How much do iteroparous perennials invest in reproduction and is this coordinated with other life-history and functional traits?

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# Abstract

1. While theoretical models predict reproductive allocation (RA) will approach 100% of available energy as a plant ages, available empirical data suggest much lower RA values in perennial plants. In this study we have two aims. First, we assess whether the discrepancy between theory and data arises from methodological differences in how growth and RA are calculated – specifically, we hypothesise RA in real plants is large when compared to growth in leaf, i.e. after excluding stem tissues and leaf turnover. Second, we hypothesise that species with cheap tissues and short lifespans will have higher average RA across their lifespan.

2. We measured investment in leaf, stem and reproductive on individuals from 14 co-occurring woody perennial iteroparous species. A fire chronosequence allowed us to use a space-for-time substitution to estimate RA schedules for each species, simultaneously measuring reproductive and vegetative production on individuals of differing age.

3. For most (11 of 14) species , we found RA eventually reached 100% of available energy, with another 2 showing values 80% . Increases in RA were associated with a decline in growth of leaf area. Comparing species, we found that species with cheap leaves matured earlier and had higher average RA, whereas delayed maturation and lower average RA were associated with greater maximum height.

4. “Synthesis”: After correcting for the cost of leaf replacement, reproductive allocation increases in perennial plants, limiting or even halting leaf area expansion. For some species, so much energy is allocation to reproduction that leaf area declines year-upon-year for multiple growing seasons preceding death.

# Introduction

A fundamental trade-off faced by all organisms is the partitioning of available mass into growth versus reproduction (Cole 1954; Harper & Ogden 1970; Cohen 1976; Kozlowski 1992). In plants, investing in growth increases height and/or leaf area, resulting in greater photosynthetic production and thereby increasing future reproductive value. By contrast, investing in reproduction increases current reproductive value, but potentially at the expense of being outcompeted in the race of for light. A plant’s lifetime strategy for reproductive allocation is thus a key trait linking its organismal function to its life history and population performance (Harper & Ogden 1970; Kozlowski 1992; Obeso 2002; Wright *et al.* 2005; Weiner *et al.* 2009; Wenk & Falster 2015; Salguero-Gómez 2017).

The importance of reproductive allocation for plant population dynamics has been highlighted recently via the compilation of full lifecycle demographic data. Salguero-Gómez *et al.* (2016) found that for 418 plant species ranging from herbs to long-lived trees, the generation time (closely linked to age at first reproduction) emerged as a strong predictor of plant population dynamics. Similarly, in large-scale analyses of plant trait data, traits related to reproductive strategy (i.e. maximum size) emerge as a major axis of variation across the worlds flora (Díaz *et al.* 2016). More generally however, it remains unclear how reproductive strategies should be quantified in cross-species comparisons, or how species differences in reproductive strategy may relate to other physiologcail traits.

In the theoretical evolutionary-ecology literature, the concept of a reproductive allocation (RA) schedule (Fig. 1) has been established for some time, and many factors are now known to influence the evolution of RA schedules in models (review by Kozlowski 1992). RA is the proportion of available mass that is invested in reproduction (versus growth) in a given year (de Wit 1978; Kozlowski 1992). An RA schedule, expressed in relation to plant size or age, then summarizes investment into growth versus reproduction across an individual’s lifetime (see Fig. 1 for examples). .

Theoretical studies have now established that a wide variety of RA schedules – and by implication life-histories – can be selected for, depending on the nature of environment, allocation-related trade-offs, and other organismal traits (reviews by Kozlowski 1992; Thomas 2011). Early theoretical studies suggested an individual’s fitness was always maximized via a bang-bang strategy: a period of first investing solely in growth and then ceasing growth and investing solely in reproduction, until death (Fig. 1a) (Cohen 1976; King & Roughgarden 1982). Bang-bang strategies are favoured both because of the compounding nature of plant growth, and because this strategy is effective under competition (Falster & Westoby 2003). The prediction for a bang-bang outcome, however, clearly does not work for most perennial plants, which – excepting a small number of specialized species (Young 2010; Thomas 2011) – exhibit “graded” or “mixed-allocation” (i.e. an iteroparous) RA strategy, consisting of a gradual shift of resources from growth to reproduction (Fig. 1b). This mismatch between theory and observation led to the discovery of factors promoting graded RA schedules. It is now known that graded responses are favoured under a variety of scenarios, including stochastic, environmental conditions (King & Roughgarden 1982); non-linearities in the response of growth, mortality or reproduction to increased investment (Charnov & Schaffer 1973; Reznick & Endler 1982; Engen & Saether 1994; Miller, Tenhumberg & Louda 2008; Mironchenko & Kozłowski 2014); or declining photosynthetic rates with plant age (Iwasa & Cohen 1989). Moreover, other features of the RA schedule, such as size at first reproduction, respond quantitatively to environmental variables and other traits (Kozlowski 1992).

Compared to the advances in the theoretical literature and in the demographic literature, little is known about actual RA schedules in wild plants. A recent review by Wenk & Falster (2015) suggests complete RA schedules exist for just a few species. Aspects of the RA schedule have been calculated or can be inferred, such as maximum allocation to reproduction, for a greater a number of species but the numbers remain small (< 50 worldwide). A substantially larger body of data exists for simple metrics like age or size at first reproduction, or maximum height (Moles *et al.* 2004; Thomas 2011), but these only provide indirect evidence on how available energy is allocated to reproduction (Wenk & Falster 2015). Of the data for iteroparous species reviewed by Wenk & Falster (2015) and Thomas (2011), maximum RA ranged widely among species, from 0.1-0.7 (fractions of available energy). More generally, perennial plants are regarded as exhibiting indeterminate growth. The implication is that plants continue to invest substantial amounts of energy in growth, even later in life.

The low values of apparent RA observed for many species pose a theoretical challenge because such values are only predicted under extreme environmental conditions. Indeterminate growth schedules, i.e. graded RA schedules where size continues to increase indefinitely (Fig 1c), are favoured by very strong non-linear feedbacks, eg. where investment in reproduction leads to a disproportionate increase in flower/seed abortion, (Miller *et al.* 2008). Otherwise, based on model outcomes, RA is expected to increase towards 1.0 once plants achieve a certain size and especially towards the end of life, even in most of the so-called graded schedules (Fig. 1b) (Kozlowski 1992; Mironchenko & Kozłowski 2014). In other words, theoretically species are predicted to grow little beyond the size at which they reproduce. The mixed allocation between growth and reproduction predicted in many models arises when the productive part of the plant degrades (through tissue turnover) between seasons. When this happens the plant builds new vegetative tissues to regain their size, but once this size is achieved, RA increases to 1.0 (Kozlowski 1992; Mironchenko & Kozłowski 2014). If the costs of tissue replacement are instead paid prior to the allocation decision, a bang-bang strategy is favoured.

Another reason reported RA values may be lower than theoretical studies predict, is that seed weight is often used as a proxy for reproductive investment (see review by Wenk & Falster 2015). However, a wide variety of other tissues are produced in order to make a viable seed, such as flowers, fruits, and pollen. Many embryos are also aborted pre-and post-fertilisation. Past research has shown that such tissues can represent a substantial energetic investment in reproduction, that often goes unaccounted in measurements of RA (Lord & Westoby 2006).

In this paper, we aim to provide the first thorough quantification of RA schedules for multiple coexisting plant species to assess whether i) maximum RA is indeed substantially less than 1.0 for perennial plant species, ii) whether species differ from one another in the type of RA schedule demonstrated, and iii) whether species with high-tissue turnover traits (low leaf mass per area) and shorter maximum height tended to reproduce earlier and more intensely. We hypothesise that for a suite of perennial plants, maximum RA will approach 1.0 when calculated after excluding energy allocated to replace tissues lost through turnover and when considering all reproductive tissues, not just seed. When measuring plant growth, it is common to consider any new tissue appearing on the plant as being “growth”. Yet much of the new leaf and stem tissue generated may be replacing tissues that were lost or shed. We therefore distinguish between growth that is replacement and expansion. Replacement maintains the current productive structure of the plant, whereas expansion increases the productive structure of the plant. In this paper we focus on total leaf mass as the primary measure for the size of the productive structure of the plant.Materials and methods

To address our questions we conducted a study in coastal heathland in eastern Australia, quantifying RA and vegetative maintenance costs for 14 dominant woody perennial species across a range of site ages, using a space-for time substitution The study species are all known to be iteroparous but otherwise differ for a collection of key life history and functional traits, including lifespan, maximum height, specific leaf area and wood density (Table 1). Because we are unable to follow individual plants for an extended period, we sampled individuals across sites differing in time since last fire. By selecting species that only regenerate from seed after fire, we could estimate the ages of the plants in each site. By combining data from multiple individuals of different age, we were then able to infer the shape of the RA schedule exhibited by a typical individual in each species.

## Study system

The study was carried out in Kuring’gai National Park – northeast of Sydney, Australia – in a fire-driven coast heath community (Kodela & Dodson 1988). Fire regimes under traditional aboriginal management are unknown, but current New South Wales National Parks and Wildlife Service (NSW NPWS) management practises seek to achieve an average interval between 7-30 years to maintain the current floristic diversity (NSW Office of the Environment 2006). The community includes perennial species that re-sprout following fire and also obligate seeders, species that are killed by fire and re-establish from seed often at first rain.

We selected 14 obligate-seeder, woody perennials that are common in the community, with asymptotic heights ranging from 0.5 m – 5 m (Table 1). These species all germinate within a year of the fire, and since the fire history of the park is well documented, the age of individuals could be estimated. The family Myrtaceae is well represented in the community, but absent from the study, as all locally common Myrtaceae re-sprout following fire and were therefore unsuitable for our study design. All sites were chosen to have minimal *Eucalyptus* cover, such that *B. ericifolia*, *H. teretifolia*, and *Allocasuarina distyla* (not included in our study because it is dioecious) would be the dominant canopy species late in succession, at heights of 3-5 m.

## Field measurements

To study estimate biomass allocation with respect to age for each species , we used a space-for time substitution, with repeat surveys conducted at a series of sites over the course of a year. The study was conducted between May 2012 - June 2013. Individuals were sampled at different ages across a fire-created chronosequence, from 3 months to 31 years. Site ages were estimated from fire records maintained by NSW National Parks and Wildlife Service. At the conclusion of the study, the approximate ages of the individuals on the six sites were: 1.4, 2.4, 5, 7, 9 and 32 years. Plants were tagged during May-June 2012 and harvested during May-June 2013, with a given individual tagged and harvested within 2 weeks of the same calendar date. Only one species, *P. lanceolata*, displayed any shoot extension during these months. These months are similarly a period of minimal reproductive activity – only *B. ericifolia*, *G. speciosa,* and (occasionally) *H. purpurea* flowered during this period – although a number of species had immature fruit from the previous year (*P. lanceolata*) or small buds that would open in the subsequent year (*B. ledifolia*, *C. ericifolium*, *E. microphylla*, *G. buxifolia*, *L. esquamatus*).

On each plant ,we estimated growth of leaf and stem tissues via a series of structural measurements. Basal stem diameter and overall height were recorded at the beginning and end of the study period. Stem diameter was recorded approximately 10 mm above the base to avoid any basal swelling. A robust shoot was designated as the leader and the number of leaves along the entire length of the leader was measured. For species with a regular pattern of small leaves, the length of stem covered with leaves was measured in lieu of the number of leaves, and a species-level estimate of “leaves per stem length” was applied to convert stem length to a leaf count (see Supplementary materials for details). At the end of the study, the number of leaves remaining along this same shoot length was reassessed to determine the number of the original leaves remaining. At the end of the study period, plants were harvested at ground level and oven dried at 60ºC for at least 1 week. Leaves and stems were separated and weighed.

On each plant ,we estimated investment in reproductive tissues by counting the number flowering parts on all individuals during repeat surveys, conducted every four weeks during cooler months and every three weeks during spring and summer. At each survey, all flowering parts were counted, including buds (by size class), flowers, young fruit (by size class), and mature fruit. For some species the size of immature and mature fruit and cones was also measured, as the final size of the structures was quite variable. The exact flowering parts considered varied considerably by species due to their diverse floral structures. Flowcharts detailing what flower parts were included for each species are provided as in the Supplementary materials (see also Wenk *et al.* 2017).

## Estimating biomass investment and allocation

Using the survey data described above we estimated investment in reproductive tissues, replacement of leaves lost via turnover, investment into leaf expansion, and investment into stem tissues, all on a dry-mass basis. Total reproductive investment was estimated from the survey data as the sum of investment in all the different flowering parts during the year. We applied an accounting algorithm to estimate the number of each part that progressed from one stage to another in the interval between censuses and then used species-level estimates of the weight for each part to estimate the dry-mass cost involved. Further details are given in the Supplementary materials and in an accompanying paper (Wenk *et al.* 2017). The total weight of leaves and stem on each plant was estimated at the beginning and end of the study. At the end of the study we measured the weight directly from dried and harvested material. We then estimated the net change in leaf mass across the study period by fitting a model of weight against age (details below) for all individuals in a species, and applying an appropriate rate of change for each individual. For each individual, the amount of leaf turnover that occurred was estimated from a subsample of leaf-loss taken from a single sub-branch and applied to the entire plant. The fractions of leaves lost on the leader shoot was calculated from the leaf count at the start and end of the study. We then assumed this ratio applied to the entire leaf canopy to determine the total yearly leaf loss. The amount invested in leaf expansion was then estimated as the difference between total leaf growth and leaf replacement. We estimated net stem growth from allometry data on stem diameter combined with actual masses taken during harvest of plants. Reproductive allocation was calculated as the fraction of investment in all reproductive tissues and leaf expansion going to reproductive tissues.

Leaf mass per area was estimated from leaves collected at three shoot ages from each of 3-5 individuals. Leaves were scanned to determine leaf area and then over dried at 60ºC for 48 hours to determine dry leaf mass.

## Statistical analyses

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Based a recent literature review (Wenk & Falster 2015) , we had a strong expectation for RA schedules to start low and increase later during life. To estimate RA schedules, we therefore fit general linear models with a logit link function, as these give the desired logistic shape. To describe patterns of leaf weight and height over time, we required models with a more flexible shape, as patterns of growth were less predictable. We therefore used a generalized additive model (GAM), a semi-parametric modelling approach that makes no assumption about the shape of the relationships, to visualize the relationships between either leaf weight or height with respect to site age. For the smoothed term in the model (age), we allowed four degrees of freedom, which resulted in biologically realistic smoothed relationships. Within the GAM, we used a penalized regression smoother to allow the final degree of smoothness to be estimated from the data (Wood 2006). Inter-specific correlations among traits were calculated using standard pearson correlations. We did not apply phylogenetic corrections to these for two reasons: 1) our purpose is to understand the variation across a set of coexisting species in their present-day ecology, as opposed to tracking the history through which species differences have arisen (Westoby, Leishman & Lord 1995); and 2) while intuitively appealing, supposed phylogenetic `corrections` are imperfect and introduce their own bias (Cooper, Thomas & FitzJohn 2016). All analyses were conducted in R 3.2.4 (R Core Team 2015).

# Results

Overall, plots of plant height versus plant age (estimated from fire records) support our approach of using a space-for time substitution to infer the growth patterns of plants over time, as for all species plant heights are either monotonically increasing or asymptoting with age (See Supplementary materials – Fig. S1). The 14 study species exhibited notable differences in major life history dimensions, with some species disappearing from the community at quite young ages while others were still thriving at the 32-year old site. Species also displayed diverse maturation ages, with three species, *B. ledifolia, H. purpurea,* and *P. linifolia*, flowering within a year of germination and one species, *P. lanceolata,* first flowering at age 7.

Fig. 2 shows patterns of total investment in leaf expansion, leaf replacement and reproductive tissues for the XX individuals in our study against their height. For most species, investment in leaf expansion represented the greatest expenditure at small sizes. At larger sizes, investment in leaf expansion dropped to zero for many species and otherwise declined below leaf replacement and reproductive investment (see points in grey regions in Fig. 2). Total investment in reproductive tissues starts at zero and then, beyond a particular height, increases with plant height.

Supporting our hypothesis, the shape of RA schedules varied enormously depending on which mass pools were considered in the *vegetative* and *reproductive* tissue pools (Fig. 3). The four panels in Fig. 3 plot the fraction of mass allocated to different tissues for individuals in the species *E. microphylla*, using different denominators and estimates of reproductive investment (see Supplementary materials Fig. S2 for other species). Fig. 3a shows the combination of tissues that some previous studies have considered when estimating RA in plants – using seed mass as the only reproductive tissue and including all of stem mass, leaf expansion and leaf replacement in the measure of *vegetative* growth. This combination of variables shows that seed mass represents only a small fraction of the total investment, even later during life (for this species around 5%). In Fig. 3b, we included the accessory costs of reproduction, which increased the reproductive component for this species up almost 40% of available mass. Across all species in this study we found that a large fraction – > 90% – of total reproductive investment went to structures other than seeds (see Wenk et al. 2017 for further analysis). In Fig. 3c, the vegetative investment pool is reduced by removing stem weight. Excluding the stem enabled us to focus on how much the productive part of the plant is growing compared to the reproductive tissues. Lastly, Fig. 3d depicts an RA schedule based on the narrowest definition of vegetative investment, comparing investment in all reproductive tissues against mass invested in expanding leaf area, the formulation used in models. Calculated in this way, maximum RA approaches 1.0 for this species, as hypothesised and suggested by evolutionary models.

Fig. 4 depicts RA schedules for all 14 study species calculated as in Fig. 3d – comparing total reproductive tissues investment with leaf expansion. All but one species (*P. pulchella)* continued to increase RA across their lifespans. Eleven of the fourteen species had a maximum RA of 1, indicating that after paying for replacement costs, surplus mass is invested almost exclusively into reproductive material later during life. Among these, six species achieved an RA of 1 at least two years before dying out, while in the other three RA=1 was only measured among the oldest plants. Across the remaining three species, two reached maximum RA values above 0.8, with only *P. pulchella* having low population level RA values due to many individuals not reproducing in any given year.

Reflecting the high values of RA observed for many species, we found that for most species total leaf area either reached a maximum or even declined at older ages (Fig. 5). By definition, once RA reaches 1, there is no longer any investment in the expansion of leaf area; the productive part of the plant has ceased to grow. All individuals also showed strong investment in leaf expansion in the years preceding reproductive maturity (Fig. 2). In some species – including *G. speciosa, H. purpurea,* and *P. linifolia –* leaf expansion fell close or to zero almost immediately after reproductive maturity; these are species that rapidly reached RA=1 following reproductive maturity (Fig. 4). At the other extreme, some species – including *E. microphylla* and *H. teretifolia –* showed modest declines in leaf expansion investment following the onset of reproduction, but continued to invest in both across many years (Fig. 2). These different investments in leaf expansion are reflected in plots of leaf area against plant age, with species like *E. microphylla and H. teretifolia* continuing to increase their total leaf area with age, while others like *G. speciosa, H. purpurea,* and *P. linifolia* reach a maximum leaf area quite early (Fig. 5). Of note, six species not only reached their maximum leaf area many years before death, but their leaf area gradually declined across multiple years, even though they were still healthy, reproducing individuals (Fig. 5) and did not decline or even increased slightly in plant height (Fig. S2). Ceasing investment in leaf expansion does not indicate these individuals were not producing new leaves. In Fig. 2, the dark green circles indicate yearly investment in leaf replacement – new leaves grown to replace shed leaves. Most individuals invested significant and increasing amounts of mass in leaf replacement with increasing plant size (Fig. 2). However, many individuals, especially the larger, older plants did not invest sufficient mass in leaf replacement to fully compensate for leaf loss, causing leaf area to decline.

Fig. 6 shows how two features of the RA schedules observed across species are correlated with the physiological trait leaf mass per area and a species maximum height. Leaf mass per area provides an indicator of the leaf turnover strategy observed within species (Wright *et al.* 2004). From the RA schedules, we calculated the age at first maturation, and also the average RA across all ages where each species was sampled. As can be seen in Fig. 6, species with lower maximum height and lower leaf mass per area tend to reproduce earlier, and invest – on average – more into reproductive each year. The lower average RA of tall, high leaf-mass-per-area species arises because they emphasis growth for a larger portion of their life.

# Discussion

In this paper we estimated RA schedules for 14 coexisting plant species, including in our calculations investment in diverse accessory tissues and separate terms for leaf replacement and leaf expansion. While easy-to-measure traits such as leaf nitrogen content and wood density now exist for many 1000’s of plant species, estimates of RA are scant because such data are very time consuming to collect . Yet, estimates of RA are needed to improve the modelling of allocation routines within vegetation models, to connect models of physiological function to datasets on demographic outcomes and dynamics, and to test and progress ecological and evolutionary theory.

Here, we found support for the evolutionary expectations that RA should approach 1.0 towards the end of life (Kozlowski 1992). The prevailing view is that RA in perennial plants is low. Our study suggests this perspective arises from a failure to both remove tissue replacement when estimating growth, and to quantify the accessory costs when estimating investment in reproduction. We show that when such adjustments are made, RA increases to more than 80% of available energy for all but one of our plant species. In fact, we found for multiple species RA was effectively greater than 100%, i.e. insufficient energy was allocated to replace leaves and the total leaf area of a plant declined after maturation. In this sense, the iteroparous perennial species included in this study have adopted a reproductive strategy not dissimilar to annuals (Mironchenko & Kozłowski 2014), just stretched over a longer time period. We also found a strong connection between a physiological trait – leaf mass per area – related to the rate of leaf turnover, and species maximum height. Below we consider how these results might generalise to other systems, and their implication for our understanding of plant strategies, individual growth, and modelling of vegetation.

As noted above, models for the evolution of RA schedules mostly predict an increase in RA towards the end of life (Kozlowski 1992; Mironchenko & Kozłowski 2014). This strategy is selected for because older individuals have limited future reproductive value, thus devaluing any investment in further growth. Yet looking across previous studies, few perennials seemed to exhibit this pattern. Here we have shown how different conclusions may be drawn, depending on which tissues are included in the estimate of RA. The evolutionary models on which our predictions are based consider the allocation of energy after any “costs” are paid. For plants, such costs would include stem and leaf respiration and replacing any tissues lost through leaf or stem turnover. Because of difficulties quantifying stem turnover, we calculated RA by comparing reproductive investment to investment in leaf growth. Calculated in this way, all but one of our species approach RA of close to or greater than 1 towards the end of life.

Considered as fraction of total productivity, the maximum amount of energy allocated to reproduction is much lower, e.g. between 20-50% of available energy (Fig. S2). These results concur with estimates obtained elsewhere (reveiws by Thomas 2011; Wenk & Falster 2015). A substantial amount of growth each year is allocated to replacing leaves lost through turnover and producing stem tissue (Fig. 2). We were unable to partition stem tissue into the amount that is replacement and the amount that is expansion, but as a first approximation we can assume a reasonable amount goes toward replacement, as vessels become exhausted. We are not the first to note that the costs of tissue turnover are high, especially for older plants (Givnish 1995), although quantifying such costs remains challenging.

Demographic data for plants has long ago established that shorter-live species invest more heavily in reproduction and begin reproducing at an earlier age. These data verify this trend using energy, not seed output, as the currency. They also demonstrate the growth cost to the plant inflicted by this investment in reproduction, as exemplified by the high average RA values exhibited by shorter-lived, shorter-statured species (Fig 6). For many, but not all, of these early reproducing, high RA species, high leaf replacement costs consume such a large fraction of total annual biomass production, that within a short period of reproductive maturity, all surplus energy is allocated to reproduction, rapidly driving RA to 1 or higher. Being able to link RA schedules, in combination with leaf replacement costs, to life history and function traits, emphasizes the importance of these measurements in understanding a plant’s growth-reproduction trade-off.

It is also worth noting, that while the amount of leaf mass peaked for most species, and then was either maintained or declined, individual height continued to increase with age for most species (Fig. S1). This behaviour may reflect one of two processes. First, continued height growth may be driven indirectly via leaf replacement: even if the leaf area of the plant is not expanding, the creation of new leaves to replace old leaves at the stem tip extends the shoot upwards. Alternatively, continued height growth may be directly favoured to prevent the plant from being overtopped by competitors. Either way, the leaf area of our plants becomes somewhat decoupled from its height at larger sizes. Similarly, stem diameter continues to increase with age, as heartwood is accumulated inside the stem (Mäkelä 1997), even if the productive amount of leaf area is no longer expanding. At the same time, we can assume that if the energy invested in reproduction were instead allocated to growth, the growth rate of stem diameter and plant height would be substantially higher. Supporting this proposition, past research has shown that reproductive allocation does indeed slow height growth (Thomas 2011).

The question arises of whether our results will generalise to other perennial species, or whether the RA strategies observed are unique to our study ecosystem? We believe our core finding – that RA values increase towards 1 for most species – will not be a particular feature of these species, but rather will be repeatable in other vegetation if similar methods are used to calculate RA. Calculating reproductive investment based on seed production only is likely to vastly underestimate RA, while including tissue replacement is likely to make growth seem larger than it really is. Additionally, we consider that the relationship between RA schedules and maximum height will generalise to other sites, as a species maximum height should be strongly constrained by its RA (Thomas 2011 p. 201; Gibert *et al.* 2016). The link between RA and the leaf trait leaf mass per area may also appear elsewhere, as generally leaf mass per area is associated with high turnover growth strategies and short lifespans (Adler *et al.* 2014).

Assuming our results do generalise to other species, the growth strategy of many perennial species may be summarised as follows: after a period investing primarily in growth, plants gradually switch to investing in reproduction. Species vary in the pace of this transition, but most eventually increase RA to 100% of available energy, while also spending enough on leaf replacement to maintain the size of the productive part of the plant (leaf area). For some species, however, the emphasis on reproduction may be so large that total leaf area declines slowly over time. Meanwhile, diameter and height continue to increase slowly, because of the accumulation of heartwood and gradual elongation of stems. Of the energy allocated to reproduction, a large portion is spent on accessory tissues.

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# Authors’ contributions

DSF and EHW conceived the idea; EHW collected the data; all authors analysed the data; EHW and DSF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

# Data accessibility

The code and replicating this analysis (and all figures) is available at https://github.com/traitecoevo/reproductive\_allocation\_kuringgai and is also archived in the repository figshare.com (doi: will be added at proof stage).

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# Figures and tables

**Table 1**: Details on study species and their physiological and life-history traits. Lifespan is the approximate age at which each species disappears from the community. 40 years is indicated as the maximum age of climax species, due to the high probability these individuals are killed by fire by this age. Age at maturity is the site age at which the majority of individuals of a species begin reproducing. Embryo-endosperm weight, Leaf mass per area, and wood density are all measured on a collection of other individuals at nearby locations. Maximum height is the height of the tallest individual in this study.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Family** | **Spp.** | **Lifespan (years)** | **Age at maturation (years)** | **Embryo + endosperm weight (mg)** | **Maximum height (mm)** | **Leaf mass per area ()** | **Wood density ()** |
| *Banksia ericifolia* | Proteaceae | BAER | 30+ | 7 | 24.06 | 2790 | 0.0224 | 0.59 |
| *Boronia ledifolia* | Rutaceae | BOLE | 9 | 1.4 | 2.1 | 770 | 0.0159 | 0.86 |
| *Conospermum ericifolium* | Proteaceae | COER | 12 | 2.4 | 0.69 | 990 | 0.0206 | 0.79 |
| *Epacris microphylla* | Ericaceae | EPMI | 30+ | 2.4 | 0.02 | 1370 | 0.0122 | 0.73 |
| *Grevillea buxifolia* | Proteaceae | GRBU | 30 | 5 | 26.7 | 1365 | 0.0146 | 0.73 |
| *Grevillea speciosa* | Proteaceae | GRSP | 20 | 2.4 | 13.48 | 1000 | 0.0169 | 0.74 |
| *Hakea teretifolia* | Proteaceae | HATE | 30+ | 7 | 8.18 | 3005 | 0.0516 | 0.57 |
| *Hemigenia purpurea* | Lamiaceae | HEPU | 20 | 1.4 | 0.3 | 703 | 0.0205 | 0.83 |
| *Leucopogon esquamatus* | Ericaceae | LEES | 30+ | 2.4 | 0.81 | 985 | 0.0129 | 0.79 |
| *Persoonia lanceolata* | Proteaceae | PELA | 30+ | 9 | 14.39 | 2140 | 0.0203 | 0.67 |
| *Petrophile pulchella* | Proteaceae | PEPU | 30+ | 7 | 2.21 | 2010 | 0.0297 | 0.66 |
| *Phyllota phylicoides* | Fabaceae | PHPH | 30 | 2.4 | 1.71 | 1630 | 0.0174 | 0.85 |
| *Pimelea linifolia* | Thymelaeaceae | PILI | 7 | 1.4 | 0.72 | 542 | 0.0086 | 0.84 |
| *Pultenaea tuberculata* | Fabaceae | PUTU | 30 | 2.4 | 1.27 | 1420 | 0.0101 | 0.89 |

**Figure 1:** Possible reproductive allocation schedules. Panels show a) a big-bang strategy; b) a graded strategy that eventually reaches full allocation to reproduction; c) a graded strategy where growth continues indefinitely. Adapted from Wenk & Falster (2015).

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**Figure 2:** Annual investment in reproduction, leaf replacement and leaf expansion for individuals from 14 study species. Species are shown in order from top to bottom based on their age at maturation (Table 1). Points show investment into different. The black lines indicate the increase in leaf replacement that would be needed for a plant to replace all of it’s lost leaf area. Note the log-scaling of x and y axes. On the y axis we have also shown in grey, locations where investment was recoded as zero for a given tissue. These values do not naturally display on a log scale and so are shown in a separated region.

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**Figure 3:** Including different biomass pools has strong effects on estimates of reproductive allocation. Panels show estimates for a single species (*Epacris microphylla*, see Fig. S2 for other species), but considering different energy pools: a) All vegetative materials, both new tissue investment and investment to replace shed tissues, are included in the vegetative components, while seed weight is used as a proxy for reproductive investment; b) All vegetative materials are included in the vegetative components and all tissues associated with reproduction (seed + accessory costs) are included in the reproductive investment pool; c) Investment in leaves to increase leaf mass and replacement of shed tissues is included in the vegetative component and all tissues associated with reproduction (seed + accessory costs) are included in the reproductive investment pool; d) Just investment in leaves to increase leaf mass is included in the vegetative component and all tissues associated with reproduction (seed + accessory costs) are included in the reproductive investment pool. The x-axis is log-scaled because most change occurs within the first few years.

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**Figure 4:** Estimated reproductive allocation schedules for the 14 study species. Species are sorted from top to bottom based on their age at maturation (Table 1). , with colours indicating site age. Fitted lines are logistic curves, with r2 value indicating the amount of variance explained.

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**Figure 5****.** Standing leaf biomass plateaus and even declines with increasing plant age. Species are sorted from top to bottom based on their Age at maturation (Table 1). The points indicate data points for the individual plants assessed, with colours indicating site age. Fitted lines are generalised additive models, with r2 value indicating the amount of variance explained.

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**Figure 6.** Coordination between maximum height, leaf mass per area and two summary features of the reproductive allocation schedules for each species: age at maturation and average RA. Each point is a species. Insets show amount of variance explained using standard pearson correlation.

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# Supporting information

**Figure S1:** Plots of plant height against estimated site age for the 14 study species. Species are sorted from top to bottom based on their Age at maturation (Table 1). The points indicate data points for the individual plants assessed, with colours indicating site age. Fitted lines are generalised additive models, with r2 value indicating the amount of variance explained.

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**Figure S2:** As in Fig. 3 but showing data for all 14 study species.

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