The shape of the RA schedule, maximum RA achieved, and age at which the maximum RA was achieved differed across the study species (Fig. 4)

Overall, 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. 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, as they fail to replace all leaves shed during the year.

1. in our species height growth does not stop with age – just tapers

* The vast majority of perennial plants are iteroparous, having multiple reproductive episodes during their lifetime.
* For almost all species height continues to increases throughout life, even though for most species leaf area asymptotes within a few years of reproductive maturity and often declines for several years before an individual’s death.
  + cannibalizing existing leaf area to increase investment in reproduction (to me, an evolutionary, not ecological argument; it is the ratio of leaves:flowers that leads to this)
* In many annual species, a plant reaches its maximum size before the onset of reproduction, then allocating its mass to seed production. The plant may survive for many additional months, as it reproduces. This is not so different from some of the shorter-lived perennial species, where they achieve their maximum leaf area (or nearly reach it), by the time of reproductive maturity. They then enter a prolonged period of reproductive investment, building at most enough leaves to replace shed tissues. For some species, it appears that their continued leaf production is simply the default construction of leaves at flowering nodes, as they have turned their attention solely to reproduction. Individual plants may persist for multiple years in this life stage – and indeed from an evolutionary perspective, a prolonged period of slow decline may be how they achieve sufficient seed output – but they are most certainly not displaying indeterminate growth.
* - Ideally, we would have separated growth in stem tissue into that arising through replacement of lost stem tissue and that arising through an expansion of the conducting tissue.

massmassmassmassmassmassmass

massmassmassmassmassmass

Methods:

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.
2. *why not stems? Hard. This is first cut. If assume pipep model, will reduce RA, but only for values < 1*
3. We focus on the division of mass 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
4. *Define surplus mass as leaf expansion + reproduction.*

# Conclusions

* Unclear if the allocation processes leading to declining leaf area are intentional or the result of allometric constraints.
  + In many species, number of flowers formed is most strongly correlated with total leaf production (replacement + expansion), not surprising since flowers form in the axils of newly formed leaves or as a cluster at the top of near growing shoot. (plot of “ovule\_count” vs “all\_leaf\_inv”)
  + For these species, there is leaf expansion, if, after replacing shed leaves and producing the accompanying number of flowers (and fruit), there is mass remaining for addition leaf growth (and yet more reproduction)
  + Alternatively there is leaf contraction, if there is not sufficient mass to replace all leaves, given the simultaneous expenditure on reproduction.
  + This would be a sensible evolved strategy, with plants rapidly accumulating significant leaf area prior to reproductive maturity, but with the onset of reproduction, species have evolved to produce a number of flowers (per leaf produced) that uses the majority of mass produced, such that there is little leaf expansion. Functional traits, especially leaf turnover rates, fine tune this process, such that different species cease leaf expansion at different times relative to reproductive onset. Traits associated with aging plants that cause productivity to decline, slowly shift the balance in the direction of leaf area loss.
* What about species that do not seem to have reproductive output driven by yearly leaf production?
  + Also, reproductive investment most closely correlated with total plant weight (quite strong correlations), even though total mass production most closely correlated with leaf area

- why plants cannibalising leaf. Actually not that unlike herbs, just over longer time period.

- how wide spread is this?

- growth often considered via stem diameter, likely to miss asymptotic production of leaf

* 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, *H. teretifolia* and *P. 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, *B. ericifolia* and *P.a 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

It is generally assumed that plants first pay the cost of replacement tissues and then divide the remaining, surplus, mass into components including leaf growth and reproduction. For the current collection of plants this was not observed for many individuals, where a plant continued to reproduce robustly, but failed to invest sufficient mass in leaf growth to fully offset shed leaves (Fig. 6). This year-upon-year cannibalism of leaf area, ostensibly to support reproductive output, suggests some mass allocation decisions are independent of actual mass supply. This could be true, for instance, of species where buds form at all leaf nodes on new shoots. The leaf growth would be replacing shed tissue, but so many buds may be initiated in the process that a plant would

Many of the study species show a linear relationship between total leaf investment (replacement and expansion) and reproductive investment once most plants in the population have reached reproductive maturity (Supp Mat). These are primarily species where flowers form in each leaf axil or species where an inflorescence forms at the tip of each growing shoot, both growth patterns where it is expected for total leaf growth and reproductive investment to occur as a pair.

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 mass 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 mass into fractions allocated to reproduction versus increased vegetative size.

(Ryan & Waring 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, Fouts & Hoch 2011 p. 2) 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, Bond & Meinzer 2004; Woodruff, Meinzer & Lachenbruch 2008; Sala & Hoch 2009).”

the decrease of light capture efficiency in mature trees (Niinemets, Sparrow & Cescatti 2005) or the decrease of the turgor pressure limiting cell expansion and reducing the carbon sink of growth (Woodruff et al. 2004). – from (Genet *et al.* 2010)

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 1996). (Becker *et al.* 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 mass reserve depletion (Dickson 1991) – in Becker 2000

Declines in leaf area in older trees have 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 mass invested in stem growth declines with size (Kaufmann & Ryan 1986; Thomas 2010).

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. In these species, it is total

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 mass 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 mass available for vegetative growth to increase plant size may be severely curtailed long before a plant approaches its end-of-life.

These factors, and others, have been addressed in theoretical models, seeking to understand how the optimal allocation of mass 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 mass expenditure to replace shed leaves and stems, becomes an ever larger proportion of a plant’s total mass budget. While the proportion of *surplus mass* allocated to reproduction may continue to increase throughout a plant’s life, the proportion of its pre-maintenance mass pool may display a different trajectory. A more inclusive calculation of RA presents several potential benefits. First, it presents a more holistic view of mass expenditure to vegetative versus reproductive materials, presenting the possibility that reproductive investment increases as a proportion of total mass investment rather than as a proportion of surplus mass. Phrased alternatively, a plant may be making decisions of mass allocation to reproduction versus vegetative material based on its mass 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 mass 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 mass 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 mass* 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 mass allocation decisions.

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)