Big questions:

1. What do we use as our measure of “investment” for RA calculations: just leaf + reproductive investment, or some measure of stem investment?
   1. Following upon this, do we want to try and divide stem growth into “replacement” (sapwood 🡪 heartwood) vs. actual growth. If we ignore stems altogether, RA is of course too high, if we use total stem growth (pretending heartwood equal value to sapwood), RA is too low. It seems that our message will be a lot stronger if we don’t completely ignore stems
   2. Currently no figures that include stem data
2. 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 (Wenk & Falster 2015). For perennial plant species, 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. In contrast, reproductive production directly and immediately increases fitness through seed production. Although 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, most perennial plant species exhibit a more nuanced transition of resources from growth to reproduction and have many years of simultaneous growth and reproduction, an iteroparous life history strategy. Moreover, they display indeterminate growth, continuing to increase in size until death.

This 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 (Wenk & Falster 2015). 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 (###). Declining photosynthetic rates with plant age (###) and relative declines in seed production at higher rates of reproductive investment (###) have also been investigated as factors leading to simultaneous investment in growth and reproduction across multiple growing seasons. 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 (###).

The growth-reproduction trade-off is best quantified as reproductive allocation (RA), the relative proportion of surplus energy that is invested in reproduction (versus growth, storage, and defence) in a given year (or growing season. *Surplus energy* is defined as the energy remaining after shed tissues (leaves, stems) have been replaced. A lifetime plot of RA summarizes the growth-reproduction trade-off as a species grows and ages, indicating that the outcome of the trade-off has shifted. While optimal energy models have indicated a collection of factors that should shift the shape of RA schedules, little empirical work exists to compare RA schedules across species. In particular, species in a community with different life history strategies are expected to have different RA schedules, but no study has compared many co-occurring species.

To this effect we have conducted a study in coastal heathland in eastern Australia, quantifying RA 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, and leaf nitrogen content. These species are also known to be iteroparous. For the members of this community, we ask:

1. Does maximum RA shift across species?
2. Does RA shift with plant size and age within a species?
3. Do species exhibit different RA schedules and do the observed RA schedules correlate with other life history data (lifespan, height, age at first reproduction)?
4. Is reproductive investment sufficiently high to impact growth?

# 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.

# 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)

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

* 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)