Big questions:

1. Do we incorporate any other data – change in height growth with reproductive onset, change in shoot extension (or new shoot leaf area). Many other factors also shift with plant age.

# Introduction

A fundamental trade-off faced by all organisms is how to partition available energy into growth versus reproduction (Obeso 2002; Wright *et al.* 2005; Weiner *et al.* 2009; Wenk & Falster 2015). Greater investment in growth translates to more rapid height increases and greater leaf area, resulting in greater access to light and higher photosynthetic yield, in turn leading to improved competitive outcomes and consequently higher survival (Wright *et al.* 2010). In contrast, reproductive production directly and immediately increases fitness through seed production, but will have a future negative effect of plant growth. Quantifying the lifetime pattern of a plant’s investment into vegetative versus reproductive tissues is a prerequisite to diverse research questions including constructing life history tables, parameterizing growth models, modelling global energy sinks, and describing what tissue types are present to consumers and decomposers within an ecosystem.

## Reproductive allocation

The growth-reproduction trade-off is most frequently quantified as reproductive allocation (RA), the proportion of surplus energy that is invested in reproduction (versus growth, storage, and defence) in a given year (Thornley 1972; de Wit 1978; Kozlowski 1992; Mäkelä 1997). *Surplus energy* is defined as the energy remaining after so-called maintenance costs, the energy diverted to replace shed vegetative tissues.

A lifetime plot of RA, termed an RA schedule, summarizes shifts in investment into growth versus reproduction as a species grows and ages, reflecting how the outcome of the trade-off shifts with plant size or age. Early theoretical explorations of this trade-off suggested an individual’s fitness was always maximized by first investing solely in growth and then ceasing growth and having a single year of reproduction followed by death (Cole 1954), termed the big-bang strategy. However, perennial plants, excepting a small number of specialized species (Young 2010; Thomas 2011), exhibit a more nuanced transition of resources from growth to reproduction and have many years of simultaneous growth and reproduction, termed an iteroparous life history strategy. Moreover, they are considered to display indeterminate growth, continuing to increase in size until death. Such species’ RA schedules are termed “graded”.

Both modelled and empirical RA schedules vary notably in shape across species, with some species displaying a distinct asymptotic maximum RA value, others continuing to increase gradually in RA until death, and a few displaying declining RA schedules, with a decrease in RA among the oldest plants (reviewed in Wenk & Falster 2015). In contrast to these graded RA schedules, big-bang species display a sudden year-upon-year transition from investing all surplus energy in growth to reproduction, immediately halting all vegetative growth and followed by death within months to a few years. For all curves, as RA approaches 1, growth to increase size effectively ceases – the plant is continuing to invest sufficient energy in vegetative tissues to maintain its current stature and leaf area, but not to increase them.

Optimal energy models have shown that RA is a sound way to illustrate the growth-reproduction trade-off. They have explored what factors lead to various graded RA schedules, showing that a gradual shift in resources from growth to reproduction is expected if environmental conditions are stochastic (King & Roughgarden 1982) or if the outcome of the growth-reproduction trade-off shifts with a factor that changes across individuals of different age, size, or other variable. Of particular note, if mortality declines with size or age, as is observed for many perennial plants across much of their lifespans (###), it is optimal for individuals to invest more modestly in both growth and reproduction across multiple years (Charnov and Schaffer 1973; Reznick and Endler 1982; Engen and Saether 1994). Declining photosynthetic rates with plant age (Iwasa & Cohen 1989), not being deciduous (Pugliese & Kozlowski 1990) and relative declines in seed production at higher rates of reproductive investment (Miller, Tenhumberg & Louda 2008) have also been modelled as factors leading to simultaneous investment in growth and reproduction across multiple growing seasons. These theoretical explorations indicate that the shape of the RA schedule, age at reproductive maturity and the maximum RA achieved reflect species’ life history strategies (e.g. mortality, seed production) and key functional trait values (e.g. leaf lifespan, photosynthetic capacity, height, seed size)

Despite the obvious importance of tabulating investment patterns across an individual’s lifetime and across species with different life history strategies and functional traits, there are a quite limited number of species for which we know the lifetime energy investment in reproductive versus vegetative tissues (reviewed in Weiner 2009, Wenk & Falster 2015) and no community-level comparative studies exist. Moreover, the studies that do exist differ in how energy allocation to vegetative and reproductive tissues is calculated, potentially leading to quite disparate values for tissue investment. As a result of the paucity of data it is difficult to identify if there are trends in how either absolute or relative investment to different tissue types shifts within individuals as they grow and age or across species with different functional traits or life history strategies.

## Changes in plant growth with age

Although RA, a ratio, is ostensibly independent of the size of the surplus energy pool being divided into reproductive versus vegetative investment, the growth-vegetation trade-off that specifies how surplus energy is divided will most certainly be influenced by energy availability, as shown in many of the optimal energy models (Iwasa & Cohen 1989; Reekie, Budge & Baltzer 2002; Katsukawa, Katsukawa & Matsuda 2002). Determining changes in NPP and surplus energy with shifts in plant size is therefore part of understanding observed RA schedules.

To first order, gross primary production (GPP) and net primary production (NPP) increase with plant size, since larger plants have a greater leaf area. Tissue replacement costs (maintenance costs) must then be paid from the pool of NPP to yield surplus energy. While GPP, NPP, and surplus energy all increase exponentially in young plants, increasing maintenance costs and a medley of changes in plant allometry and physiological traits complicate the relationship between plant size and energy production as plants grow. In particular, the surplus energy pool may increase from young to mid-sized individuals, but then decline from mid-aged to older individuals. This pattern will be influenced by various characteristics observed in older and taller plants, including declining leaf area (Ryan, Binkley & Fownes 1997; Kashian, Turner & Romme 2005; Nock, Caspersen & Thomas 2008) (Bond-Lamberty et al. 2002, Leuschner et al. 2006), decreasing photosynthetic capacity (Ryan *et al.* 1997; Day, Greenwood & White 2001; Niinemets 2002; Thomas 2010), increasing hydraulic limitations (###), crown abrasion (Ryan *et al.* 1997), and declining nutrient supply (###). These changes lead to the well-established observation that GPP asymptotes as plants reach middle age and declines in older stands (Gower, McMurtrie & Murty 1996; Ryan *et al.* 1997; Drake *et al.* 2011; Tang *et al.* 2014). Empirical evidence suggests respiration shifts in tandem with GPP, leading to a proportional decline in NPP (Gower *et al.* 1996; Ryan *et al.* 1997; Tang *et al.* 2014). Surplus energy will in turn asymptote, or perhaps even decline as maintenance costs continue to rise while GPP does not. Indeed, several of the variables listed above will result in lower photosynthase production for a given leaf area, thereby increasing the proportion of NPP being spent on tissue replacement costs, in turn leading to relative declines in surplus energy.

It follows that as a plant grows and ages, the initial investment in reproduction for earlier-maturing plants will occur at a time when there is high rate of vegetative production…

and both its leaf area and RA increase, there is a rapid increase in the pool of energy invested in reproduction and a declining rate of increase in the pool of energy invested in growth to increase size, such that plant growth rapidly asymptotes with the onset of reproduction (###Thomas).

These data suggest that many perennial species will show a gradual decline in the pool of energy available to grow to a bigger size*, before* considering that a proportion of surplus energy is being siphoned to reproduction and that the proportion being allocated to reproduction will be increasing as plants get big and old. Surprisingly, increased relative investment in reproduction (increased RA) is generally omitted as an explanation for declines in leaf area with increasing plant age. Many ignore any mention of reproductive investment (###Drake) and while others indicate that a shift of resources to reproduction with age is a hypothesis which needs more data (Ryan *et al.* 1997; Becker, Meinzer & Wullschleger 2000; Day *et al.* 2001; Tang *et al.* 2014). Indeed, it is possible that small declines in surplus energy availability in middle-aged to older plants, in conjunction with increased RA, might mean that reproductive investment rapidly consumes much of the pool of surplus energy explaining. This lack of surplus energy would feedback to put a rapid end to increases in plant height and leaf area – or worse. Indeed, Genet (Genet, Bréda & Dufrêne 2010) observed that the age-related declines in growth were not fully offset by increased reproduction, such that the decline in growth was greater than the increase in reproduction.

## Study

Determining how species differ in their energy investment to key tissue pools, vegetative maintenance costs, vegetative growth, and reproductive investment, is necessary to understanding why, across species, a given age, height, or basal diameter translates differently to leaf area, leaf production, and seed production across species. We suggest that different investment patterns and growth-reproduction trade-off outcomes reflect consistent differences in life history strategies and key functional trait values. In particular, we hypothesize that

1. That species will exhibit different RA schedules and the observed RA schedules will correlate with other life history data, such as lifespan, height, and age at first reproduction. In particular:
   1. Shorter lived species will show a more rapid onset of reproduction and higher maximum RA.
2. Proportional energy investment into vegetative tissue replacement, vegetative tissue growth, and reproductive tissue investment shifts as a species ages, such that:
   1. The proportion of NPP attributed to surplus energy initially increases, but then asymptotes or declines with age.
   2. Reproductive investment will be sufficiently high to impact growth to increase size well before the end of a plant’s life.
3. Key RA schedule values, such as maximum RA and age at reproductive maturity correlate with functional trait values.

To address these questions we conducted a study in coastal heathland in eastern Australia, quantifying RA and vegetative maintenance costs for 14 dominant perennial species at 6 ages. These species differ for a collection of key life history and functional traits, including lifespan, maximum height, specific leaf area, wood density, and leaf nitrogen content. These species are also known to be iteroparous.

# Methods

## Study system

This study was carried out in Kuring’gai National Park, just to the northeast of Sydney, Australia.

1. Field Methods
2. calculating RA based only on leaf investment and reproductive investment
   1. including stem weight would cause RA to decrease dramatically for most species, because actual stem diameters and weights must continue to increase each year that any shoot growth occurs, even though the volume of functional wood (sapwood) may be stable or declining.
3. We focus on the division of energy investment into leaf replacement, leaf growth, and reproduction, for two reasons. First, leaf mass is a much between predictor of the following year’s total production than is the total standing biomass of the plant. This is because much of the stem biomass is functionally dead heartwood. The mass of heartwood increases ### each year, ###. We are unable to divide the yearly increase in stem biomass into the incremental increase in sapwood versus heartwood. The increase in sapwood mass should reflect the increased

# Results

1. diverse RA values across species (Figure 1a)
2. all species show increase in RA with age (Figure 1b)
3. diverse RA schedules across species – fit into predicted categories, some determinate others indeterminate (Figure 2)
4. declining leaf area in many species; others plateau; a few keep increasing (Figure 3); however in our species height growth does not stop with age – just tapers
5. initial leaf weight is a good predictor of NPP
6. Only for long-lived species is surplus energy strongly correlated with leaf\_weight - and even for these species NPP and total leaf investment much more strongly correlated, because of strong correlations between maintenance and leaf\_weight and the huge size of the maintenance pool
7. For 10 of the 14 species, initial leaf weight is significantly correlated with the number of ovules initiated (Supp Material, r2>0.3 for these species). Indeed, this measure of plant size was a better predictor of the number of ovules initiated than was the total investment in new leaves, both those replacing shed material and those increasingly a plant’s leaf area

At the broadest level, all species display a fundamentally identical trajectory of investment in leaves versus reproductive tissues as they grow and age: as seedlings and saplings they invest solely in stem and leaf growth, increasing rapidly in height and leaf area. They have high shoot extension rates and consequently high increase in leaf area per shoot. At some age, notably different across the study species, plants reach reproductive maturity. As the plants initiate investment in reproductive material and subsequently increase allocation to reproduction, they all show a marked decline in relative investment in leaf growth. Indeed, all plants exhibit a cross-over in absolute investment in increased leaf area versus year reproductive production across their lifetime. Notably, for ten of the 14 species, total leaf area declines year-upon-year starting at some age. That is, these species have negative leaf growth for part of their lifetime, cannibalizing existing leaf area to increase investment in reproduction, as they fail to replace all leaves shed during the year.

Although all study species broadly follow the same lifetime developmental pathway of investing first in height and leaf growth and later in reproduction, the magnitude and timing of their investment in different tissues types is diverse. Figure 1 plots investment in leaves versus reproductive materials for all study individuals, illustrating that different individuals of a species have notably different RA values. Across species (Figure 1a), individuals have different absolute investment in both leaves and reproductive materials, reflecting size differences across the study species, but broadly all have similar RA ranges. When the same data are plotted by the age of the individual (Figure 1b), a quite different pattern becomes apparent: Younger individuals have quite modest RA values, while RA values exceed 0.75 and approach 1 for many of the oldest individuals studied, indicating they are investing all available resources in reproduction.

The RA schedules for the 14 species suggest that the species have disparate life history strategies. Species RA schedules fall into five of the six curve types proposed: big bang, asymptotic, gradual-determinate, gradual-indeterminate, and declining.

Different study species show different leaf area trajectories with age (Figure 3).

# Discussion

* For almost all species height continues to increases throughout life, but for most species leaf area asymptotes within a few years of reproductive maturity and often declines for several years before an individual’s death.
* Declining leaf area with age/size
  + notable how many species show a decline in leaf area within a year of initiating reproduction.
    - These species display a bang-bang schedule, but continue to survive for a number of year’s post reproductive onset, just with a continued year-upon-year decline in leaf area.
  + Two of the four species that are dominant canopy members late in succession, *Hakea teretifolia* and *Petrophile pulchella*,are the only study species that continued to demonstrate strong investment in leaf area at 30 years of age. The other two canopy species, *Banksia ericifolia* and *Persoonia lanceolata*, have negative investment in leaf area at the oldest site, with many *P. lanceolata* individuals displaying minimal growth.
  + There are two additional understory species that continued to be common within the oldest site, *Leucopogon* and *Epacris*, both members of the heath family (Ericaceae). Although leaf investment for both these species was much lower at the oldest site, many individuals of both species did continue to exhibit positive leaf investment together with high reproductive investment.
* Leaf area is a better predictor of future investment than is total plant weight. Since leaf area represents the plants photosynthetic capacity, this should be no surprise.
  + For many species both are fairly poor, but more or less across the board, leaf area is better
  + This means that is total leaf area is declining with size, plants are on a slow trajectory to death as soon as they begin cannibalizing leaf area to support reproductive investment
* It is widely assumed that large perennial species continue increasing in size throughout their lifetimes. If leaf area is used as the measure of plant size, this is not true for these study species.

- Many authors acknowledge that reproductive investment is an understudied sink contributing to declines in various plant growth measures (i.e. GPP, NPP, leaf area) with age (Ryan *et al.* 1997; Day *et al.* 2001; Tang *et al.* 2014). A growing collection of literature has stand-level carbon-flux data, demonstrating that older stands have declining GPP. Some of the growth-related explanations for this decline, such as hydraulic limitation with increasing height and declining photosynthetic rates with plant age (refs###) are unlikely to be influenced by reproductive investment. Others, including declining leaf area and declining height growth (increasing competition) with age, may be a direct response to increased reproductive allocation (Ryan *et al.* 1997; Becker *et al.* 2000; Genet *et al.* 2010). Only with detailed individual or stand-level data on

# Figure captions.

Figure 1. Investment in increased leaf area versus reproductive output (both on a year basis) for all reproducing individuals within the population. Panel (a) colours the individuals by species and panel (b) colours the individuals by age. Note that leaf investment values are scaled as positive in these plots. See methods for details on the transformation. (*Lizzy: I can also create this figure using the same data as in Figure 2, where the data aren’t scaled – it results in some very odd RA values among individuals with negative leaf investment. Not at all sure about the best approach here.)*

For A. saccharum, age (which varied from 30 to 160 years) was a significantly better predictor of LAI decline than dbh. (Nock *et al.* 2008)

Calculating RA as a proportion of surplus energy makes the implicit assumption that a plant is first investing a proportion of net primary productivity (NPP) to maintain its current size and then divvying the remaining energy into fractions allocated to reproduction versus increased vegetative size.

RyanM.G. WaringR.H.. 1992. Stem maintenance and stand development in a subalpine lodgepole pine forest Ecology

Sala: “Another area of study that has focused on C as a primary driver of productivity is the research that has been done on the mechanisms underlying the well-known age- and size-related growth declines in trees and forests (Ryan et al. 1997). The two classical groups of hypotheses to explain size/age-related declines of growth rates in trees and stands focused on the extent to which growth declines occurred as a result of reduced C supply via photosynthesis (assimilation hypotheses) or an increase of C demand due to increases of the respiratory load (respiration hypotheses; see Sala et al. 2011 for a discussion). However, both of these groups of hypotheses rest on the same assumption: that growth declines are due to limiting C availability. This perspective is now questioned based on current research indicating that alternative factors (e.g., turgor, long-distance transport of assimilates, nutrients) contribute to growth limitations in tall trees (Woodruff et al. 2004, Sala et al. 2011, Woodruff and Meinzer 2011b).”

the decrease of light capture efficiency in mature trees (Niinemets et al. 2005) or the decrease of the turgor pressure limiting cell expansion and reducing the carbon sink of growth (Woodruff et al. 2004). – from Genet

Becker et al. 2000 –shouldn’t assume hydraulic limitations main reason height growth ceases

In adult trees, allocation of photosynthate to flower and seed production has priority over primary and secondary stem growth (Oliver & Larson 1990). - in Becker 2000

On very poor sites, heavy seed production can even eliminate annual ring production (Matthews 1963). – in Becker 2000

“When height growth ceases to offer a competitive

advantage through avoidance of shading, then

(genetically programmed) resource allocation will be

adjusted to enhance tree survival and reproduction,

not necessarily wood production.” Becker 2000

large fruit crops may decrease vegetative growth during both fruiting and non-fruiting years because of energy reserve depletion (Dickson 1991) – in Becker 2000

Declines in leaf area in older trees maybe has been noted by different measurements including increased canopy gap fraction (Quinn & Thomas 2015), decreaing LAI (Nock *et al.* 2008), ###. In addition, older trees have a lower ratio of branch biomass to main stem biomass than do younger trees (Liu, Fox & Xu 2002; Lehtonen *et al.* 2004)

(Sheil *et al.* 2017): So why would growth ultimately decline? …and the proportion of intercepted energy invested in stem growth declines with size (Kaufmann & Ryan [1986](http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12775/full#fec12775-bib-0055); Thomas [2010](http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12775/full#fec12775-bib-0130)).

Plants in low light conditions has lower RA - (Delerue *et al.* 2013)

Reproductive investment can also be summarized by reproductive value (RV) curves that plot total yearly reproductive investment against plant size and show, for most perennial species, that reproductive investment increases with plant size, asymptoting as plant’s age (Weiner *et al.* 2009). RV curves do not however depict the growth-reproduction trade-off, for they consider a plant’s size not vegetative growth.

Overall, if the proportion of NPP going to maintenance costs increases sharply with age or NPP does not keep pace with increases in leaf area and stem architecture, the surplus energy pool may rapidly asymptote – or even decline – impacting growth, reproductive investment, and potentially RA. RV curves suggest that although reproductive investment plateaus with plant size, it rarely declines. In addition to the outcome of the growth-reproduction trade-off this reflects simple allometric constraints for many species: the number of buds initiated is often closely linked with the deployment of leaves. Since flowers to the point of pollination can account for the majority of reproductive investment (refs###), many species reproductive investment will be closely linked to investment in vegetative growth, both maintenance costs and new growth. The increasing maintenance costs and reproductive investment, suggest that the pool of energy available for vegetative growth to increase plant size may be severely curtailed long before a plant approaches its end-of-life.

A few species display declining RA schedules, with a decrease in RA among the oldest plants, interpreted as a mechanism for older plants to survive until their habitat becomes more favourable for high reproductive production and growth (Kohyama 1982; Nakashizuka, Takahashi & Kawaguchi 1997; Ehlers & Olesen 2004).

* PROBABLY NEED A PARAGRAPH LISTING SOME INFORMATION ON WHAT DIFFERENCES WE EXPECT ACROSS SPECIES. RIGHT NOW JUST INCLUDED IN HYPOTHESES
* (Thompson & Stewart 1981) – call RA measure of greatest importance as well
* (Primack 1987)

Becker, P., Meinzer, F.C. & Wullschleger, S.D. (2000) Hydraulic limitation of tree height: a critique. *Functional Ecology*, **14**, 4–11.

Cole, L.C. (1954) The population consequences of life history phenomena. *The Quarterly Review of Biology*, **29**, 103–137.

Day, M.E., Greenwood, M.S. & White, A.S. (2001) Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, **21**, 1195–1204.

Delerue, F., Gonzalez, M., Atlan, A., Pellerin, S. & Augusto, L. (2013) Plasticity of reproductive allocation of a woody species (Ulex europaeus) in response to variation in resource availability. *Annals of Forest Science*, **70**, 219–228.

Drake, J.E., Davis, S.C., Raetz, L.M. & DeLUCIA, E.H. (2011) Mechanisms of age-related changes in forest production: the influence of physiological and successional changes. *Global change biology*.

Ehlers, B.K. & Olesen, J.M. (2004) Flower production in relation to individual plant age and leaf production among different patches of *Corydalis intermedia*. *Plant Ecology formerly `Vegetatio’*, **174**, 71–78.

Genet, H., Bréda, N. & Dufrêne, E. (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, **30**, 177–192.

Gower, S.T., McMurtrie, R.E. & Murty, D. (1996) Aboveground net primary production decline with stand age: potential causes. *Trends in Ecology & Evolution*, **11**, 378–382.

Iwasa, Y. & Cohen, D. (1989) Optimal growth schedule of a perennial plant. *The American Naturalist*, **133**, 480–505.

Kashian, D.M., Turner, M.G. & Romme, W.H. (2005) Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequence. *Ecosystems*, **8**, 48–61.

Katsukawa, Y., Katsukawa, T. & Matsuda, H. (2002) Indeterminate growth is selected by a trade-off between high fecundity and risk avoidance in stochastic environments. *Population Ecology*, **44**, 265–272.

King, D. & Roughgarden, J. (1982) Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theoretical Population Biology*, **22**, 1–16.

Kohyama, T. (1982) Studies on the *Abies* population of Mt. Shimagare II. Reproductive and life history traits. *The Botanical Magazine Tokyo*, **95**, 167–181.

Kozlowski, J. (1992) Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology & Evolution*, **7**, 15–19.

Lehtonen, A.A., Sievänen, R.A., Mäkelä, A.B. & Mäkipää, R.C. (2004) Potential litterfall of Scots pine branches in southern Finland. *Ecological Modelling*, **180**, 305–315.

Liu, W., Fox, J.E.D. & Xu, Z. (2002) Biomass and nutrient accumulation in montane evergreen broad-leaved forest (Lithocarpus xylocarpus type) in Ailao Mountains, SW China. *Forest Ecology and Management*, **1**–**3**, 223–235.

Mäkelä, A. (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science*, **43**, 7–24.

Miller, T.E.X., Tenhumberg, B. & Louda, S.M. (2008) Herbivore‐Mediated Ecological Costs of Reproduction Shape the Life History of an Iteroparous Plant. *The American Naturalist*, **171**, 141–149.

Nakashizuka, T., Takahashi, Y. & Kawaguchi, H. (1997) Production-dependent reproductive allocation of a tall tree species *Quercus serrata*. *Journal of Plant Research*, **110**, 7–13.

Niinemets, U. (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology*, **22**, 515–535.

Nock, C.A., Caspersen, J.P. & Thomas, S.C. (2008) Large ontogenetic declines in intra-crown leaf area index in two temperate deciduous tree species. *Ecology*, **89**, 744–753.

Obeso, J.R. (2002) The costs of reproduction in plants. *New Phytologist*, **155**, 321–348.

Primack, R.B. (1987) Relationships Among Flowers, Fruits, and Seeds. *Annual Review of Ecology and Systematics*, **18**, 409–430.

Pugliese, A. & Kozlowski, J. (1990) Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts. *Evolutionary Ecology*, **4**, 75–89.

Quinn, E.M. & Thomas, S.C. (2015) Age-related Crown Thinning in Tropical Forest Trees. *Biotropica*, **47**, 320–329.

Reekie, E.G., Budge, S. & Baltzer, J.L. (2002) The shape of the trade-off function between reproduction and future performance in *Plantago major* and *Plantago rugelii*. *Canadian Journal of Botany*, **80**, 140–150.

Ryan, M.G., Binkley, D. & Fownes, J. (1997) Age-related decline in forest productivity: Pattern and process. *Advances in Ecological Research*, **27**, 213–262.

Sheil, D., Eastaugh, C.S., Vlam, M., Zuidema, P.A., Groenendijk, P., van der Sleen, P., Jay, A. & Vanclay, J. (2017) Does biomass growth increase in the largest trees? Flaws, fallacies and alternative analyses. *Functional Ecology*, **31**, 568–581.

Tang, J., Luyssaert, S., Richardson, A.D., Kutsch, W. & Janssens, I.A. (2014) Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences*, **111**, 8856–8860.

Thomas, S.C. (2010) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree Physiology*, **30**, 555–573.

Thomas, S.C. (2011) Age-related changes in tree growth and functional biology: the role of reproduction. *Size- and Age-Related Changes in Tree Structure and Function* (eds F.C. Meinzer, B. Lachenbruch & T.E. Dawson), pp. 33–64. Springer Netherlands, Dordrecht.

Thompson, K. & Stewart, A.J.A. (1981) The measurement and meaning of reproductive effort in plants. *The American Naturalist*, **117**, 205–211.

Thornley, J.H.M. (1972) A model to describe the partitioning of photosynthate during vegetative plant growth. *Annals of Botany*, **36**, 419–430.

Weiner, J., Campbell, L.G., Pino, J. & Echarte, L. (2009) The allometry of reproduction within plant populations. *Journal of Ecology*, **97**, 1220–1233.

Wenk, E.H. & Falster, D.S. (2015) Quantifying and understanding reproductive allocation schedules in plants. *Ecology and Evolution*, **5**, 5521–5538.

de Wit, C.T. (1978) *Simulation of Assimilation, Respiration and Transpiration of Crops*. Centre for Agricultural Publishing and Documentation.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. & Foster, R.B. (2005) Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology*, **21**, 307–315.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M. & Zanne, A.E. (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, **91**, 3664–3674.

Young, T.P. (2010) Semelparity and iteroparity. *Nature Education Knowledge*, **3**, 2.

These factors, and others, have been addressed in theoretical models, seeking to understand how the optimal allocation of energy to growth versus reproduction shifts as an individual grows and ages and under what conditions the outcome is indeterminate growth and multiple reproductive events (###).

However, with increasing plant size, the energy expenditure to replace shed leaves and stems, becomes an ever larger proportion of a plant’s total energy budget. While the proportion of *surplus energy* allocated to reproduction may continue to increase throughout a plant’s life, the proportion of its pre-maintenance energy pool may display a different trajectory. A more inclusive calculation of RA presents several potential benefits. First, it presents a more holistic view of energy expenditure to vegetative versus reproductive materials, presenting the possibility that reproductive investment increases as a proportion of total energy investment rather than as a proportion of surplus energy. Phrased alternatively, a plant may be making decisions of energy allocation to reproduction versus vegetative material based on its energy pool prior to replacing shed tissue. This in turn allows for the possible outcome that a plant’s vegetative mass ceases to increase at some size or age, as tissue replacement becomes so high that it consumes the entire energy budget for vegetative tissues. In such instances, the plant should be categorized as displaying determinate growth, yet, contrary to convention, would not have reached its end of life. In more extreme instances, a plant’s reproductive investment may be sufficiently large to leave insufficient energy to replace all shed tissues, leading to a *decrease* in plant size year-upon-year. Decreasing leaf area cannot be a long-term strategy, but may allow a plant to have higher reproductive output for several years at the end of its life. If a plant ceases to increase its vegetative size, RA, calculated as a proportion of *surplus energy* reaches 1 and if a plant’s vegetative size declines, RA exceeds 1. If plants display such growth trajectories, the conventional RA calculation will not accurately depict a plant’s energy allocation decisions.

Yearly leaf replacement