictor of seedling
growth (Poorter *et al.* 2008), thought unlikely to directly affect growth of large plants
(Ruger *et al.* 2012), and been negatively related to individual growth and fecundity
(Adler *et al.* 2014). Wood density has previously been highlighted as one of the most
important traits influencing adult woody plant growth (King *et al.* 2005; Falster &
Westoby 2005a; Poorter *et al.* 2008; Ruger *et al.* 2012; Reich *et al.* 2014) but also found
to be a poor predictor of inherent growth rates (Herault *et al.* 2010). Leaf traits appear to
have particularly unclear implications for growth; some studies reporting strong support
(Kitajima 1994; Falster & Westoby 2005a; Sterk, Poorter & Schieving 2006; Reich *et al.*
2014; Kunstler et al 2016), whilst others report poor or ambiguous relationships (Poorter
*et al.* 2008; Paine *et al.* 2015) and assert no justification for using leaf economics traits to
describe growth rates (Ruger *et al.* 2012). Leaf nitrogen has previously been related to
growth, where species with fast growth rates tending to have high leaf nitrogen (Poorter,

Trait-based growth research typically takes advantage of long term monitoring data sets
from well-sampled, dense and productive forests, such as temperate and tropical forests,
where access to light represents a major resource gradient (Thomas 1996; Kobe 1999;
King et al. 2005; Condit et al. 2006; Sterck et al. 2006; Poorter et al. 2008; Herault et al. 2011; Ruger et al. 2012; Prior & Bowman 2014). The bias of trait-growth rate studies to mesic systems is a bias towards systems with high light competition and frequently dominated by tall, non- or weakly-resprouting species. Vegetation without a strong vertical light profile may show different growth strategies in response to contrasting resource gradients. Prior & Bowman (2014) found that asymmetric-size competition for light was greater at high productivity sites. Areas of relatively scarce resources, resulting in low productivity, or frequent disturbance are often understudied from a functional trait-based perspective. This impedes a truly general understanding of height growth strategies.

In the Mallee region of south-eastern Australia, fire responses of broad vegetation associations and growth forms have been well described (Bradstock & Gill 1993; White 2006; Giljohann et al. 2015), and despite many papers on mallee eucalypt demography (Wellington 1984; Wellington & Noble 1985a; Noble 1985; Wellington & Noble 1985b; Clarke et al. 2010), and studies focused on Callitris sp. (Bradstock, Bedward & Cohn 2006), and Triodia sp. (Rice & Westoby 1999, Gilijohann et al. 2017), quantitative data on individual growth responses for many of the common plant species remain limited (Pausas et al. 2004). We know little about the coexistence and height-growth trajectories of species in the Mallee region.

We use data from this high-light, low precipitation and low productivity region of South Eastern Australia which is on the border of temperate and semi-arid fire-regime (Murphy
et al. 2013) to complement the growing literature on trait-based growth models. This ecosystem differs substantially from tropical forest systems, where previous trait-growth work has been published, with an estimated net primary productivity of Mallee ecosystems in Australia of 0.9 t C ha$^{-1}$ year$^{-1}$ within a gradient of productivity in Australia ranging from Tussock Grasslands (0.3 t C ha$^{-1}$ year$^{-1}$) to Eucalypt Woodlands (2.2 t C ha$^{-1}$ year$^{-1}$) and rainforest (7.9 t C ha$^{-1}$ year$^{-1}$) (Murphy et al. 2013). We model plant height using a hierarchical approach, where traits are incorporated into our model as linear predictors of growth parameters. Relating growth characteristics to functional traits in a flexible yet formal manner such as this not only increases our understanding of trait-growth rate relationships but also aids our ability to draw predictive inferences from them, particularly for species for which we may have few data. We believe this is an important research endeavor intrinsically, but could also have consequences for decisions about many plant species but where managers only have limited data for few species. An example of this is plant growth and life history trajectories in fire-prone environments.

We test trait-growth relationships by examining the influence of specific leaf area, woody density, seed size and leaf nitrogen content on three aspects of plant growth; maximum relative growth rate, age at maximum growth and asymptotic height. We do this in a light-saturated and disturbance-prone environment with woody semi-arid plant species, to test the theory of an ‘arms race for light’ outside of low-light, mesic forests. Finally we demonstrate how formally incorporating functional traits into models can aid in predicting growth strategies of plant species.
Methods

The study area is in Murray Sunset National Park, Victoria (34.7683° S, 141.8542° E), a large conservation area within the semi-arid Murray Mallee region of South-Eastern Australia. This region of Victoria has hot dry summers and cold winters. Mean annual rainfall is 290 mm, falling mostly in the cooler months from May-November, and mean maximum daily temperatures ranging from 15.4 °C in July to 32.3 °C in January (BOM).

Two main soil formations occur in this area, The Lowan Sands and The Woorinen Formation, which differ in colour, sand grain size and grain surface features driven largely by differing clay content (Pell, Chivas and Williams 2001). The landscape is dominated by dune/swale systems, which reflect subtle but important variation in soil characteristics and moisture availabilities (White 2006).

The vegetation and fire histories of the Murray Mallee region of South-Eastern Australia have previously been comprehensively mapped (Haslem et al. 2012; Avitable et al. 2013). The most common vegetation type of the region is ‘tree mallee’ which is characterised by small multi-stemmed eucalypts (‘mallees’) with a shrubby and grassy understorey (Haslem et al. 2012). Within this broad vegetation type, three distinct classes occur; Triodia mallee, Chenopod/Shrubby mallee and Heathy Mallee (White 2006; Haslem et al. 2012). Large wildfires are a prominent disturbance in this region with 40% of tree mallee vegetation in the region being burnt in the last 40 years, however, only a small percentage (<3%) has burnt more than once during this period (Avitable et al. 2013).
This study took advantage of fire histories within Murray Sunset National Park (Avitable et al. 2013) to conduct a chronosequence study of plant species growth over time (Falster & Westoby 2005a; Muir, Vesk & Hepworth 2014). Eleven areas varying in time-since-fire (1, 2, 4, 8, 13, 15, 26, 33, 36, 46, 86 years), were selected within a relatively small region of Murray Sunset National Park, sites encompassed a range of post-fire ages whilst restricting the amount of edaphic variation, and all areas were within *Triodia* Mallee.

Between three and five different patches within a ‘time-since-fire’ area were surveyed, totaling 50 surveys across 11 areas. Eighteen woody plant species were selected that had at least three individuals across each of the 50 survey sites, a total of 1250 individual plants were sampled.

**Size Measurements**

We measured heights of at least five (and up to 10) individuals per species in each time-since-fire area. Many species in this region resprout after fire, but for species with post-fire seed regeneration, separate measurements were made on seedling and resprouting individuals. It is easy to determine seeded individuals from resprouting individuals when plants are young, but as they age it becomes increasingly difficult to have confidence of whether an individual seeded or resprouted. Additionally, we thought it likely that resprouters would generally outpace reseeders due to their underground resource stores, and so modeling both functional types together might conflate growth rates based on functional traits and inherently different growth mechanisms (Falster & Westoby, 2005a).

Due to this, *Eucalyptus oleosa*, *Eucalyptus gracilis* and *Melaleuca lanceolata* (the
resprouting species) were left out of the trait-based multi-species model, and their growth was modeled separately to represent the resprouting species. Canopy length, canopy width and basal diameter of the biggest stem were also measured for each individual of each species; we focussed our analysis on height-growth to complement the growing literature of height-growth, mainly from more temperate ecosystems. Regressions showing the relationships between these alternative size variables to canopy height are in the appendix (Appendix Figs S2, S3 and S4).

Measuring plant traits

Guidance on sample sizes for measuring plant traits were followed from Cornellissen et al. (2003), and we took five samples (ie five leaves or five stem sections) from each of five individual plants for each species. Specific leaf area (SLA; mg mm$^2$), the one-sided leaf surface area of fresh leaves divided by the mass of leaves oven-dried at 65°C for 48 h was measured for at least five leaves from each of five individuals for each species. Leaf nitrogen concentrations (Nmass; %) were calculated on five fully expanded leaves taken from well-lit positions on each of five individuals per species. Leaves from each species were then pooled and finely ground for nitrogen analysis. Total nitrogen concentration based on mass (%) was measured using complete combustion gas chromatography performed by The Surface and Chemical Analysis Network at The University of Melbourne. Stem tissue density (dry mass per unit fresh volume; mg mm$^{-3}$) was measured using 40-60 mm long, stem segments from at least five individuals per species. Samples were collected in the field and refrigerated before processing as soon as feasible.
Stem tissue density was then determined following Archimedes principle using the protocol from Cornellissen et al. (2003). Seed mass (mg) was measured for as many species as possible with field-collected seed, oven-dried and weighed. Seed mass data was also supplemented from the literature and a global seed mass database (Moles & Westoby 2003). See Table 1 in Appendix for list of all species and their mean trait values.

A hierarchical, trait-based nonlinear growth model

We modeled the growth of species using a hierarchical multi-species non-linear growth model, which formally incorporates plant traits as species-level predictors of growth. Our chosen model has biologically interpretable parameters; the maximum height achieved, the maximum relative growth rate (maximum RGR), which is measured in units of cm/cm/yr (Atwell 1999) and the time at which this maximum growth occurs, measured in years.

In deciding which functional traits to include in our models we drew on literature to generate hypotheses of trait effects on growth. Specifically that wood density, seed mass and leaf traits would be influential traits affecting growth trajectories (Falster & Westoby 2005a; Reich et al. 2014), whereby seed mass should be most influential on initial growth (Moles & Westoby 2006), stem density of achievable height (Falster & Westoby 2005a; Falster & Westoby 2005b) and leaf traits throughout the whole growth process (Sterck, Poorter & Schieving 2006; Reich et al. 2014), leaf nitrogen being important for the pace and the timing of maximum growth (Poorter, Remkes & Lambers 1990). Our final model
had stem density and SLA influencing maximum height, nitrogen leaf content and seed mass on age at maximum growth and seed mass on maximum relative growth rate. These enter into our multi-species model in a way similar to that of Pollock et al. (2011).

We chose to use the three-parameter sigmoidal model form due to the biological interpretable parameters and its use in previous studies (Thomas 1996; Falster & Westoby 2005a) and the increased information due to a parameter specifying age at maximum relative growth rate. As well as biologically interpretable parameters, our model choice sought to adequately represent the growth of all species modeled. One consequence of modeling multiple species and growth forms together is that some species are better fit than others. We display some model fits to raw data of our chosen model (Fig. 1a-f). We compared our three-parameter sigmoidal model to four other possible growth models; two two-parameter models (Power and Exponential) and one other three-parameter model (Logistic), plus our chosen Hillslope model with log time (Appendix Table S2). We used Bayesian inference employing Markov chain Monte Carlo (MCMC) methods with the open-source software package JAGS version 3.3.0 (Plummer 2003) run via the statistical software environment R version 2.15.2 (R Development Core Team, 2015) with the package R2jags (Su & Yajima 2015). Please see the Supporting Information for a more detailed model description.

Predictions

We used modeled relationships between growth parameter and traits to make predictions for real species for which we have no growth data but we do have trait data and also hypothetical species based on trait information only. We did this by including our real
species and our ‘hypothetical species’ into our dataset, with missing height values, but with trait values included for them in the dataset. In a Bayesian framework, these missing data values are estimated with predictive distributions. For our real species we used their measured trait data collected from the field. For our hypothetical species, we use extreme trait values that lay with two standard deviations of those observed in our trait data set. We present a tall, fast and early growing species (low stem density 0.65 mg mm\(^{-3}\), low SLA 2.55 mg mm\(^{-2}\), small seed mass 0.430 mg and low leaf nitrogen content 0.97%); a tall, late and slower growing species (low stem density 0.65 mg mm\(^{-3}\), low SLA 2.55 mg mm\(^{-2}\), heavy seed mass 100 mg, high leaf nitrogen 4.67%); a short, late and slow growing species (high stem density 0.87 mg mm\(^{-3}\), high SLA 6.53 mg mm\(^{-2}\), heavy seed mass 21.86 mg, high leaf nitrogen 2.91%); and a short, early and fast growing species (high stem density 0.87 mg mm\(^{-3}\), high SLA 6.53 mg mm\(^{-2}\), small seed mass 0.350 mg and low leaf nitrogen 0.97%).

Results

Growth trajectories

Maximum height of woody species in the Mallee ranged between short woody shrubs such as _Halgania cyanea_ (Boraginaceae), reaching an average maximum height of approximately 40 cm and the tallest species _Codonocarpus cotinifolius_, which reached average maximum heights of approximately 5 m. The four next tallest woody species, which dominate the overstorey canopy are _Callitris verrucosa_ (321 cm), _Eucalyptus_...
gracilis (258 cm), *Eucalyptus oleosa* (268 cm) and *Melaleuca lanceolata* (209 cm) (Fig. 2). The seed-derived individuals of the resprouter species have much slower relative growth rates, achieve these later and have lower heights compared to their resprouting individuals (Fig. 2a-b). The species that achieved the maximum growth earliest had the fastest maximum relative growth rates and that reached the greatest eventual heights were *C. verrucosa* and *C. cotinifolius* and then the resprouting species (Fig. 2). Of the seed-derived species data, one clear trade-off existed whereby high relative growth rates (parameter b) were negatively correlated (Pearson’s correlation coefficient of -0.73) with age at maximum growth rate (parameter c), so species that grew relatively quickly always reached their maximum growth rate early (Appendix Fig. S3).

**Growth variation among species**

All species modeled had height-growth characterized by maximum relative growth rates of between 3 cm/cm/yr and 7 cm/cm/yr, onset of maximum growth occurring between one and two years following disturbance, and asymptotic heights of between 40 cm and 500 cm (Figs 2 and 3). The fastest growing species were the two resprouting eucalypts, which both had maximum relative growth rates of 6.7 cm/cm/yr, and these species also reached their maximum relative growth rate the earliest, at 1.2 years of age. Resprouting plants in the Mallee accelerated faster to achieve higher maximum growth and higher maximum heights compared to seed-derived conspecifics and to other non-resprouting species (Fig. 3). There was a clear difference between the growth rates and the age at maximum growth between the seed-derived plants of resprouting eucalypt species - *E.*
gracilis and E. oleosa - and their resprouting counterparts. Resprouting eucalypt
individuals had nearly two-fold higher maximum growth rates (6.98 and 6.91 cm/cm/yr
respectively for resprouters and 3.56 and 3.66 cm/cm/yr for seed derived cohorts) and
achieved these by half the age of the seed derived individuals (2.21 and 2.01 years
respectively for resprouters and 1.11 and 1.11 years for seed derived cohorts).
The tallest species, C. cotinifolius, had one of the fastest growth rates, reaching its
maximum height of 468 cm at 1.8 yrs at a rate of 4.5 cm/cm/yr (Fig. 3). This species
unusual relative to the other species in our dataset as it is known as a polycarpic fire
ephemeral and characteristically has relatively short life spans and very rapid growth
(Pate et al 1985). The second tallest species, Callitris verrucosa (Cupressaceae) had a
below average growth rate. All other species had mean asymptotic heights between 40
cm and 3.2 m. The next tallest suite of species were all resprouters, the two eucalypt
species and Melaleuca lanceolata (Myrtaceae). The slowest growing species was
Beyeria opaca (Euphorbiaceae) with a maximum growth rate of 3.2 cm/cm/yr. In these
data, there appears to be little evidence for a clear succession of leaders. For example,
both E. gracilis (Myrtaceae) and E. oleosa (Myrtaceae) were always the tallest species at
a site, apart from C. cotinifolius at two years. In the Mallee, seed-derived individuals of
short species could reach their maximum growth either early or late. Species that grew
fast could achieve both tall and short heights. There were, however, no tall species that
had low maximum growth rates (Fig. 3, Fig. S1 Appendix).

The greatest variation between species was in the parameter asymptotic height (Standard
Deviation = 0.494). There was relatively little variation between species in age at
maximum relative growth rate (SD = 0.13) and the least variation between species was for maximum relative growth rate (SD = 0.02).

**Trait effects on growth parameters**

Leaf, seed and stem traits all explained some variation in sub-models for the three growth parameters (Fig. 4a, see Table S2 Appendix for further details). Effect sizes were largest for asymptotic height, which is the parameter that varied most between species. Smaller effect sizes were found for the other two parameters, reflecting the smaller variation to explain. The largest single effect size was for stem density on maximum height. Seed mass had smaller effects and those of leaf traits were of intermediate size, but highly uncertain.

Species with lighter seeds achieved faster relative growth rates and did so earlier (Fig 4a, b, d). Species with high leaf Nitrogen content and heavy seeds were likely to be the slowest to reach maximum growth (Fig 4c, d). In general, species with low stem densities and low specific leaf area reach greater asymptotic heights (Fig 4 e, f).

*Codonocarpus cotinifolius* appeared an outlier, having high SLA and yet achieved a tall height, but it has an unusually low stem density, nearly 4 standard deviations below the mean value of this community. Species traits explained similar amounts of variance in the parameters; maximum growth rate has $R^2 = 0.65$, age at maximum growth $R^2 = 0.66$ and maximum asymptotic height $R^2 = 0.59$. Stem density and specific leaf area varied the most, with stem density having the largest and strongest effect size. Seed mass and
nitrogen content both had little variation around the mean parameter value but had relatively small effect sizes (Fig. 4a).

Predictions based on traits

We used the modeled relationships from our hierarchical trait-growth model to predict the growth trajectory of two real species (*Dodonaea viscosa* and *Myoporum platycarpum*) for which we only have field collected trait data as well as four hypothetical species, which represent different regions of ‘trait space’ from within our dataset (Fig. 5). These scenarios mostly differ in maximum height within the first three years and these height values commonly range between 50 cm and 250 cm.

Discussion

Mallee growth trajectories

The theoretical arms race for light suggests that two prominent gradients of competition for light exist; a vertical gradient where species compete at one point in time and a temporal gradient, where over time, each species will have some dominating time in the sun (Falster & Westoby 2003). Falster & Westoby (2005) and Muir (pers. comms) found distinct periods of prominence across species in forest systems where shorter species temporarily out-pace taller species, but are subsequently overgrown, allowing a temporal partitioning of dominance between species after disturbance. Our results suggest that this does not occur in Mallee, and all species in this system have relatively fast growth rates and trajectories compared to growth of species in other ecosystems such as open
coastal woodland (Falster & Westoby 2005) and damp forest (Muir et al. 2014) (Figs 2 and 3). All species in the Mallee reached an average asymptotic height after 5 years and there were no distinct prolonged overlapping series of species within the canopy (Fig. 2). Light is abundant in this ecosystem and direct competition for light appears to be less pronounced in the temporal species dynamics. In fact, two of the tallest species, *Eucalyptus gracilis* (Myrtaceae) and *Eucalyptus oleosa* (Myrtaceae), reach their period of maximum growth the earliest, at 1.2 yrs and have the fastest maximum relative growth rates (Fig. 3), which allows these species to share competitive dominance in the upperstorey. Mallee eucalypts resprout from lignotubers and have multi-stemmed growth forms (Noble 1985; White 2006). Our results suggest these attributes contribute to these species' persistence in this environment, as they resprout readily after fire and maintain their height dominance over all other species apart from the short lived *Codonocarpus cotinifolius* (Gyrostemonaceae) and the slower growing *Callitris verrucosa* (Cupressaceae) (Figs 2 and 3). When growth trajectories of the seed-derived individuals of the resprouting species were compared to their resprouting counterparts, the resprouting individuals achieved taller heights, younger ages of maximum growth and faster relative growth (Fig. 3), reflecting well appreciated principles of resprouting species being strong competitors due to large underground energy reserves stored below ground in lignotubers (Bellingham & Sparrow 2000; Pausas & Keeley 2014). These resprouting cohorts also appear to fit the description of ‘super-species’, which grow fast, achieve tall heights and live a long time (Huston & Smith 1987). However, seeding species also demonstrate fast growth rates, which may reflect an adequate share, or less competition for post fire resources, light and space, for both resprouters and non-
resprouters in this system. But the question remains, if light is not limiting, then why
grow so fast?

Falster & Westoby (2005) suggest there may be strong selection for traits that maximise
height growth rate, and thereby light acquisition, in vegetation undergoing frequent
disturbance. When light is not a limiting resource, fast growth may not be a race for light
but instead reflect an ability to start either reproducing or storing resources quickly in the
face of unpredictable disturbance or environmental fluctuations such as drought
(Bellingham & Sparrow 2000). Our data contains both resprouters and non-resprouters
and both syndromes have the ability for rapid height growth; resprouters have persistent
underground resources that facilitate high competitive ability in fertile environments and
non-resprouters have rapid seedling growth and early emergence postfire (Pausas &
Keeley 2014). The trait composition in our study site may reflect an ‘intermediate’
position in regards to fire frequency, productivity and rainfall, as resprouters dominate
the canopy and non-resprouters dominate the understory woody vegetation and all
species demonstrate rapid post-fire height-growth (Fig. 2). Co-existence of these two
strategies is expected when there has been long-term variation in environmental
conditions or patchy disturbance that may differentially benefit the survival of seedlings
or adults, for example long terms trends in fluctuating water availability (Bellingham &
Sparrow 2000; Pausas & Keeley 2014). One of the most important considerations for an
individual plant is that it is able to re-occupy a site and take advantage of abundant but
short pulses of resources before the next disturbance event (Bellingham & Sparrow 2000)
and if there is a time constraint on growth, rates of growth are often fast (Arendt 1997).
Our results suggest that both the resprouters and the non-resprouters in the Mallee region are capable of achieving rapid height-growth.

Trait relationships with growth parameters

In theory, the rate of individual plant growth and when this growth occurs directly influences species position and length of time at a competitively dominant position or ‘at the top’, where it has the access to the most light (Huston & Smith 1987; Loehle 2000; Falster & Westoby 2003). We found trends suggesting that smaller seeded species are likely to grow faster per year and reach their period of maximum growth rate earlier than larger seeded species. Species with low leaf nitrogen are also likely to reach a period of fastest annual growth before others. Species with low stem densities and low specific leaf area will generally grow taller than species with high stem densities and high SLA. Our results seem consistent with some literature, for example Adler et al. (2014) found that species with low wood density, small seeds, high SLA and rapid leaf turnover rates (indicative of resource exploitation as a high priority) are expected to grow faster. This suite of traits leading to fast growth is indicative of plants prioritising short-term gains over long-term benefits and are thought to possess a higher capacity to change their growth rates to changing resource conditions (Adler et al. 2014). This may be particular relevant to species in resource-poor, disturbance-prone or areas with pronounced environmental variation, such as mallee vegetation, where resources (ie rainfall) and disturbance (ie fire) fluctuate.
Predictions based on trait-relationships

The ability to move from descriptive to predictive science is a goal of much trait-based research (Ruger et al. 2012; Adler et al. 2014). The formal incorporation of traits into our hierarchical and biologically interpretable multi-species model, allows us to make predictions of growth trajectories based on trait values and hence estimate the growth parameters for species we have few data for but can access some easily measurable traits; either from existing trait databases, or with a targeted field collection. For example, we can predict a growth trajectory for a species with low stem density, low SLA and small seeds and demonstrate that this species is likely to achieve a greater height compared to other species and it will reach its maximum growth rate earlier. We can also use only trait information to predict the growth curves of species which may occur locally, but for which we do not have growth data (Fig. 5). We were able to conduct this type of prediction because we chose to use a semi-mechanistic and hierarchical model that allows overall trends in growth to be consistent between species with modeled variation, but also specific trait effects to have a variable impact on each of our growth parameters. An important future research goal is to determine how robust trait based predictions are across different species, between different sites. Additionally, understanding the differences in growth strategies between different light environments and how these change through time across ecosystems would be a fascinating area of comparative ecology.

This study is one of a handful to examine how plant functional traits influence growth
trajectories and complements existing literature by focusing on a high light, disturbance-
prone and low productivity region. We built a hierarchical multi-species model of plant
growth with biologically interpretable parameters; maximum growth rate, age at
maximum growth rate and asymptotic height achieved. Including functional traits as
predictors of these growth parameters allows us to formally capture the role of seed size,
stem density, leaf nitrogen content and specific leaf area in species pace and timing of
growth and their competitive dominance. There are multiple ways this approach may be
extended, such as specifically incorporating environmental variables and intra-specific
trait information. We believe this is a good first start in developing relatively simple
models that can be used to describe multi-species growth trajectories, but also produce
testable predictions about growth trajectories based on easy to collect functional data.

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Figure 1. Plant height over times since fire and hierarchical model fits showing reseeding species a) *Acacia bractybotrya* (Mimosaceae), b) *Westringia rigida* (Lamiaceae), c) *Halgania cyanea* (Boraginaceae), d) *Beyeria opaca* (Euphorbiaceae), e) *Acacia montana* (Mimosaceae), and f) *Eremophila glabra* (Myoporaceae). The black dots represent observations.
Figure 2. Modeled height growth trajectories for 18 semi-arid woody plant species after fire. Resprouting species and their seed-derived growth comparison in (a), whereby blue dashed lines are modeled growth based on resprouting individuals, dashed black lines are seed derived plants from resprouting species. Non-sprouting species in (b), and species were modeled to 40 years, but all species reached asymptotic height by ten years, so we only display these values and include a close up of the growth trajectories from 0.5 to 3.5 years; the period where the most rapid growth occurs for all species in (c).
Figure 3. Species estimates for the three separate growth parameters in rank order; a) maximum growth rate, b) age at maximum growth and c) maximum height. The shaded panels at the base of each figure show the cross-species mean. The black dots and lines represent non-resprouting species, the blue dots and lines represent the separately modeled re-sprouting species. Error bars are 95% credible intervals. Species names are abbreviated to the first letter of the genus and species: Beyeria opaca (Bo), Westringia rigida (Wr), Eremophila glabra (Eg), Phebalium squamulosum (Ps), Olearia muelleri (Om), Acacia montana (Am), Callitris verrucosa (Cv), Acacia wilhelmiana (Aw), Senna artemisioides subsp zygophylla (Sa), Dodonaea bursarifolia (Db), Acacia brachybotrya
(Ab), *Olearia pimeleoides* (Op), *Olearia subspicata* (Os), *Halgania cyanea* (Hc),

*Codonocarpus cotinifolius* (Cc), *Melaleuca lanceolata* (Ml), *Eucalyptus oleosa* (Euco),

*Eucalyptus gracilis* (Eucg).
Figure 4. Coefficients estimates (effect sizes) for linear predictors in the three submodels, which describe how traits influence the growth parameter. (a) Positive coefficients (numbers larger than 0) indicate a positive relationship between the trait values and the growth parameters. Bars represent 95% credible intervals. We also show 50% credible intervals with the light grey bars. (b-f) Partial dependency plots representing the effect of one trait on one growth parameter with all other parameters and coefficients held at their mean. (b) Seed mass had a negative influence on maximum growth rate, (c,d) leaf nitrogen content and seed mass positively influenced age of maximum growth, (e,f) stem
density and SLA negatively influenced asymptotic height. Along the x-axis are the scaled and centered trait values and along the y-axis are the parameter values for each species. This trait-based growth model was constructed using only non-resprouting species. See Table S4 (appendix) for further details on effect sizes.
Figure 5. Example predicted height growth trajectories based on traits. (a) is a prediction of the growth trajectory of *Acacia brachybotrya* (Mimosaceae) which we have limited data for in our dataset. The black dots represent the height data for this species, the black line represents the fitted growth curve in our hierarchical model, the gray line represents using *A. brachybotrya* traits only to predict its growth. (b) represents two real species, *Dodonaea viscosa* (Sapindaceae) and *Myoporum platycarpum* (Myoporaceae), for which we have trait data but no height data and their predicted growth curves based on their traits. (c) two hypothetical species, where we have used trait values representing fast/slow and tall/short strategies. We present a tall, fast and early growing species (low stem density, low SLA, small seed mass, and low leaf nitrogen); a tall, late and slower growing species (low stem density, low SLA, heavy seed mass, high leaf nitrogen); a short, late and slow growing species (high stem density, high SLA, heavy seed mass, high leaf nitrogen); and a short, early and fast growing species (high stem density, high SLA, small seed mass and low leaf nitrogen). See methods for quantitative trait values. All predicted relationships are based on median predicted parameter values.
Appendix

Table S1. Mean trait values for 18 species from Murray Sunset National Park, the numbers in parentheses next to species names are the number of individuals sampled for trait measurements.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Specific leaf area (mg mm$^{-2}$)</th>
<th>Stem density (mg mm$^{-3}$)</th>
<th>Seed mass (mg)</th>
<th>Nitrogen content (%)</th>
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<tr>
<td>Mimosaceae</td>
<td>Acacia bractybotrya (16)</td>
<td>4.11</td>
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<td>Mimosaceae</td>
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<td>Mimosaceae</td>
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<td>Gyrostemnaceae</td>
<td>Codonocarpus cotinifolius (5)</td>
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<td>0.32</td>
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<td>4.67</td>
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<td>0.86</td>
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<td>Asteraceae</td>
<td>Olearia pimeleoides (25)</td>
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<td>2.91</td>
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<td>Asteraceae</td>
<td>Olearia subspicata (15)</td>
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<td>Rutaceae</td>
<td>Phebalium squamulosum (15)</td>
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<td>0.83</td>
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<td>Mimosaceae</td>
<td>Senna artemisoides subsp. zygophylla (10)</td>
<td>1.68</td>
<td>0.87</td>
<td>12.15</td>
<td>1.59</td>
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<td>Lamiaceae</td>
<td>Westringia rigida (20)</td>
<td>3.01</td>
<td>0.87</td>
<td>1.25</td>
<td>1.68</td>
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</table>
Figure S1. Scatter plots of model parameters and functional traits, the numbers in the top right corner of each panel are the Pearson’s correlation coefficient.
Figure S2. Regressions showing relationships and R squared values between species structural attributes – canopy height (cm), canopy width (cm), canopy length (cm) and species basal diameter (mm) measured for all species.
Figure S3 – The relationships between species height (cm) and canopy length (cm) for each species.
Figure S4 – The relationships between height (cm) and basal diameter (mm) measured for each species.
Table S2. Alternative non-linear model forms, convergence, Deviance Information Criteria (DIC), the effective number of parameters (pD), mean R squared values of observed versus predicted heights across all species (Naïve Rsq) and mean R squared values of observed versus predicted heights based on internal cross validation, where each species was left out of the training dataset and it’s heights predicted (CV Rsq) and key references for model forms.

<table>
<thead>
<tr>
<th>Model</th>
<th>Equation</th>
<th>Convergence</th>
<th>DIC</th>
<th>Naïve Rsq</th>
<th>CV Rsq</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Power</td>
<td>( aT^b )</td>
<td>50000</td>
<td>9759.1</td>
<td>0.792</td>
<td>0.001</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Exponential</td>
<td>( a + b \log(T) )</td>
<td>50000</td>
<td>8687.7</td>
<td>0.815</td>
<td>0.000</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Logistic</td>
<td>( a/(1 + \exp(-bT + c)) )</td>
<td>100000</td>
<td>9276.1</td>
<td>0.780</td>
<td>0.011</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Hillslope log(T)</td>
<td>( a/(1 + \exp(-b(T - c))) )</td>
<td>90000</td>
<td>8772.7</td>
<td>0.784</td>
<td>0.518</td>
<td>Tjørve 2009</td>
</tr>
<tr>
<td>Hillslope</td>
<td>( a/(1 + \exp(-b(T - c))) )</td>
<td>90000</td>
<td>8723.0</td>
<td>0.779</td>
<td>0.514</td>
<td>Tjørve 2009</td>
</tr>
</tbody>
</table>
Figure S5. Plant height data over times since fire and hierarchical model fits showing resprouting species a) *Eucalyptus oleosa*, b) *Eucalyptus gracilis* and c) *Melaleuca lanceolata*. The black dots represent field-collected data; the blue stars for the resprouting species represent heights of seedlings; the blue dots represent randomly selected height data points from individuals of indeterminate origin to use as asymptotic height estimates for the seeders of the same species.
Table S3: Linear trait model statistics - Gelman’s R squared values represent the proportion of variance in the response explained by the predictors for each level of a multi-level model, values approaching 1 are better. Pooling factors assess the contribution of within group estimates (species level data) versus population estimates (all data combined), a pooling factor of less than 0.5 indicates the model is using more within group information than population mean information. As models improve, both Gelman’s R squared and the pooling factor should approach 1.

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Sub-model</th>
<th>Gelman’s R squared</th>
<th>Pooling factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic height (a)</td>
<td>$\log(a_j) = \exp(\beta_0 + \beta_1 \times SD_j + \beta_2 \times SLA_j + \epsilon_j)$</td>
<td>0.57</td>
<td>0.19</td>
</tr>
<tr>
<td>Maximum relative growth rate (b)</td>
<td>$\log(\delta_j) = \exp(\beta_0 + \beta_1 \times SM_j + \epsilon_j)$</td>
<td>0.77</td>
<td>0.64</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>$\log(c_j) = \exp(\beta_0 + \beta_1 \times N_j + \beta_2 \times SM_j + \epsilon_j)$</td>
<td>0.83</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Table S4. Effect sizes of Figure 4 displaying the growth parameter, traits that influence that parameter as corresponding for Figure 4 and the mean effect size with lower and upper bounds of 95% credible interval.

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Trait</th>
<th>Mean standardised effect size (95% credible intervals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic height (a)</td>
<td>Stem density</td>
<td>- 0.58 [-0.99, -0.20]</td>
</tr>
<tr>
<td>Asymptotic height (a)</td>
<td>Specific leaf area</td>
<td>- 0.19 [-0.57, 0.19]</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>Seed mass</td>
<td>0.08 [-0.02, 0.19]</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>Leaf nitrogen</td>
<td>0.05 [-0.05, 0.15]</td>
</tr>
<tr>
<td>Maximum relative growth rate (b)</td>
<td>Seed mass</td>
<td>- 0.06 [-0.14, 0.03]</td>
</tr>
</tbody>
</table>
Appendix

Detailed statistical modeling methods

While a multi-species hierarchical approach is not as simple as single species regressions, we believe the added complexity is worthwhile, as explained and unexplained variance can be partitioned between the observation and the species level, and species with few data can still be included. Furthermore this approach is relatively simple compared to fully mechanistic models, which can be hard to parameterise with empirical data. Similar approaches have been used for hierarchical models of plant resprouting (Vesk 2006), quantifying distributions of demographic rates in tropical forests (Condit et al. 2006) and species distributions (Pollock et al. 2011). We believe this represents a practical approach to describing the growth of multiple plant species.

We were interested in the height growth of plant species; our observations were heights (cm) of individual plants for each species across time (yr). Because plant heights are finite, height growth must be nonlinear, and as such so must our model. Our model had a hierarchical structure corresponding to two levels of variation: between species and between individuals. The strength of hierarchical modeling is that it allows explained and unexplained variation to be partitioned within and between multiple levels (in this case, species and individual) of a dataset. It does this by allowing parameters to vary between levels by assuming they are drawn from a common distribution (Condit et al. 2006, Gelman & Hill 2007, Ruger et al. 2012). The advantage of this is that rare or data-scarce species can also be modeled from these common distributions. When field data are scarce for less common species, the ability to retain species with few observations is attractive. A hierarchical model structure also allows specifying sub-models for model parameters (Pollock et al. 2011). In our case, functional traits are formally included as species-specific linear predictors of the growth parameters in a Hillslope growth model (Tjørve 2009). This approach reveals not just plant growth through time for individual species, but also how functional traits contribute to inter and intra-species variation in growth and represents a more, but not fully, mechanistic understanding of how traits affect the function of plants.

A hierarchical, nonlinear growth model

We modeled the growth of species using a hierarchical multi-species non-linear growth model, which formally incorporates plant traits as species-level predictors of growth.

We have an observation model (Eq. 1.1), in which the heights of individual plants are drawn from a lognormal distribution. The lognormal distribution reflects the natural constraints of height data, which are only positive numbers, with relatively few extreme height values (Limpert, Stahel & Abbt 2001):

\[ H_i \sim lnorm(\mu_i, \sigma^{-2}) \]  
Equation 1.1
Where \( H \) is the observed height (cm) for each individual \( i \), which is drawn from a lognormal distribution with mean \( \mu_i \) precision \( \sigma^{-2} \).

We have a **process model**, where each of our modeled height observations is estimated from a growth model. A range of possible growth models exist (Tjørve 2003; Tjørve & Tjørve 2010; Paine *et al.* 2012) and our aim was not to systematically compare every growth model, but instead to choose one that has biologically relevant parameters (Thomas 1996; Falster & Westoby 2005a). We chose a sigmoidal model referred to as the Hillslope equation (Tjørve 2009), which is re-paramaterisation of a logistic equation with three parameters (Eq 1.2):

\[
\mu_{ij} = \frac{\alpha_{ij}}{(1 + \exp\left[-\beta_{ij} (T_i - c_{ij})\right])}
\]

**Equation 1.2**

Where \( \mu \) is the observed height of individual plant \( i \) of species \( j \) (cm) and \( T_i \) is the observed time since fire (yr) of each individual \( i \), and \( \alpha, \beta, \) and \( c \) are species-specific constants. These are biologically interpretable and will be referred to from here as the maximum height achieved (\( \alpha \)), the slope (\( \beta \)) represents the maximum relative growth rate (maximum RGR), which is measured in units of cm/cm/yr (Atwell 1999) and the time at which this maximum growth occurs (\( c \), the location parameter) measured in years.

Each of the three parameters in our process model of growth are estimated via **parameter sub-models**, equations 1.3 – 1.5. Mean parameter values are estimated by species-specific linear models, with species trait values as covariates to influence each of the parameters and with intercepts varying by species. In deciding which functional traits to include in our models we relied on previously published literature to generate hypothesis of trait effects on growth. Specifically that wood density, seed mass and leaf traits would be influential traits affecting growth trajectories (Falster & Westoby 2005a; Reich *et al.* 2014), whereby seed mass should be most influential on initial growth (Moles & Westoby 2006), stem density of achievable height (Falster & Westoby 2005a; Falster & Westoby 2005b) and leaf traits throughout the whole growth process (Sterck, Poorter & Schieving 2006; Reich *et al.* 2014). Initially we let all traits influence each parameter in our growth model, and used a process of backwards selection to test different trait-parameter combinations. Our final model had stem density and SLA influencing maximum height, nitrogen leaf content and seed mass on age at maximum growth and seed mass on maximum relative growth rate, (see equations 3 - 5).

\[
\log(\alpha_j) = \exp[\beta_0 + \beta_1 \times SD_j + \beta_2 \times SLA_j + \epsilon_j] \quad \text{Equation 1.3}
\]

\[
\log(\beta_j) = \exp[\beta_0 + \beta_1 \times SM_j + \epsilon_j] \quad \text{Equation 1.4}
\]
\[ \log(c_j) = \exp(\beta_0 + \beta_1 \times N_j + \beta_2 \times SM_j + \varepsilon_j) \]

Equation 1.5

Where the \( \varepsilon \) terms represent separate species-level random effects and describe the residual departure of species from the fixed effects.

We used Bayesian inference employing Markov chain Monte Carlo (MCMC) methods with the open-source software package JAGS version 3.3.0 (Plummer 2003) run via the statistical software environment R version 2.15.2 (R Development Core Team, 2015) with the package R2jags (Su & Yajima 2015). Priors for parameters were normally distributed, centered on zero with a standard deviation of 0.0001. We used positive half Cauchy distributions truncated at 0, with prior mean 0 and prior scale 25 for the observation error and random effects (Gelman 2006). We initialized our model by using mean parameter values taken from single species non-linear models. We logged trait values and then centered and scaled our trait data by one standard deviation before modeling.

**Model choice**

As well as biologically interpretable parameters, our model choice sought to adequately represent the growth of all species modeled. One consequence of modeling multiple species and growth forms together is that some species are better fit than others. We compared our three-parameter sigmoidal model to four other possible growth models; two two-parameter models (Power and Exponential) and one other three-parameter model (Logistic), plus our chosen Hillslope model with log time. To compare these models, we looked at DIC and R squared values between predicted and observed heights for each species. Additionally we performed internal cross validation for each model, where each species was left out of the training dataset and then it’s height over time predicted and observed and predicted heights assessed by R squared values (Appendix Table S2).

Overall, the Hillslope model had the lowest DIC and performed well in internal cross validation (Appendix Table S2). We did not consider four, five or six parameter models, because we were cautious of over-parameterisation with our relatively small empirical dataset. We chose to use the three-parameter sigmoidal model form due to the biological interpretable parameters and its use in previous studies (Thomas 1996; Falster & Westoby 2005a) and the increased information due to an extra parameter specifying age at maximum relative growth rate. We do not consider these alternative models further.

We display some model fits to raw data of our chosen model (Fig. 1a-f).

For the resprouting species, heights of seedlings were measured when the seedling origins were obvious in the field. However, past approximately ten years this became difficult to distinguish and measurements were made on resprouters only. For this reason, and also because we were unsure about using a multi-species model of growth which included both seed derived individuals and resprouters we chose to model the resprouters separately; we present the resprouter data in the Appendix Fig. S2. In order to incorporate the seedlings of resprouter species for comparison against the resprouter growth trajectories, we randomly sampled some top heights from the resprouting individuals (grey circles, Appendix Fig. S2) to use in our model. This approach assumes
that resprouting and seed derived individuals of resprouting species achieve similar top
heights. The sigmoidal model for resprouter species tended to under predict the
asymptotic height of *Eucalyptus oleosa* and *Eucalyptus gracilis* (Appendix Fig. S2).

**Model checking**

Three chains were monitored to ensure convergence, which was assessed both visually
and via the Brooks-Gelman-Rubin convergence diagnostic (Brooks & Gelman 1998).
We evaluated model fit through visual checks of predicted versus observed heights and
by comparing Deviance Information Criteria (DIC, Spiegelhalter *et al.* 2002) between
alternative models. We evaluated the fit of our species-specific linear sub-models by
calculating Gelman’s R squared statistic (this statistic can be interpreted like a classical R
squared statistic, whereby it tells us the proportion of variance in the response explained
by the predictors for each level of a multi-level model) and pooling factors (which
assesses the contribution of mean model group estimates versus data) for each submodel
(Gelman & Pardoe 2006), these statistics are reported in the Appendix Table S3. We plot
coefficient estimates with 95% and 50% credible intervals of the linear predictors in our
growth parameter sub-models. While the effect sizes are sometimes small (effect sizes
can be seen in Fig 4a and Appendix Table S4) we discuss the trends apparent in the data,
particularly as we chose our predictor variables based on a priori information based on
previous trait-based work (see methods).

**References**

Atwell, P. Kriedemann, & C. Turnbull), pp. 188. Macmillan Education, Australia.


persistence and maximum height among plant species in a post-fire succession. *Oikos,
111*(1), 57–66.


(comment on article by Browne and Draper). *Bayesian Analysis, 1*, 515 – 534.

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<tr>
<td>Asteraceae</td>
<td>Olearia subspicata (15)</td>
<td>3.5</td>
<td>0.82</td>
<td>0.8</td>
<td>2.09</td>
</tr>
<tr>
<td>Rutaceae</td>
<td>Phebalium squamulosum (15)</td>
<td>3.09</td>
<td>0.83</td>
<td>1.143</td>
<td>1.76</td>
</tr>
<tr>
<td>Mimosaceae</td>
<td>Senna artemisioides subsp. zygophylla (10)</td>
<td>1.68</td>
<td>0.87</td>
<td>12.15</td>
<td>1.59</td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>Westringia rigida (20)</td>
<td>3.01</td>
<td>0.87</td>
<td>1.25</td>
<td>1.68</td>
</tr>
</tbody>
</table>
Figure S1. Scatter plots of model parameters and functional traits, the numbers in the top right corner of each panel are the Pearson’s correlation coefficient.
Figure S2. Regressions showing relationships and R squared values between species structural attributes – canopy height (cm), canopy width (cm), canopy length (cm) and species basal diameter (mm) measured for all species.
Figure S3 – The relationships between species height (cm) and canopy length (cm) for each species.
Figure S4 – The relationships between height (cm) and basal diameter (mm) measured for each species.
Table S2. Alternative non-linear model forms, convergence, Deviance Information Criteria (DIC), the effective number of parameters (pD), mean R squared values of observed versus predicted heights across all species (Naïve Rsq) and mean R squared values of observed versus predicted heights based on internal cross validation, where each species was left out of the training dataset and it’s heights predicted (CV Rsq) and key references for model forms.

<table>
<thead>
<tr>
<th>Model</th>
<th>Equation</th>
<th>Convergence</th>
<th>DIC</th>
<th>Naïve Rsq</th>
<th>CV Rsq</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Power</td>
<td>$aT^b$</td>
<td>50000</td>
<td>9759.1</td>
<td>0.792</td>
<td>0.001</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Exponential</td>
<td>$a + b \log(T)$</td>
<td>50000</td>
<td>8687.7</td>
<td>0.815</td>
<td>0.000</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Logistic</td>
<td>$a/(1 + \exp(-b(T + c)))$</td>
<td>100000</td>
<td>9276.1</td>
<td>0.780</td>
<td>0.011</td>
<td>Tjørve 2003</td>
</tr>
<tr>
<td>Hillslope log(T)</td>
<td>$a/(1 + \exp[-b(\log(T) - c)])$</td>
<td>90000</td>
<td>8772.7</td>
<td>0.784</td>
<td>0.518</td>
<td>Tjørve 2009</td>
</tr>
<tr>
<td>Hillslope</td>
<td>$a/(1 + \exp[-b(T - c)])$</td>
<td>90000</td>
<td>8723.0</td>
<td>0.779</td>
<td>0.514</td>
<td>Tjørve 2009</td>
</tr>
</tbody>
</table>
Figure S5. Plant height data over times since fire and hierarchical model fits showing resprouting species a) *Eucalyptus oleosa*, b) *Eucalyptus gracilis* and c) *Melaleuca lanceolata*. The black dots represent field-collected data; the blue stars for the resprouting species represent heights of seedlings; the blue dots represent randomly selected height data points from individuals of indeterminate origin to use as asymptotic height estimates for the seeders of the same species.
Table S3: Linear trait model statistics - Gelman’s R squared values represent the proportion of variance in the response explained by the predictors for each level of a multi-level model, values approaching 1 are better. Pooling factors assess the contribution of within group estimates (species level data) versus population estimates (all data combined), a pooling factor of less than 0.5 indicates the model is using more within group information than population mean information. As models improve, both Gelman’s R squared and the pooling factor should approach 1.

Table S4. Effect sizes of Figure 4 displaying the growth parameter, traits that influence that parameter as corresponding for Figure 4 and the mean effect size with lower and upper bounds of 95% credible interval.

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Sub-model</th>
<th>Gelman’s R squared</th>
<th>Pooling factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic height (a)</td>
<td>$\log(a_J) = \exp[\beta_0 + \beta_1 \times S_j + \beta_2 \times SLA_j + \epsilon_j]$</td>
<td>0.57</td>
<td>0.19</td>
</tr>
<tr>
<td>Maximum relative growth rate (b)</td>
<td>$\log(\delta_J) = \exp[\beta_0 + \beta_1 \times S_j + \epsilon_j]$</td>
<td>0.77</td>
<td>0.64</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>$\log(c_J) = \exp[\beta_0 + \beta_1 \times N_j + \beta_2 \times SM_j + \epsilon_j]$</td>
<td>0.83</td>
<td>0.46</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Trait</th>
<th>Mean standardised effect size (95% credible intervals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic height (a)</td>
<td>Stem density</td>
<td>- 0.58 [- 0.99, - 0.20]</td>
</tr>
<tr>
<td>Asymptotic height (a)</td>
<td>Specific leaf area</td>
<td>- 0.19 [- 0.57, 0.19]</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>Seed mass</td>
<td>0.08 [- 0.02, 0.19]</td>
</tr>
<tr>
<td>Age at maximum growth rate (c)</td>
<td>Leaf nitrogen</td>
<td>0.05 [- 0.05, 0.15]</td>
</tr>
<tr>
<td>Maximum relative growth rate (b)</td>
<td>Seed mass</td>
<td>- 0.06 [- 0.14, 0.03]</td>
</tr>
</tbody>
</table>
376x161mm (72 x 72 DPI)
341x229mm (72 x 72 DPI)
Author/s: Thomas, FM; Vesk, PA

Title: Growth races in The Mallee: Height growth in woody plants examined with a trait-based model

Date: 2017-11-01

Citation: Thomas, FM; Vesk, PA, Growth races in The Mallee: Height growth in woody plants examined with a trait-based model, AUSTRAL ECOLOGY, 2017, 42 (7), pp. 790 - 800

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