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. Early theoretical explorations of this trade-off suggest an individual’s fitness is 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.

Quantifying the lifetime pattern of relative investment in vegetative versus reproductive tissues is a prerequisite to diverse research questions including parameterizing growth models, modelling global energy sinks, and describing what tissue types are present to consumers and decomposers within an ecosystem. Despite the obvious importance of investment patterns, there are a quite limited number of species for which we know the lifetime energy allocation to 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 the relative investment to different tissue types shifts across species with different functional traits or within individuals as they grow and age.

In both empirical datasets and theoretical work, 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. Calculating RA as a proportion of surplus energy makes the implicit assumption that a plant is first investing energy to maintain its current size and then divvying the remaining energy into fractions allocated to growth versus increased vegetative size.

A lifetime plot of RA, termed a RA schedule, summarizes the growth-reproduction trade-off as a species grows and ages, showing how the outcome of the trade-off shifts with plant size or age. Both modelled and empirical RA schedules vary notably in shape across species, with some species displaying a distinct asymptotic maximum RA value and others continuing to increase gradually in RA until death (Wenk & Falster 2015). 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). 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, 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. 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.

Optimal energy models 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.

For instance, if mortality declines with size or size, 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 (Ryan, Binkley & Fownes 1997; Niinemets 2002; Thomas 2010; Drake *et al.* 2010), 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 investigated 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)

Models have shown that RA is a sound way to illustrate the growth-reproduction trade-off, but they do not consider how the proportion of energy dedicated to tissue replacement versus surplus energy shifts across or within species and how this impacts reproductive investment and in turn RA. Plant traits and plant size (or age) will impact the size of the surplus energy pool, by impacting net primary production (NPP) and tissue replacement costs. Indeed, larger plants face an increasing cost of replacing shed tissues and leaves, on an absolute and often proportional basis, as their ever-larger canopy of leaves and framework of branches shed and need to be replaced. In addition, the observed decline in photosynthetic rates with age (refs###) will decrease NPP relative to leaf area, leading to a relative decrease in the surplus energy pool. Variation in the relative size of the surplus energy pool is also expected across species. For instance, species with short leaf lifespans must invest a larger proportion of NPP in leaf replacement, leaving a relatively smaller pool of surplus energy (refs###).

(Ryan *et al.* 1997) – reasons for declining leaf area with age include crown abrasion in taller trees and competition; has data that show rapid decline, but notes that most other studies display more gradual decline in leaf area; no explicit mention of effect of reproductive investment; pattern not displayed by tropical stands

RyanM.G.WaringR.H.. 1992. Stem maintenance and stand development in a subalpine odgepole 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).”

From Genet 2010 – 1 of 3 explanations for decreasing carbon assimilation with age: decreasing leaf area, assessed at stand (Ryan

et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005,

Leuschner et al. 2006) and tree scales (Nock et al. 2008),

Becker et al. 2000 – suggest shift of resources to reproduction with age is a hypothesis which needs more data; 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

large fruit crops may decrease vegetative

growth during both fruiting and non-fruiting years

because of energy reserve depletion (Dickson 1991) – in Becker 2000

Genet 2010 – growth declines with age; growth declines not offset by increased reproduction – i.e. decline in growth greater than icrease in reproduction

----------- NOT HAPPY WITH TEXT BELOW HERE----------------------

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.

* PROBABLY NEED A PARAGRAPH LISTING SOME INFORMATION ON WHAT DIFFERENCES WE EXPECT ACROSS SPECIES. RIGHT NOW JUST INCLUDED IN HYPOTHESES

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 a given photosynthetic yield translates differently to plant height, leaf area, 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. 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 asymptotes or declines with age.
   2. That reproductive investment will be sufficiently high to impact growth to increase size well before the end of a plant’s life.
2. 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.
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.

# 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.)*

* (Thompson & Stewart 1981) – call RA measure of greatest importance as well
* (Primack 1987)

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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