Chapter 2
Age-Related Changes in Tree Growth and Functional Biology: The Role of Reproduction

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Abstract Population biologists have generally assumed that reproduction entails a reduction in growth, future reproduction, and/or increase in mortality: such "costs of reproduction" are central to life-history models that predict patterns of reproductive allocation, growth curves, and other aspects of plant ontogeny. However, the apparent importance of biophysical processes (such as hydraulic limitation effects) has led to a widespread view that physiological effects of reproduction play a minor role, if any, in driving age-related patterns of tree growth and functional traits. This chapter assesses available data to detect and measure the role of reproduction on tree functional biology, where possible by use of meta-analysis to integrate results across studies. Trees generally show a long period of pre-reproductive growth, and a pattern of increasing reproductive allocation with size, as predicted by life-history theory. The widespread existence of substantial physiological costs of reproduction in trees is indicated by several sources of comparative data. (1) Reproductive allocation generally increases with tree size, and recent studies suggest that >40% of fixed carbon may be allocated annually to reproductive structures in mature forests. (2) There are ~100 species of monocarpic trees in which rapid senescence is triggered by a single reproductive event. (3) Dendrochronological studies comparing stem growth increment to measures of fruit production across years, generally find negative correlations, even when statistically accounting for environmental effects such as growing season temperature and precipitation. These studies also document carry-over effects, in which intense reproductive events reduce tree performance over multiple years. (4) Shoots near reproductive structures generally show reduced shoot extension growth, leaf size, and leaf N content, among other changes. There is also some evidence that leaf traits related to carbon gain (such as leaf size, photosynthetic capacity and leaf N) increase with size among small pre-reproductive trees,

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but decrease following reproduction. (5) Studies of sexual dimorphism in dioecious tree species generally find patterns consistent with a higher cost of reproductive in female (pistillate) individuals, which show reduced growth. Analyses of growth curves of some dioecious tree species also indicate sexual dimorphism in patterns of growth decline late in tree ontogeny, consistent with a strong role of reproduction in determining the form of growth declines. In conclusion, reproduction cannot be dismissed as of only minor importance as a determinant of age-related trends in tree functional biology. The physiological mechanisms for reproductive effects, their comparative biology, and their interactions with other processes that limit growth deserve much greater research attention.

1 Introduction

Trees are remarkable organisms in many respects, their size, longevity, and strong interactions with global biogeochemistry being some of the traits in which trees reign superlative among extant life forms. A less commonly noted but equally remarkable aspect of tree biology is their prolonged and often prolific reproductive output. With few exceptions, trees show an initial juvenile period in which no reproductive structures are produced, followed by an adult phase lasting decades to centuries characterized by periodic bouts of reproduction that continue throughout the tree's lifespan (Harper and White 1974). The reproductive output of trees is commonly a central driver of community processes in forest ecosystems. For example, mast fruiting patterns in the forests of Southeast Asia and parts of the temperate zone largely determine population dynamics of regenerating seedlings, of organisms that depend on seeds as resources, and through trophic cascades have large impacts on many organisms within the ecosystem (e.g., Ostfield et al. 1996; Jones et al. 1998; Curran and Leighton 2000). Historically, the capacity of forests to produce acorns and beech mast (used for pannage, the fattening of domesticated pigs in forests), was the main "ecosystem function" by which the forests of Europe were valued (Shaw 1940; Rackham 1980; Birrell 1987).

A pronounced dichotomy exists in the literature on age-related changes in tree growth and physiology as it relates to reproduction. On the one hand, there is a well-developed literature focused on life-history strategies as a basis for predicting patterns of reproductive and growth dynamics of trees and other perennial plants (e.g., Kozlowski and Uchmanski 1987; Iwasa and Cohen 1989; Clark 1991; Thomas 1996a; Iwasa 2000; Zhang 2006). A fundamental assumption in essentially all of this work is that there are "costs" of reproduction that result in tradeoffs between tree growth and reproductive output (Obeso 2002). This literature has generally not explicitly considered biophysical limitations to tree growth (but see Mäkelä 1985). In contrast, much of the recent ecophysiological literature examining "age-related" patterns of growth and physiology has tacitly assumed that biophysical processes such as water transport are the primary causal agents of growth and physiological patterns, and has ignored, downplayed or dismissed reproductive "costs" as playing any important role (e.g., Gower et al. 1996; Ryan et al. 1997; Bond 2000; Bond et al. 2007; Kutsch et al. 2009).

There are some strong arguments, both theoretical and empirical, that both reproductive "cost" effects and biophysical limitations may be of importance in driving age-related patterns of tree growth and physiology, but also that the relative importance of these factors varies among species and with environmental conditions. Weiner and Thomas (2001) compared efforts to identify "the" physiological basis for limitations of tree size to efforts in prior decades to identify the (sole) limit to population growth in populations of organisms. Through much of the early history of population ecology it was assumed that there must be some main factor that acted to limit population carrying capacity, with proponents of differing camps arguing, for example, that density-dependent competition, predation, or abiotic factors were most likely to be that single limiting factor (Andrewartha and Birch 1954). This historical debate in the literature was ultimately settled by the realization that different factors were clearly of central importance in different populations of organisms.

An important theoretical argument related to constraints on tree growth is the hypothesis that selection should act such that multiple limiting factors generally will occur (Bloom et al. 1985). In contrast to the assumption codified as "Liebig's Law of the Minimum", if plant growth is under positive selection pressure, then selection will act to favor phenotypes that are less limited by that particular resource. If another resource then becomes limiting, selection will similarly act to reduce limitations of that resource, with the ultimate result being that plants are equally co-limited by a set of resources. The original hypothesis of Bloom et al. has been critiqued from a variety of perspectives: in particular, access to or uptake of different resources may be interdependent (Gleeson and Tilman 1992), and the assumption that one resource may be "bought" by another resource in excess may not hold (Bazzaz et al. 1987). However, there is empirical evidence that co-limitation of plant growth by at least two resources (though often with one dominant limitation) is common (Chapin et al. 1987; Elser et al. 2007). Studies of mature trees and forests, mainly focused on nutrient limitation, have likewise commonly found co-limitation (e.g., Tanner et al. 1998; Gradowski and Thomas 2006, 2008; Paoli and Curran 2007; Vadeboncoeur 2010). Reproductive costs are similar to other limitations of plant growth in that selection should act to reduce their costs, thus potentially enhancing the importance of other limiting factors. However, the selection scenario articulated by Bloom et al. (1985) should ultimately act through reproductive fitness rather than growth, since growth in an evolutionary context is the means by which an organism can achieve reproductive success. Thus, evolutionary theory predicts that multiple resources should constrain tree growth early in ontogeny, but that effects of reproductive allocation should become increasingly important as trees age. A single causal agent for age-related declines in growth or for associated changes in physiological processes is very unlikely from this perspective.

The main objective of this review is to examine the empirical evidence for costs of reproduction in trees, where possible using meta-analyses of data from published studies. I start with a short overview of the salient aspects of life-history theory as applied to trees, and of empirical data on patterns of size-dependent reproduction in trees. I then review comparative studies on monocarpic trees, as these species constitute a special case where reproduction is apparently closely linked to rapid senescence. I then consider (1) dendrochronological studies in which tree ring series have been related to long-term data on reproductive output, (2) studies of canopy growth in which patterns of shoot extension and physiology have been related to production of reproductive structures on tree shoots or branches, and (3) studies of dioecious tree species that have compared growth patterns and functional biology of male (staminate) and female (pistillate) individuals. Finally, I summarize the ensemble of results of different approaches to evaluating reproductive effects on age-related patterns of tree growth and physiology, and suggest important avenues for future work.

2 Life History Theory and Tree Reproduction: An Overview

Life-history theory as applied to patterns of age-related growth and reproduction generally starts with an assumption of a “principle of allocation” (Levins 1968): specifically, that resources are finite, and that resources allocated to reproduction must have some commensurate negative consequence to growth processes. An important distinction has also generally been made between “reproductive allocation” and “reproductive effort”. Reproductive allocation is the “proportion of the total resource supply devoted to reproductive structures” (Bazzaz et al. 2000). Reproductive effort is a more holistic concept of the total resources diverted from vegetative growth as a consequence of reproduction. From evolutionary first principles, there is an expectation that reproduction must entail some fitness cost (i.e., to future growth, survivorship, or reproduction): an organism that has “free” reproduction will be selected to increase reproduction to a point where there is at least some cost. There is also an expectation that reproductive effort generally will exceed reproductive allocation, since there are physiological costs in the development of any tissues above and beyond those represented by carbon, nutrients, and energy in the tissues themselves. These costs (sometimes labeled “somatic costs of reproduction”: Bazzaz et al. 2000; Obeso 2002) may include energetic construction costs, costs associated with transport of metabolites, and “opportunity costs” of meristem allocation and storage prior to allocation.

A useful starting point for theoretical analyses to predict age-related patterns of growth and reproduction is annual semelparous plants (Cohen 1968, 1976). In cases where there is a predictable termination of the life cycle (e.g., the end of the growing season), the optimal strategy for reproductive investment is generally a “bang-bang” strategy: all resources are invested in somatic growth, and then there is a complete shift to complete resource allocation to reproduction. This strategy is an evolutionary stable strategy in a game-theoretical context: a population of phenotypes with a “graded” reproductive investment pattern will be invaded by a phenotype with a “bang-bang” strategy. However, in the case where there is uncertainty in the termination of the life cycle (e.g., a stochastic growing season), graded reproductive investment is favored (King and Roughgarden 1982). In all cases the optimal strategy involves a pattern of increasing reproductive allocation with age (and size).

The generalization of life-history models to consider long-lived perennials, such as trees, has been based on treating reproductive allocation as a series of allocation decisions made over sequential growing seasons (Kozlowski and Uchmanski 1987; Iwasa and Cohen 1989; Iwasa 2000). Within each growing season allocation strategies follow a similar logic to that of an annual plant: resources initially captured are initially allocated to somatic structures, and then increasingly to reproductive structures. This pattern is predicted to occur both within each growing season, and through ontogeny. There is strong empirical evidence that increases in reproductive effort with age are, with very few exceptions, the rule in animals (Roff 1992). Increases in the costs of reproduction though plant ontogeny have also been found in several herbaceous plants (Reekie and Bazzaz 1992; Worley and Harder 1996; Hemborg and Karlsson 1998), but no consistent size or developmental trends were found in several other studies (Obeso 2002; Cheplick 2005). The relevant empirical data for woody perennial plants appear not to have been synthesized.

3 Size at Onset of Maturity

One basic but important prediction of the life-history theories outlined above is that trees should show a prolonged juvenile period, particularly in environments where early allocation to reproduction would come at high cost to future growth and reproduction. While a long juvenile period of trees has been casually noted by generations of plant biologists (Harper and White 1974), quantitative analyses have been surprisingly limited. An empirical challenge has been the lack of long-term data on reproductive status, since the most direct method for assessing age- and size-dependent reproductive status would be to follow cohorts of trees through time. Although notes on age at first reproduction are commonly made of trees grown in arboreta or in breeding trials (and are the usual basis for age to reproduction given in silvics manuals and similar sources), quantitative analyses for natural tree populations are very scant.

If trees consistently reproduce (or can be recognized as reproductive) following reproductive onset, then a function describing the probability of reproduction as a function of size (or age) in a given reproductive episode will correspond to the cumulative distribution function of size (or age) at first reproduction (Thomas 1996b). This property allows the distribution of size at reproductive onset to be estimated using static data. Analyses using this approach indicate great variation among species and between forests in reproductive size thresholds (Thomas 1996b; Davies and Ashton 1999; Wright et al. 2005). The relative size at onset of maturity (RSOM) may be quantified as the ratio of height at onset of maturity to maximum (asymptotic) height (Thomas 1996b). RSOM also shows high variation among tree species, with reported values ranging from ~0.2 to 0.8. (Thomas 1996b, 2010; Davies and Asthon 1999; Wright et al. 2005). Comparative analyses have examined variation in size at onset of maturity in terms of variation among species, ecological groups, and forests. One consistent pattern is that trees that attain a large stature (i.e., have a large asymptotic maximum height) are larger at onset of maturity either

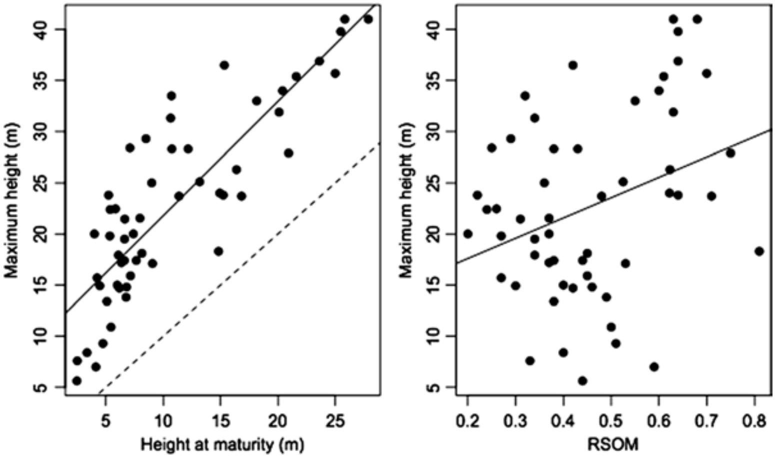

Fig. 2.1 Relationship between tree height at maturity and asymptotic height among 54 tree species, compiling data across studies (mainly of tropical tree species: Thomas 1996b, 2010; Davies and Asthon 1999; Wright et al. 2005). Least-squares linear regression lines are shown as *solid lines*; the *dotted line* indicates a 1:1 relationship for maximum height and height at maturity. Correlations are significant in both cases (absolute height at maturity: $r=0.847$; $P<0.001$; RSOM: $r=0.330$; $P=0.015$)

in absolute or relative terms (Thomas 1996b; Wright et al. 2005). One may also view this pattern in terms of maximum size as the dependent variable: tree species that show a smaller size at onset of maturity (expressed either in absolute terms or as RSOM) reach a smaller maximal height (Fig. 2.1). This pattern is consistent with a systematic cost of reproduction such that early reproduction limits maximum tree size; however, the correlation is relatively weak (r = 0.330).

4 Size-Dependence of Reproductive Allocation and Effort

Predictions of life-history theory are generally that reproductive allocation should increase with age and size in iteroparous organisms (Williams 1966; Kozlowski and Uchmanski 1987; Iwasa and Cohen 1989). Although it is possible to construct models that predict declines in reproductive allocation with age, scenarios in which this occurs are considered biologically unrealistic (Roff 1992). The size-dependence of reproductive allocation is generally most informatively analyzed using allometric methods (Weiner 1988; Weiner et al. 2009; Cheplick 2005). An allometric relationship between reproductive and somatic biomass with a slope >1 would indicate a pattern of increasing reproductive allocation with size. Data most typically are available for numbers or biomass of reproductive structures as a function of stem diameter. If one assumes tree biomass (M) scales with stem diameter (D) as $M=D^{8/3}$, then life-history theory would correspondingly predict an exponent of $\alpha > 8/3$ for an allometric relationship between reproductive biomass (R) and stem diameter (i.e., $R = D^{\alpha}$) (Thomas 1996a).

Although more information is available for herbaceous plant species (Weiner et al. 2009) – in particular for lifetime reproduction – a number of studies have presented data on reproductive allometry of crop sizes per reproductive event in natural populations of trees. Reported relationships are quite variable, and there is often very high variability among individuals in reproductive output, necessitating large sample sizes to reveal allometric patterns. Several studies have reported values of $\alpha \sim 2$ (Studies reporting exponents in the range of 1.7–2.2 include: Peters et al. 1988; Niklas 1993; Hirayama et al. 2004), and this value has been widely assumed in forest simulation models (Pacala et al. 1993), and in analyses of propagule dispersal kernels (Ribbens et al. 1994; Caspersen and Saprunoff 2005; Muller-Landau et al. 2008). In contrast, several studies of tropical tree species have estimated much higher exponent values: Alvarez-Buylla and Martinez-Ramos (1992) report $\alpha = 3.3$ for the neotropical pioneer *Cecropia obtusifolia*, and Thomas (1996a) found an average $\alpha = 5.3$ among 32 species of sub-canopy tree species in Malaysia. It is possible that the large variability in allometric slopes among studies may be driven by differences in size-dependence access to resources. In particular, vertical gradients in light availability may greatly enhance size-dependence of reproduction in sub-canopy tree species.

In addition to showing greater reproductive output within any given reproductive event, larger trees generally reproduce more frequently than smaller trees. Many studies have documented this pattern in a wide range of species and ecosystems, with examples ranging from Malaysian sub-canopy trees (Thomas and LaFrankie 1993) to tropical alpine dwarf trees (Kudo and Suzuki 2004). Among forest canopy trees positive relationships between size and reproductive frequency have been documented for *Nyssa sylvatica* in New Jersey USA (Cipollini and Stiles 1991), *Bischofia javanica* in the Bonin Islands of Japan (Yamashita and Abe 2002), *Shorea acuminata* in Malaysia (Naito et al. 2008), and *Chrysophyllum lucentifolium* (Sapotaceae) in Brazil (Fonseca et al. 2009). Where analyses have been conducted, size-dependent increases in reproductive frequency have been found to be independent of effects of canopy position or crown illumination (Cipollini and Stiles 1991; Fonseca et al. 2009).

Although most studies have described monotonic increases in reproduction with tree size, apparent decreases in total crop sizes of reproductive structures among very large trees have also been reported. Such a decrease might be expected if declines in net carbon fixation and/or meristem production are not compensated for by increases in reproductive allocation. However, it does not appear that any formal statistical analysis documenting a "hump-shaped" relationship between tree size and reproductive output has been presented (e.g., Greene and Johnson 1994; Gullison et al. 1996; Kainer et al. 2006; Naito et al. 2008), and patterns interpreted as decreases may simply represent increased variability with tree size, as is obvious in many data sets (e.g., Gullison et al. 1996; Kainer et al. 2006). Perhaps the most convincing data showing systematic decreases in reproductive output with tree size has been presented for *Aquilaria* spp. (Thymeleaceae) (Soehartono and Newton 2001), however again there is no formal statistical test. Increased variability in reproductive output among individuals with increasing tree age size in some cases is clearly related to biotic interactions. For example, Kainer et al. (2006) describe large increases in average liana load with tree size in *Bertholletia excelsa* (Lecythidaceae), and negative effects of lianas on reproduction; however, very large (>100 cm dbh) trees with low liana loads showed the highest reproductive output.

There are several reasons why simple allometric analyses of crop sizes do not give an adequate picture of reproductive allocation patterns through tree ontogeny. First, much of the "biomass" of large trees can consist of non-living heartwood tissue. In addition, very large trees of many species show pronounced crown thinning and loss of branches (e.g., Nock et al. 2008), such that stem diameter may not estimate biomass accurately. Plants may be considered as a population of modules (reiterated morphological units, such as a leaf with subtending shoot: Watkinson and White 1985), providing an alternative basis for quantifying size-dependent patterns of reproductive allocation in plants. Studies that have followed this approach have consistently found a pattern of increasing allocation of meristems to reproductive structures with increasing size or age in woody plants (Acosta et al. 1997; Lopez et al. 2001).

Theoretical studies of life history evolution have generally treated reproductive allocation as the total resources invested in reproduction, which corresponds to reproductive effort rather than allocation per se (Bazzaz et al. 2000). The size- and/or age-dependence of reproductive effort in trees, as distinct from reproductive allocation, has received little explicit attention in either theoretical or empirical studies. Reproductive costs other than direct resource investment in reproductive structures should include physiological costs associated with the transport of carbon and nutrients, construction respiration costs, and physiological costs associated with maintenance of turgor during the development of reproductive structures. A similar set of biophysical constraints that pertain to development and physiological function of leaves in tall tree canopies, such as effects of hydraulic path length effects, should pertain to reproductive structures as well. There is thus a strong basis to expect that the non-allocation fraction of reproductive effort (somatic cost of reproduction) should increase with tree size. This reasoning suggests that reproductive effort actually shows stronger increases with tree size than suggested by studies to date based on either allometric or module-based analyses.

4.1 Direct Assessments of Size-Dependent Carbon Partitioning

What is the proportion of carbon fixation allocated (or "partitioned" *sensu* Litton et al. 2007) to reproductive structures, and how does this change with tree size and age? Early studies suggested that this fraction was generally quite low (e.g., <15%: Linder and Troeng 1981; Dick et al. 1990a, b), supporting a conclusion that reproductive allocation was unlikely to be an important determinant of age-related growth declines (Ryan et al. 1997). The allometric data cited above do not give sufficient information to evaluate carbon partitioning, as the amount of carbon fixed and allocated to growth of other tissues (or to storage) has not generally been quantified. While relevant studies are scarce, Hirayama et al. (2008) present data showing increasing biomass allocation to reproduction with tree size in three species of Japanese *Quercus* ($P < 0.01$; linear model analysis of data for mast fruiting year presented in their Table 2.1), with annual biomass allocation to reproduction of the largest trees sampled in each species estimated at 32–79% during a mast year. In another recent study Genet et al. (2010) provide estimates based on a chronosequence of *Fagus sylvatica* stands, with assessments of woody tissues growth, and non-structural carbohydrates in addition to reproductive structures. The proportion of annual fixed carbon in reproductive structures increased from ~5% or less in stands <25 years in age, to ~40% in stands >120 years. There is thus recent evidence that carbon allocation to reproduction increases substantially with tree size/age, and is, at least episodically, much higher than previously suggested.

5 Moncarpic Trees

Plants that show a single bout of reproduction shortly followed by senescence and death are termed monocarpic[1]. It has been incorrectly reported in recent papers (Poorter et al. 2005; Read et al. 2006) that there are only four genera and ~30 species of monocarpic trees known, but this is a serious underestimate. There are at least six arborescent palm genera that include strictly monocarpic species (Dransfield et al. 2008a): *Arenga* (20 species, all hapaxanthic, 4 monocarpic), *Caryota* (13 species, all hapaxanthic, 10 monocarpic), *Corypha* (6 species, all monocarpic), *Metroxylon* (6 of 7 species hapaxanthic, 5 monocarpic), *Wallichia* (10 species, all hapaxanthic, 1 monocarpic), *Raphia* (20 species, all hapaxanthic, roughly 1/3 monocarpic), and *Tahina* (monotypic), the last discovered in Madagascar in 2007 (Dransfield et al. 2008b). In addition, two other arborescent palm genera show a hapaxanthic but not strictly monocarpic habit: *Eugeissona* (6 species), and *Nannorrhops* (monotypic). Among dicotyledonous trees, monocarpy has been noted in *Cerberiopsis* (Apocynaceae: 1 of 3 species monocarpic) (Read et al. 2006, 2008), *Spathelia* (Rutaceae: ~15 species, at least 2 monocarpic) (Rodrigues 1962; Groppo et al. 2008), and *Tachigali* (Leguminosae: Caesalopiniodeae; ~20 species, mostly monocarpic) (Foster 1977; Poorter et al. 2005). The large tropical genera

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[1] Trees in which individual stems die following reproduction are termed hapaxanthic; in the case of palms that form stem clusters many groups are hapaxanthic, but only species showing a single-stemmed habit are strictly monocarpic (Dransfield et al. 2008a).

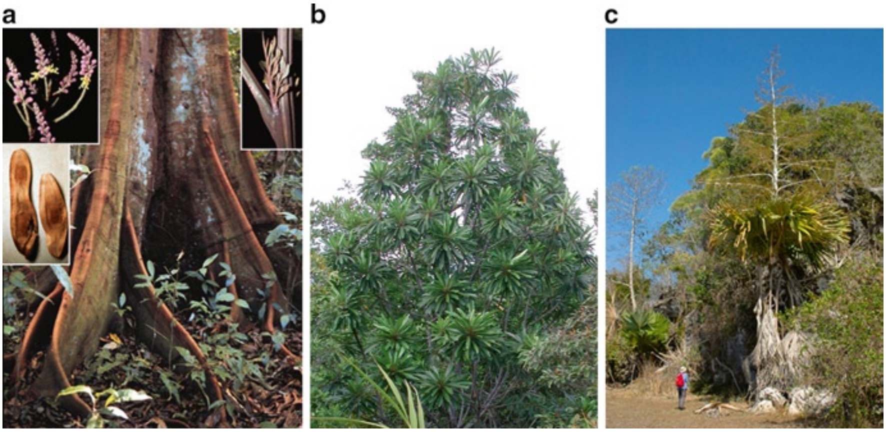

Fig. 2.2 Examples of the ~100 known species of monocarpic trees, in which a single episode of reproduction is followed by rapid senescence and death. (**a**) *Tachigali versicolor* (Leguminosae: Caesalopiniodeae), a common tree at Barro Colorado Island, Panama; (**b**) *Cerberiopsis candelabra* (Apocynaceae) endemic to New Caledonia and forming extensive monospecific stands; (**c**) *Tahina spectabilis* (Dransfield et al. 2008b) recently discovered in northwestern Madagascar. Photo credits: (**a**) Robin Foster; (**b**) Jennifer Read; (**c**) John Dransfield

Strobilanthes and *Mimulopsis* (both Acantheaceae) also include monocarpic species; while many species are multi-stemmed shrubs, some grow to be sizeable single-stemmed trees (e.g., *Mimulopsis arborescens*). Additional monocarpic species occur in montane forests in Africa but have received almost no study: these include *Oreacanthus mannii*, *Acanthopale decempedalis*, *Isoglossa glandulosa*, *I. nervosa* (all Acanthaceae), and *Plectranthus insignis* (Lamiaceae) (Duncan Thomas and David Kenfack, *personal communication*). Subtropical examples of monocarpy include several species of rosette trees of the genus *Echium* (Boraginaceae) (Böhle et al. 1996). There are thus likely over 100 species of monocarpic trees in at least 15 genera (Fig. 2.2). This tally does not include the many examples of short-lived tropical trees that reproduce continuously (or nearly so) after the onset of reproduction, and so approach a monocarpic life history.

Monocarpic tree species provide an important set of examples in which the physiological impacts of reproduction completely determine future plant development. Although there are very few formal comparative studies (Poorter et al. 2005; Read et al. 2006, 2008), monocarpic trees appear to be characterized by systematic differences from co-occurring polycarpic trees. Characteristics of monocarpic tree species include: high resource investment in reproductive structures; rapid growth; high growth response to increased light availability; low mortality rates, at least at certain life history stages; and an early age (though not size) at reproduction (Poorter et al. 2005). It has been noted that reproduction in at least some monocarpic tree species is triggered by damage. *Cerberiopsis candelabra* is characteristically a mass-flowering species: entire stands will flower and die synchronously (Read et al. 2008). However, damaged individuals of *C. candelabra* will commonly flower out of synchrony (Read et al. 2006).

Some monocarpic trees (such as *Corypha* spp.) have a single non-branched stem that eventually produces a terminal inflorescence (i.e., the Holttum architectural model of Hallé et al. 1978). However, this is not the case in most monocarpic trees, and meristem limitation alone does not appear to be a sufficient mechanism in most cases. An early proposed mechanism for the coordinated reproduction and senescence observed in monocarpic plants was the "nutrient drain hypothesis": that plant resources are so drained by reproductive structures that insufficient resources remain to sustain other physiological functions (Molisch 1938). However, physiological studies of monocarpic species (mainly agronomic crops) indicate that reproduction does not entirely consume all labile carbon or other resources (Kelly and Davies 1988). A more recent formulation of the nutrient drain hypothesis is that nutrient and carbon sinks related to reproductive development show a feedback with vegetative sinks that disrupts future vegetative development (Kelly and Davies 1988). It has also, more speculatively, been hypothesized that senescence in moncarpic plants may be induced by a signal (e.g., a "death hormone" produced in reproductive structures) that initiates whole-plant senescence (Leopold 1961; Noodén et al. 1997). No such substance has been identified, and it is not clear why plants would evolve such a process. There are some cases in which the nutrient drain hypothesis, even in modified form, does not appear to be a viable explanation (Kelly and Davies 1988). A role for biotic agents has also been suggested. Read et al. (2006) cored *C. candelabra* trees at the time of flowering, and found wood to be consistently characterized by a dark-stained, watery rot compared with clean, pale wood in non-reproductive individuals. This observation suggests that in *C. candelabra* a biotic agent having severe detrimental effects may trigger reproductive onset, or that trees lose rapidly the capacity for pathogen defense following reproduction.

In summary, cases of monocarpic reproduction in trees offer several potentially important insights into effects of reproduction on tree growth and physiology more generally. First, reproduction clearly is capable of causing complete loss of physiological function (though the mechanism is unclear). Monocarpic trees appear to have arisen multiple times from polycarpic ancestors. One would therefore, from an evolutionary perspective, expect to find intermediate cases where reproduction has drastic, though not fatal, effects. Second, the "nutrient drain hypothesis", that death following reproduction in monocarpic plants is driven directly by allocation of all available resources to reproduction, has not been supported. It follows that reproductive costs can substantially outweigh the direct effects of resource allocation. Third, recent evidence that monocarpic trees show unusual combinations of high growth yet low mortality compared to co-occurring polycarpic species (Poorter et al. 2005) suggests that iteroparous reproduction in general results in costs in terms of slower growth and/or higher mortality compared to what is possible given biophysical constraints alone. Fourth, there are intriguing but anecdotal observations that death in at least some monocarpic tree species may be linked to biotic factors associated with reproduction.

6 Empirical Evidence for the "Costs of Reproduction" in Polycarpic Trees

The development of reproductive structures on a plant can affect a wide range of growth and physiological processes (Table 2.1), with implications for current and future survivorship and reproduction. Most, but not all, of these effects are consistent with the hypothesis of a tradeoff based on costs of reproduction to current or future growth. Observed effects on vegetative growth range from reductions in diameter increment and shoot elongation, to increased shoot mortality and meristem initiation. Reductions in leaf size and changes in leaf morphology, chemistry, and physiology have also been widely observed.

Table 2.1 Observed effects of reproduction on tree functional traits based on correlations within or among woody plants

	Effect	References
Growth:	Reduced stem diameter increment	Table 2.2
	Reduced shoot elongation	Table 2.3
	Reduced leaf initiation	Dick et al. (1990a)
	Increased shoot mortality	Gross (1972)
Morphology:	Reduced leaf size	Tappeiner (1969), Tuomi et al. (1982), Caesar and MacDonald (1984), Chapin and Moilanen (1991), Karlsson (1994), Miyazaki et al. (2002), Leal and Thomas (2003)
	Increased crown transparency	Innes (1994)
	Reduced leaf mass per area	Caesar and MacDonald (1984), Miyazaki et al. (2002)
Gas-exchange:	Reduced net photosynthesis	Karlsson (1994), Karlsson et al. (1996), Obeso et al. (1998), Miyazaki et al. (2002), Wheelwright and Logan (2004)
Leaf and shoot chemistry:	Reduced leaf N	Newell (1991), May and Killingbeck (1992), Karlsson (1994), Leal and Thomas (2003)
	Reduced stem N	Newell (1991)
	Increased leaf C:N ratio	Leal and Thomas (2003)
	Reduced leaf chlorophyll content	Leal and Thomas (2003)
	Increased chlorophyll A:B ratio	Leal and Thomas (2003)
	Reduced labile C	Newell (1991), Miyazaki et al. (2002), Ichie et al. (2005)

6.1 Correlation vs. Causation in Analysis of Reproductive Costs

The majority of data related to cost of reproduction in woody plants has been based on correlations observed in nature. In some cases a negative correlation between growth and reproduction may not indicate causation: in particular, if an environmental factor has a positive effect on growth but a negative impact on reproduction (or vice-versa) this can produce a negative correlation that might be spuriously interpreted as a tradeoff (Bell 1980). A recent example of this has been documented in Californian oak species in which rainfall is positively affects diameter increment but negatively affects acorn production (Knops et al. 2007). However, environmental factors commonly have positive effects on both growth and reproduction (e.g., Woodward et al. 1993; Despland and Houle 1997), a pattern that would in general obscure actual tradeoffs. Ideally analyses that control for major environmental drivers or experimental approaches should be used. Unfortunately, it is essentially always the case that the full set of important environmental drivers of tree growth and reproduction are not known a-priori. Experimental approaches are logistically challenging with trees, and may produce artifacts: for example, bud removal experiments may result in wounding responses.

Much of the data pertaining to reproductive effects on tree growth and physiology are based on observations and correlations that do not take into account environmental correlations; the review and meta-analyses presented thus may confound environmental correlations with direct reproductive effects. However, it is likely that environmental factors are at least equally likely to affect growth and reproduction in the same as in opposite directions; thus, environmental influences are most likely to result in increased variance within and (particularly) among studies. In this regard a pooled analysis (and especially a formal meta-analysis) is much less likely to be influenced by environmental covariance patterns than is any given study considered individually. In the following sections I also specifically compare results to available experimental studies and to studies in which attempts have been made to control for environmental factors.

6.2 Meta-analyses: Literature Search and Analytic Methods

For effects on which there is a relatively extensive pertinent literature (>7 species and >7 separate publications), I present meta-analyses of available data to assess the generality of the hypothesized patterns. The sample of studies utilized is based on tracing back references in prior publications, in addition to a systematic search of electronic databases. Meta-analyses of relationships are based on a pooled analysis of correlation coefficients, following Hunter and Schmidt (1990) (see also Field 2001). The Hunter-Schmidt statistic $(\overline{r})$ is simply a weighted mean correlation calculated as:

$$\overline{r} = \frac{\sum_{i=1}^{k} n_i r_i}{\sum_{i=1}^{k} n_i}$$

where r_i and n_i are the observed correlation and sample size of the i^{th} study, and the summations are made among k studies. The significance is tested using a Z statistic ($\overline{r}$ divided by its standard error), with the associated probability calculated using the standard normal distribution (Field 2001). This is a "random effects" analysis, and so does not assume uniformity of relationships across studies. In many cases correlation coefficients were directly presented; in others they were calculated from original data or from data digitized from figures. In some cases reproduction was treated as a categorical variable, and correlations were calculated with non-reproductive stems or individuals scored as zero, and reproductives as 1. Analyses are restricted to publications that present data on trees that have not been subjected to breeding programs. There is, for example, a large literature on relationships between growth, physiology, and fruit production in alternate-bearing (climacteric) apples and other fruit trees. These agronomic taxa have been specifically bred for extreme expression of reproductive traits (and often for reduced stature), and therefore might be expected to show extreme tradeoffs between growth and reproduction.

6.3 Dendrochronological Studies

The diameter growth of trees in the temperate zone (and, as is increasingly being documented, of many trees in the tropics) is recorded by growth rings demarcated by latewood formed prior to the winter or dry season quiescent period. Diameter (or basal area) increment can be allometrically scaled to, and generally provides a good approximation of, tree biomass growth. Given that the reproductive output of trees generally shows high inter-annual variability, long-term records of tree reproductive output, in conjunction with dendrochronological analyses of tree ring series, provide a valuable source of information to detect and quantify the effects of reproduction on tree growth.

Meta-analysis results for studies examining tree ring increment in relation to reproductive output reveal a consistent pooled negative correlation (Table 2.2). The Hunter-Schmidt $\overline{r}$ (–0.230) is significantly less than zero at $P<0.001$. Negative patterns are also found for conifers and angiosperms considered separately: for conifers the Hunter-Schmidt $\overline{r} = -0.271$ ($P<0.001$), and for angiosperms the Hunter-Schmidt $\overline{r} = -0.134$ ($P<0.001$). The lower value for angiosperms is largely attributable to low correlations found for California oaks (Knops et al. 2007), which represent 5 of 7 samples. The mean correlation is also significantly negative

Table 2.2 Summary of dendrochronological studies included in meta-analysis examining the correlation of reproductive output (variously measured across studies) with tree ring increment across years

Species	Location	Years	r	Reference
Abies grandis	BC Canada	28	–0.317	Eis et al. (1965)
Abies lasiocarpa	Washington USA	28	**–0.044**	Woodward et al. (1993)
Abies lasiocarpa	Oregon USA	28	**–0.222**	Woodward et al. (1993)
Dacrydium cupressinum	New Zealand	33	**–0.304**	Norton and Kelly (1988)
Nothofagus truncata	New Zealand	33	**–0.303*****	Monks and Kelly (2006)
Picea abies	Norway	40	**–0.648*****	Selas et al. (2002)
Pinus banksiana	Quebec Canada	24	0.310	Despland and Houle (1997)
Pinus sylvestris	Spain	11	–0.140	Alonso et al. (2007)
Pseudotsuga menziesii	BC Canada	28	–0.765***	Eis et al. (1965)
Tsuga mertensiana	Washington USA	28	**–0.122**	Woodward et al. (1993)
Tsuga mertensiana	Oregon USA	28	**–0.163**	Woodward et al. (1993)
Quercus lobata	California USA	13	**0.048**	Knops et al. (2007)
Quercus douglasii	California USA	13	**0.007**	Knops et al. (2007)
Quercus agrifolia	California USA	13	**–0.107**	Knops et al. (2007)
Quercus chrysolepis	California USA	13	**0.159***	Knops et al. (2007)
Quercus kelloggii	California USA	13	**0.078**	Knops et al. (2007)

Correlation values listed in ***bold*** are partial correlations that correct for climate effects (or comparable analyses based on indexing). The Hunter-Schmidt $\bar{r} = -0.225 \pm 0.021$ ($P = 0.0001$)

Significant trends for studies considered individually are indicated by asterisks: $*P<0.05$; $**P<0.01$; $***P<0.001$

if one considers only studies that have included climate variables as covariates: Hunter-Schmidt $\bar{r} = -0.208$ (P<0.001). Although the data analyzed include prominent examples of null results reported in the literature (e.g., Despland and Houle 1997; Alonso et al. 2007; Knops et al. 2007), these studies tended to be of shorter duration and thus have reduced influence on the overall calculations. The finding of a highly significant meta-analysis result, in spite of the fact that relatively few studies are significant considered individually (Table 2.2), is common in cases where sample sizes of individual studies are low and/or the signal to be detected is either weak or variable among studies (Hedges and Olkin 1985). Detection of prevailing trends under these conditions is a main motivation for meta-analysis generally.

Several additional relevant studies were noted but not included in the meta-analysis due to either a small series length, insufficient reporting of data, or lack of access to some older publications. Consistent with the studies in Table 2.2, these studies generally find negative correlations between tree ring increment and reproductive output (generally fruit or cone production): for *Abies balsamea* in New Brunswick, Canada (Morris 1951), *Pinus sylvestris* and *Picea abies* in Sweden (Eklund 1954, 1957), *Pinus ponderosa* in Colorado, USA (Linhart and Mitton 1985), *Pseudotsuga menziesii* in BC, Canada (El-Kassaby and Barclay 1992), and *Fagus crenata* in Japan (Hoshino et al. 2008 – notably based on a 48 year time series). A few additional null results have also been reported: for *Pinus ponderosa* in Washington State USA (Daubenmire 1960), *Pinus sylvestris* in Poland

(Chalupka et al. 1976), and another (much shorter-duration) study of *Fagus crenata* in Japan (Yasumura et al. 2006).

Dendrochronological studies coupled with long series of reproductive measurements also provide a valuable avenue for analyses of time-lagged effects of reproduction, and of the interactions between climate variability, reproduction, and tree growth. A number of studies have employed auto-regressive moving average (ARIMA) models or similar techniques to examine lagged effects of reproduction on growth. For example, Woodward et al. (1993) detected lagged effects of coning on growth over the following 2 years in two montane conifer species. However, other studies have found effects only in the year of fruit or cone production (e.g., Selas et al. 2002).

Several studies have simultaneously considered climatic variability and reproduction as predictors of long-term tree growth patterns. Woodward et al. (1993) examined relationships for two conifers (*Abies lasiocarpa* and *Tsuga mertensiana*) between cone counts and the residuals of a growth index value that was adjusted both for size trends (as per standard dendrochronological indexing methods) and temperature and precipitation data. They report consistently negative correlations based on this approach (Table 2.2). Monks and Kelly (2006) found that the partial negative correlation between growth and reproduction in *Nothofagus truncata* was strengthened when climate variables were included in a predictive model. In contrast, Knops et al. (2007) found in five species of Californian oaks (*Quercus* spp.) that inclusion of precipitation as a predictor resulted in partial correlations between growth and reproduction not different from zero (and one case of a small apparent positive partial correlation between growth in reproduction). In the case of Californian oaks, dry conditions during the early growing season appear to inhibit growth while enhancing pollination success (Knops et al. 2007), a pattern that seems likely to be system-specific.

6.4 Reproductive Allocation and Shoot Extension Within Tree Crowns

Negative correlations between shoot extension growth and production of reproductive structures have been widely reported in the literature. The first observations on this phenomenon appear to date to Morris (1951); most often data have been recorded in terms of annual shoot length increment of internodes produced the year following a given reproductive event (e.g., Gross 1972; Fox and Stevens 1991), but the specific measures of reproduction and growth vary among studies.

The meta-analysis of available data provides remarkably consistent support for a general negative trend between shoot or branch growth and the quantity or mass of reproductive structures (generally fruit or cones) present (Table 2.3). All reported correlations are negative, four of eight being significant considered individually. The Hunter-Schmidt $\overline{r}$ (–0.341) is significantly less than zero at $P<0.001$. Additional studies that did not present simple correlations (or data allowing calculations) have

Table 2.3 Summary of studies included in meta-analysis examining the correlation of stem increment and reproductive output within tree crowns

Species	Location	N	r	Reference
Alnus hirsuta var. *sibirica*	Japan	206	–0.270**	Hasegawa and Takeda (2001)
Alnus hirsuta var. *sibirica*	Japan	49	–0.630***	Hasegawa and Takeda (2001)
Betula alleghaniensis	Ontario Canada	15	–0.518	Gross (1972)
Betula papyrifera	Ontario Canada	15	–0.859	Gross (1972)
Pinus radiata	Australia	6	–0.295	Cremer (1992)
Pinus strobus	Ontario Canada	26	–0.170	Leal and Thomas (2003)
Pseudotsuga menziesii	California USA	10	–0.838***	Tappeiner (1969)
Salix alaxensis	Alaska USA	92	–0.232*	Fox and Stevens (1991)

The Hunter-Schmidt mean $r = -0.341 \pm 0.013$ ($P = 0.0000015$)

Significant trends for studies considered individually are indicated by asterisks: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

likewise generally found negative relationships (Henriksson and Ruohomäki 2000), although null results have also been reported (e.g., Bañuelos and Obeso 2004). A number of studies also describe substantial variation among populations and sites, such that negative relationships between reproduction and shoot extension are present in some populations but not others, possibly related to local variation in soil resources or other factors (e.g., Obeso 1997).

As in the case of dendrochronological studies of reproductive effects, the analysis in Table 2.3 is based on correlative data. Thus positive responses of both reproduction and growth to environmental heterogeneity might be expected to mask an underlying tradeoff (Obeso 2002; Karlsson et al. 2006). In addition, physiological integration should also generally act to obscure patterns at the shoot or branch level (Bañuelos and Obeso 2004). Experimental approaches, primarily based on removal of reproductive buds, have also been employed to test for reproductive costs at the branch and whole-tree level. Fox and Stevens (1991) in a bud removal experiment failed to find experimental evidence for negative effects of reproduction on growth in *Salix alaxensis*, in spite of a weak negative correlation between extension growth and reproduction. A follow-up experiment found a compensatory response to removal of either reproductive or vegetative buds, leading to the suggestion that bud removal is not a valid experimental approach to detect or measure reproductive costs due to artifacts related to wounding responses (Fox 1995). Nevertheless, similar studies have detected increased vegetative growth following reproductive bud removal in other woody plants (Houle 2001; Karlsson et al. 2006).

6.5 Reproduction and Shoot Demography Within Tree Crowns

Meristems are generally genetically predetermined to develop as vegetative or reproductive structures, and there is thus a potential for reproduction to limit future growth and development through meristem limitation. Reproduction may also

Fig. 2.3 Crown dieback following heavy production of catkins in *Betula alleghaniensis* (From Gross 1972: used by permission)

sufficiently drain resources to result in subsequent crown dieback. Substantial crown dieback following episodes of very high seed production was observed in *Betula alleghaniensis* by Gross (1972): individuals with high a high proportion of catkins per terminal bud site showed progressively lower shoot growth in the subsequent year, and 3 of 4 individuals with >95% of terminal buds bearing catkins showed branch dieback (Fig. 2.3). This pattern was observed very extensively in the study region, with an estimated 20–50 cm loss of the upper crown common following an intensive regional reproductive episode (Gross 1972). Studies of reproductive effects on shoot demography are particularly logistically difficult in trees, and this remarkable early research has not been replicated to date. A few studies have been conducted on small-statured, accessible trees (e.g., Maillette 1987), but have not detected significant negative effects of reproduction on shoot demography.

6.6 Leaf-Level Gas-Exchange, Chemistry and Morphology

Proximity of reproductive structures could either act to enhance net photosynthesis by reducing feedback inhibition, or to reduce carbon uptake due to nutrient allocation effects. Enhanced photosynthesis in leaves near reproductive structures has been commonly found in herbaceous plants and cultivated fruit trees (e.g. DeJong 1986; Urban et al. 2003). However, reported proximity effects of reproductive structures on net photosynthesis in non-cultivated trees appear to be generally negative (Karlsson et al. 1996; Obeso et al. 1998; Miyazaki et al. 2002; Wheelwright and Logan 2004). This may be due to relatively higher nutrient limitation in natural as compared to cultivated systems. Patterns of leaf chemistry appear to be consistent with fruits and seeds constituting a significant local sink for nutrients, in particular nitrogen. Reduced leaf N and reduced chlorophyll content in leaves that develop in proximity to reproductive structures has been reported in *Pinus strobus* by Leal and Thomas (2003), who also report a large increase in the chlorophyll a:b ratio. Such an increase is a predicted consequence of chlorophyll degradation, since chlorophyll b is converted to chlorophyll a prior to further breakdown (Folley and Engel 1999; Hörtensteiner 2006).

Ontogenetic patterns of leaf traits with tree size provide additional indirect evidence for effects of reproduction. Ontogenetic declines in the area of individual leaves have been widely observed in comparisons of saplings vs. mature trees (Thomas and Ickes 1995). However, the first leaves produced in tree ontogeny are typically very small, likely as a result of constraints imposed by seed resources. Average leaf size thus reaches a peak at an intermediate tree size. In a number of tree species this peak occurs approximately at the size of reproductive onset (Alvarez-Buylla and Martinez-Ramos 1992; Thomas and Ickes 1995), though in others the peak clearly falls earlier in development (Reich et al. 2004; Panditharathna et al. 2008; Thomas 2010). If biophysical processes, such as hydraulic effects on leaf turgor, were directly driving changes in leaf size, an increase in size early in ontogeny would not be expected; nor would one predict any association of this pattern with reproductive onset.

While many published studies addressing ontogenetic change in leaf gas-exchange have compared seedlings or saplings vs. mature trees (Bond 2000; Thomas and Winner 2002), there have been surprisingly few efforts to characterize gas-exchange over the entire course of tree ontogeny (Niinemets 2002; Nabeshima and Hiura 2008). In a recent effort to address this gap, I found that light-saturated photosynthesis and leaf N reach a peak at intermediate tree sizes closely approximating the size at onset of maturity in three species of temperate deciduous trees (Fig. 2.4). In contrast, leaf traits that reflect investment in structure and defense, including leaf mass per area, leaf thickness, leaf tissue density, and leaf C content increased monotonically with tree size. Qualitatively similar patterns were found in the three tree species examined (Thomas 2010).

6.7 Belowground Processes

Agronomic studies of fruit trees suggest that there is commonly a very strong tradeoff between root growth and fruit development. For example, in alternate-bearing apple trees, allocation in non-fruiting years is largely directed to root growth; root pruning is widely used to induce reproduction in non-fruiting years (Ferree et al. 1991). Very few studies of non-cultivated trees have been undertaken. A masting event in

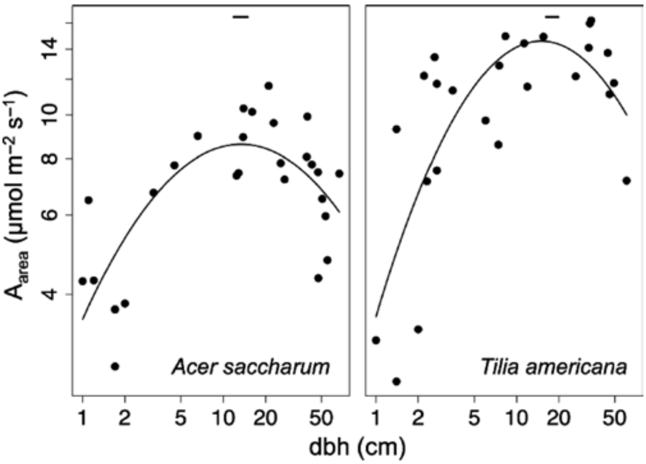

Fig. 2.4 Light saturated photosynthesis (A_{area}) as a function of stem diameter at 1.3 m height (dbh) in *Acer saccharum* and *Tilia americana*. In both cases the peak in A_{area} is closely coincident with the size (dbh) at reproductive onset (14.3 cm in *A. saccharum* and 19.8 cm in *T. americana*: shown by horizontal bars ± 95% CI). *Dotted line* is a 2nd-order polynomial fit to log-log transformed data (Modified from Thomas 2010)

Dryobalanops aromatica (Diptercarpaceae) did not result in detectable declines in root carbohydrate levels (Ichie et al. 2005).

6.8 Reproduction Effects That Don't Fit into a "Costs" Framework

There are a variety of physiological consequences of reproductive activity that do not fit easily into a "costs" framework. Reproductive structures serve as strong sinks for carbon, and in some cases photosynthetic rates of leaves near to reproductive structures can be enhanced, as a consequence of local carbon sink strength reducing feedback inhibition effects (Gifford and Evans 1981), and other factors (Urban et al. 2003). Reproductive structures can also supply much of their own carbon demands through photosynthesis (Bazzaz et al. 1979; Aschen and Pfanz 2003) particularly through refixation of CO_2 generated by construction respiration. Estimates of the proportion of the total C requirements internally generated by developing fruit average ~ 16%, but few measurements have been made on trees (Aschen and Pfanz 2003). Photosynthesis of reproductive structures and carbon refixation are both considered cases of adaptations of plants to offset reproductive costs (Obeso 2002). Development of reproductive structures will also have impacts on biomechanical support, within-crown shading, and plant hormonal balance that may or may not qualify as "costs".

6.9 Sexual Dimorphism of Functional Traits in Dioecious Trees

An additional form of "natural experiment" for evaluating the effects of reproduction on growth patterns and tree functional traits is to compare the sexes of dioecious tree species. The production of pistillate flowers, fruit and seed generally entails a much higher allocation of biomass and mineral nutrients (especially N) than does the production of staminate flowers alone; likewise female cones of conifers require greater investment, particularly of N, than do male cones (McDowell et al. 2000). Thus, the costs of reproduction have generally been predicted (and widely observed) to be higher in pistillate individuals. There have been several recent reviews that focus in whole or in part on sexual dimorphism in plants (Dawson and Geber 1999; Obeso 2002; Case and Ashman 2005); here I review some main results and specifically highlight studies that examine sex differences in ontogenetic patterns.

Dioecious trees (and dioecious plants generally) commonly show pronounced differences between the sexes in leaf-level physiological traits, such as photosynthetic capacity, leaf N, water use efficiency, and tissue water relations (Dawson and Geber 1999; Case and Ashman 2005). A now-classic result is the finding that female trees differ in responses to water stress, with males showing more conservative water use strategies under xeric conditions (Dawson and Bliss 1989). This pattern is a predicted consequence of evolved response to higher reproductive costs of water and nutrient supply to developing seeds and fruits, and has been found in numerous woody dioecious plant species (Dawson and Bliss 1989; Dawson and Ehleringer 1993; Dawson and Geber 1999; Espirito-Santo et al. 2003; Dudley 2006). Female trees, as a consequence, commonly show greater drought sensitivity than males, and may be differentially distributed to more mesic habitats (e.g., Dawson and Ehleringer 1993; Dudley 2006). One may infer from these results that female reproductive function in non-dioecious species must have comparably large impacts on whole-tree function; moreover, increasing reproductive allocation with tree size should result in strong size x sex interactive effects on drought sensitivity. Along these lines, strong interactive effects of sex and size on diameter increment responses to precipitation have recently been found in a dendrochronological study of *Juniperus thurifera* in Spain (Rozas et al. 2009).

The slope of the relationship between growth rate and tree size (following the peak of the differential form of the growth curve) has been considered a signature characteristic of age-related declines tree growth (e.g., Bond et al. 2007). A strong role for reproductive effort in driving age-related decline tree growth would thus be indicated not simply by differences between the sexes in average growth rates, but specifically differences in the slope of this decline. Wheelwright and Logan (2004) provide one of the only pertinent data sets available, on the dioecious tree *Ocotea tenera*, which shows both lower growth rates among female trees, and a much steeper decline in growth with increasing size in female trees (Fig. 2.5). A similar pattern has also been reported for the dioecious shrub *Rhamnus alpina* (Bañuelos and Obeso 2004). Higher growth and/or reduced mortality of male trees late in ontogeny has also been inferred from an elevated

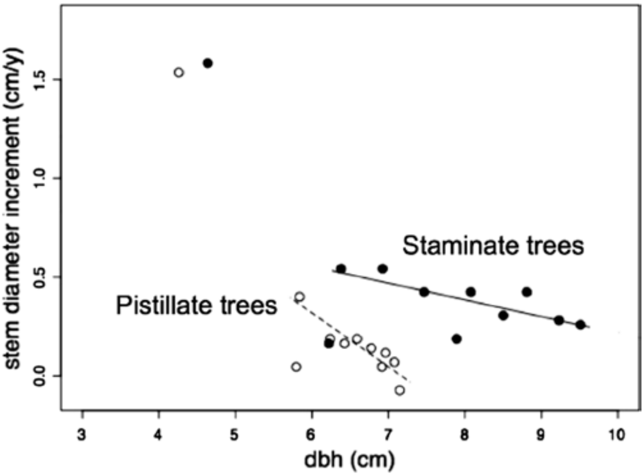

Fig. 2.5 Patterns of decline in diameter increment in males (staminate: *solid symbols*) vs. females (pistillate: *open symbols*) in a natural population of the tropical tree *Ocotea tenera*. Linear regressions for the later phase of growth (excluding the first two annual measurements in each case) are shown: for males (*solid line*) $y = 1.063–0.085x$; for females (*dotted line*) $y = 1.954–0.273x$. Slopes differ significantly between sexes (ANCOVA $P < 0.001$). Data are re-analyzed from Fig. 2.1 of Wheelwright and Logan (2004)

ratio of male to female trees observed in large size classes of tropical dioecious trees (Thomas and LaFrankie 1993).

6.10 Interactions Between Reproduction and Biotic Factors

Although costs of reproduction have figured centrally in analyses of sexual dimorphism in plants, males and females may also show differential evolutionary responses to other factors. In particular, male reproductive success depends on pollen transfer; there may, for example, be strong selection for increased male height in trees with wind-dispersed pollen or height-dependent access to pollinators (Lloyd and Webb 1977). Higher growth rates in males (e.g., Fig. 2.5), may thus potentially be related to sexual selection as well as direct physiological costs. In addition, male and female plants may show differential levels of and tolerance of herbivory, with slow-growing females generally being better defended (Jing and Coley 1990; Ågren et al. 1999; Verdu et al. 2004). There may also be effects of reproduction on growth and physiology mediated by herbivores or pathogens that primarily attack reproductive structures themselves. For example, the ash flower gall mite (*Eriophyes fraxiniflora*) attacks male flowers in many species of *Fraxinus*, but can cause extensive deformation of both flowers and leaves (Wawrzynski and Ascerno 1990). Such sex-specific effects in dioecious taxa suggest similar large secondary effects of reproduction more generally that are mediated by biotic agents.

7 Synthesis and Some Implications for Future Studies

The body of research reviewed is remarkably consistent in indicating that the "costs of reproduction" in trees are not trivial. Eight independent sources of data support this contention: (1) Among species, trees that show a smaller size at onset of maturity tend to show a smaller maximum size; (2) As is the case with most other organisms, various sources of data suggest that reproductive allocation generally increases with tree size; (3) Monocarpic trees provide a set of clear examples in which reproduction catastrophically impacts future growth and development, and comparisons with polycarpic trees suggest that repeated reproduction carries a consistent cost in terms of growth potential; (4) Dendrochonological analyses indicate an overall pattern of negative correlations between tree growth and reproduction, and in some cases of carry-over effects of reproduction that persist for >1 year; (5) Shoot extension growth within tree crowns is generally reduced when in close proximity to reproductive structures, (6) There are likewise frequently local negative effects of reproductive structures on leaf size, N content, and photosynthetic capacity within tree crowns; (7) Leaf size, N content, and photosynthetic capacity commonly increase with tree size early in ontogeny, but show decreases only after reproductive onset; (8) In dioecious tree species, females generally show reduced growth, and growth analyses indicate that females can show much steeper reductions in growth growth rate with tree size than do males.

Can such costs of reproduction explain, at least in part, the general pattern of age-related declines in growth in trees? The meta-analyses presented above (Tables 2.2 and 2.3) indicate pronounced negative effects of reproduction on tree growth, but do not directly assess whether these negative effects increase with tree ontogeny. However, two lines of reasoning suggest that reproductive effects must increase with tree ontogeny, and likely do contribute to age-related declines in growth. Trees universally show a long period of pre-reproductive growth during which negative effects of reproduction cannot be present (Fig. 2.1). Therefore negative effects of reproduction on growth must at a minimum be expressed as a "step function", being present only after reproductive onset. In addition, the widespread pattern of increasing reproductive output and frequency with tree size and age suggests that the negative consequences of reproduction on growth also must generally increase with tree size and age. It has previously been argued that because tree reproduction is intermittent, reproductive cost effects are unlikely to explain any continuous decline in growth (Ryan et al. 1997). However, studies reviewed here have found evidence for carry-over effects of reproduction in prior years on current growth (Woodward et al. 1993) and shoot survivorship (Gross 1972).

How large is the effect of ontogenetic increases in reproductive allocation on tree growth? A recent study of *Fagus sylvatica* by Genet et al. (2010) indicates an increase in annual carbon allocation of from <5% in young trees to ~40% in trees >120 years, with a concomitant decrease in carbon allocation to stem growth. However, the direct mechanistic relevance of these data depend on whether the growth of large trees is carbon limited. Recently, a pattern of increasing non-structural carbohydrate concentrations in old trees (Sala and Hoch 2009) and observations of little or no growth enhancement to elevated CO_2 in mature trees (Körner et al. 2005) have both been interpreted as indicating a lack of carbon limitation. However, the *Fagus* stands studied by Genet et al. (2010) showed no age-related trend in non-structural carbohydrate concentration. Moreover, since concentrations of N and other mineral nutrients are generally higher in reproductive than somatic tissues, reproductive allocation could impact growth even in "carbon-saturated" trees. As noted above, observed physiological effects of leaf proximity to reproductive structures commonly include reduced leaf N, chlorophyll content, and photosynthetic capacity, all suggesting strong impacts of N allocation.

A direct test of the effects of tree reproduction on age-related trends in growth and physiology is in theory possible if one could experimentally inhibit reproduction through all or part of a tree's lifespan, and compare patterns to a control population. Experimental approaches for inhibiting reproduction could range from bud removal experiments to genetic modification methods, which have particular promise in *Populus* (Brunner and Nilsson 2004). This type of experiment has been utilized extensively in studies aimed at quantifying the costs of reproduction in short-lived herbaceous plants (e.g., Reekie and Bazzaz 1987a, b, c), and some woody shrub species (e.g., Houle 2001; Karlsson et al. 2006). While comparable experiments on trees appear never to have been undertaken, they may be feasible in short-lived, small-statured species. Candidate tree species for such experiments might include small-statured ephemeral pioneer trees, such as members of the genera *Trema* (Ulmaceae), *Clerodendrum* (Verbenaceae), and *Carica* (Caricaceae), and *Salix* (Salicaceae) or *Populus* (Salicaceae) in the temperate zone. Such experiments would also offer a valuable platform to better understand physiological mechanisms, including the relative importance of carbon limitation.

Dendrochronological studies linked to long-term records of tree reproduction – and where possible with experimental manipulations – will likely continue to present the best opportunities to understand effects of reproduction on age-related trends in tree growth and functional biology. Four types of dendrochronological studies stand out as offering great potential. First, additional analyses that link climate variability to trends in both tree reproduction and increment growth across a variety of species are essential. Work to date has not specifically sought to quantify the possible role of reproduction in driving age-related changes in growth patterns, and the common practice of removing age-related trends prior to analysis is likely to obscure such patterns. Studies of this type would be particularly novel and potentially revealing in tropical regions, where consistent annual rings are much more common than has commonly been believed (Worbes 2002). Second, studies of growth pattern differences between the sexes of dioecious species offer an important and under-explored avenue for understanding reproduction in relation to age-related trends in growth and physiology. Third, monocarpic trees provide a unique potential for comparative studies on age-related growth and physiology, in that there are no possible effects of reproduction until the end of the life cycle. It would be particularly interesting to examine whether patterns of age-related growth and physiology differ between monocarpic and polycarpic members of such genera as *Tachigali* and *Cerberiopsis*. Finally, there is a near complete absence of studies examining relationships between reproduction and root growth and functional biology in non-cultivated trees.

In all future dendrochronological studies it will be important to statistically partition effects among alternative causal processes, including direct climate effects and reproduction (Knops et al. 2007). In addition, it would be useful to partition "age-related" trends in tree growth to explicit age vs. size effects, in datasets where there is appreciable orthogonal variation in age vs. size. As an example of this approach, in black spruce (*Picea mariana*) declines in diameter increment through ontogeny, and of the capacity to show release responses following harvests, were principally attributable to tree age rather than size (Thorpe et al. 2007).

In terms of research applications, reproductive effects on tree growth have long been considered a potential breeding target for enhancing growth and yield (e.g., Ledig and Linzer 1978; El-Kassaby and Barclay 1992; Strauss et al. 1995). Breeding for trees with low reproductive effort is likely to be a much easier objective than breeding to reduce effects of biophysical limitations to growth, since the objective is essentially a loss of function. There is also considerable interest in breeding for reproductive sterility in genetically engineered trees, to limit possible genetic pollution effects (Strauss et al. 1995; van Frankenhuyzen and Beardmore 2004; Brunner et al. 2007). From an environmental management perspective, a better understanding of the links between growth and reproduction of trees is important in the context of anthropogenic climate change and other major perturbations of forest ecosystems. Reproductive development of trees is commonly more sensitive to climatic variables (and to different climatic variables) than is growth (e.g., Woodward et al. 1993; Despland and Houle 1997; Knops et al. 2007), and reproduction may likewise show stronger responses to rising CO_2 (e.g., LaDeau and Clark 2001). Global change impacts on tree reproductive output may thus have greater ecological impacts on forest community interactions and biodiversity than changes in total biomass accumulation (e.g., Ostfield et al. 1996; Jones et al. 1998; Curran and Leighton 2000).

In conclusion, reproductive effects should be looked at as one among a suite of processes that impact patterns of age-related growth and functional biology of trees. Given the centrality of reproduction and reproductive costs in life-history theory, research to better understand the physiology and comparative ecology of reproductive effects, and their interaction with biophysical limitations to tree growth, should be a priority for future research.

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