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AGE–SIZE PLASTICITY FOR REPRODUCTION IN MONOCARPIC PLANTS

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Abstract. Empirical and theoretical investigations of monocarpy have usually addressed the question of minimum or threshold sizes for reproduction. However, the range of flowering sizes observed in many monocarpic species is extraordinarily large (well beyond what can be called a "threshold"), and the sizes of flowering and nonflowering plants may overlap greatly. We attempt to explain these reproductive patterns in terms of optimal reaction norms predicted by simple deterministic life history models. We assume that individuals differ in their growth trajectories due to the heterogeneous quality of microsites and ask how the optimal age and size at flowering varies with environmental variation in growth and for different assumptions about fecundity and mortality. Under two very different growth functions (one with no age- or size-related decline in growth rate and another with such a decline as size approaches an asymptote), the optimal reaction norms imply considerable plasticity for size at reproduction, particularly when poor growth is associated with higher mortality or lower asymptotic size. Deterministic models such as these may be more applicable to long-lived than to short-lived monocarps, because fitness potential should be less affected by stochastic variability in yearly growing condition in the former than in the latter. We consider the case of a tropical monocarpic and masting tree species, *Cerberiopsis candelabra* (Apocynaceae), and show that our model results can account for wide ranges of reproductive size and overlap in size of flowering and nonflowering plants, in accord with observation. We suggest that empirical attention to norms of reaction across growth environments will be a more profitable approach than investigation of size thresholds per se.

Key words: growth trajectory; life history; monocarpy; reaction norm; reproductive age; reproductive size; semelparity.

INTRODUCTION

The contrast between monocarpy (semelparity) and polycarpy (iteroparity) has drawn frequent attention in life history models (Cole 1954, Charnov and Schaffer 1973, Schaffer 1974, Young 1981, Takada 1995), but a theory to explain life history variation within monocarpic species (that is, plasticity across environments) is less well developed. In this article, we consider plasticity in the fundamental life history "decision" of monocarpic plants: when to flower and hence die. We wish to expand attention beyond the question of size thresholds per se to include the more complete notion of age–size norm of reaction for flowering. In particular, we are interested in monocarpic trees, an unusual life form among monocarpic plants. Recent work has produced major advances in understanding life history plasticity in short-lived, herbaceous monocarps (Metcalf et al. 2003), but monocarpy encompasses many long-lived habits, including giant rosettes (Young 1984, Tissue and Nobel 1990) and canopy trees with branching and secondary growth (Veillon 1971, Foster 1977, Poorter et al. 2005).

Large variation in size at flowering is a common occurrence among monocarps, including facultative biennials (Wesselingh et al. 1997), long-lived monocarpic rosettes (Young 1984, Tissue and Nobel 1990), and monocarpic trees (Foster 1977, Read et al. 2006). Our data on *Cerberiopsis candelabra* (see Plate 1), a monocarpic canopy tree endemic to New Caledonia, dramatically illustrate the issues that arise from this variability (Read et al. 2006). Across 18 populations of *C. candelabra* surveyed in a masting year, flowering occurred in trees as small as 5 cm dbh and as large as 79 cm dbh, with nearly complete overlap of the size range of nonreproductive individuals, 5–64 cm dbh. In four populations, the largest tree on the site was nonflowering, and in two populations nonflowering trees were larger, on average, than reproductive ones (although the difference in means was not statistically significant). Patterns of variation like this require an explanation.

Our current knowledge of monocarpy derives overwhelmingly from facultative biennials and other short-lived herbaceous monocarps, often plants of dunes, pastures, or disturbed sites in seasonal temperate habitats. For example, 16 of the 17 species listed in Table 1 of the review of monocarpy by Metcalf et al. (2003) fit this description (the exception being the tropical bromeliad, *Puya dasylirioides*). Much of the

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theoretical and empirical study of monocarpy is focused on questions motivated by these kinds of plants, such as the role of overwinter survival rates, vernalization requirements for flowering, and why facultative biennials delay flowering (Werner 1975, Kachi and Hirose 1985, de Jong et al. 1989, Wesselingh et al. 1997, Rees et al. 1999, Sletvold 2005). This last issue, in particular, has dominated the empirical study of monocarpy.

The flowering behavior of facultative biennials tends naturally to focus attention on size thresholds. Few biennial species are strictly biennial (Kelly 1985). Most flower as two-year-olds under cultivation, while in natural habitats they often defer reproduction to later growing seasons (Silvertown 1984). This pattern is usually explained by a minimum size requirement for flowering: a plant is biennial only when a favorable environment allows it to reach the critical size quickly. A roughly similar pattern occurs in the timing of amphibian metamorphosis (Wilbur and Collins 1973), a life history decision analogous to flowering in monocarpic plants. When larval growth rates are increased (by higher food levels or reduced competition, for example), most amphibians show earlier metamorphosis at a larger size, i.e., a plastic response to environmental change. It is curious that theoretical explanations of this life history transition in animals have usually been framed in terms of age–size norms of reaction (Wilbur and Collins 1973, Day and Rowe 2002, Rose 2005), while the onset of flowering in plants has been examined largely in terms of size thresholds alone. Even when age- and size-dependency of flowering are considered together, they are often seen as alternatives (Lacey 1986).

There must be some minimum vegetative size that can sustain flower and fruit production in any plant. For example, Tissue and Nobel (1990) demonstrated that rosettes of the monocarpic *Agave deserti* must reach a size >1000 g dry mass in order to flower. Smaller rosettes could flower precociously if they were attached to larger rosettes, but not if the rhizomal connection were severed so that they could not receive a carbon subsidy. In this case, the size of the smallest independently flowering rosette is probably a good estimate of the critical vegetative size required for reproduction (a "physical threshold" in the terminology of Day and Rowe [2002]). But some *A. deserti* plants flowered at sizes up to 10 000 g dry mass. Why does this 10-fold range occur, and why is it not twofold or 100-fold? A physical threshold does not, by itself, explain much about the causes of intraspecific variation in flowering size.

Another perspective on such variation is to postulate that individuals have idiosyncratic thresholds, revealed in empirical data as an increasing probability of flowering with increasing plant size. Logistic regression of such data can be interpreted as a cumulative probability function. Differentiation of this cumulative function yields an underlying frequency distribution, which can be interpreted as a distribution of thresholds, an interpretation consistent with polygenic variation for threshold size (Wesselingh and de Jong 1995, Metcalf et al. 2003). But this approach, while clearly valuable, only partially addresses the life history questions surrounding flowering size. Even if genetic variation underlies idiosyncratic thresholds, we would still wish to know how selection on life history shapes the genetic variation, in particular whether there is an adaptive basis for it.

We believe that a clearer theoretical picture of monocarpy emerges from attention to both size and age at reproduction, as well as to the growth trajectory that links size with age. Our approach emphasizes the adaptive nature of reaction norms across multiple (micro-) environments that provide different opportunities for growth. Any individual's age and size at reproduction lie at some point along its growth trajectory. A curve connecting these points across a range of individual trajectories is the norm of reaction for flowering. Our goal in this article is to find optimal norms of reaction for monocarpy and see if they are consistent with empirical observations of wide variation in flowering size and overlap between reproductive and nonreproductive individuals. If there is a strict size threshold for reproduction, the norm of reaction would form a horizontal line across a size-by-age plot, i.e., flowering plants would always be larger than nonflowering plants, but age at flowering might vary widely. Alternatively, if there is a strict age threshold, the norm of reaction would be a vertical line on the size-by-age plot, and reproductive plants would always be older than nonflowering plants, but sizes could vary, and therefore overlap, if growth trajectories differ. More complex mechanisms that trigger reproductive onset in relation to size and age would produce more complex reaction norms.

A focus on reaction norms may be more applicable to long-lived monocarps than to herbaceous ones, even though both types of plants undoubtedly experience variation in growth conditions due to microsite heterogeneity. But a single summer is a substantial portion of the life span of a facultative biennial, and, in temperate habitats, a single winter may impose very high mortality. In these conditions, a "one-year look-ahead" contingent on current size might capture the essential life history prospects faced by a herbaceous monocarp (Rees et al. 1999, Metcalf et al. 2003). In contrast, a monocarpic tropical forest tree must sustain several decades of growth before it acquires the reproductive benefits of a position in the canopy (Poorter et al. 2005). Potential size in the long term (i.e., the growth trajectory), rather than current size per se, is more likely to determine flowering strategies in longer-lived monocarps. Nonetheless, we develop a general model for optimal flowering size in monocarps that has no a priori assumption about life span.

Optimal Flowering Model

In the models below, we determine the norms of reaction that maximize a plant's net reproductive rate, R_0. This is an appropriate measure of fitness when population or metapopulation size is stationary and individuals are subject to density-dependent mortality (provided the density dependence does not affect the life history trait under consideration) (Roff 1992, Kozłowski 1993, Brommer 2000). These conditions are likely to be met by plants in which mortality is concentrated in the seed and seedling stages.

Consider a life history with probability $l(t)$ of survival to age t and fecundity $b(t)$ at age t. Survival and fecundity may be more strongly linked to size than to age in modular organisms (Harper 1977), so it will be more intuitive to employ the equivalent size-based life history functions. If plant size, s, increases monotonically with age, then an inverse function exists in which age is a strictly increasing function of size. Thus, it is possible to convert $l(t)$ and $b(t)$ to $L(s)$ and $B(s)$ for size-specific rather than age-specific survival and fecundity. The net reproductive rate of a monocarpic plant that flowers at size $s = \sigma$ is given by $R_0 = L(\sigma)B(\sigma)$. Maximization of R_0 requires

$$L(\sigma)B'(\sigma) = -L'(\sigma)B(\sigma) \tag{1}$$

in which the primes indicate derivatives with respect to s. The condition in Eq. 1 succinctly encompasses the fundamental "gamble" governing monocarpy (Metcalf et al. 2003): flowering should occur when the marginal fitness increment from increased fecundity following further growth (the left-hand side) is exactly balanced by the marginal fitness decrement due to reduced survival to larger size (the right-hand side).

Growth trajectory, s(t)

Plant growth typically follows a sigmoid curve, which can be represented by several equations, including the logistic (Hunt 1982). However, Day and Taylor (1997) have cautioned against life history modeling in which all phases of the life history are consolidated in a single growth equation. They argue that the timing of maturity may bring on the declining growth captured by sigmoid or asymptotic curves, rather than evolving within an independent context of declining growth. Therefore, they recommend that pre-reproductive growth be modeled as a power function of current size. But there are reasons to suspect that plants may experience declining growth rates long before and independently of reproductive maturity. This is a ubiquitous pattern among trees and seems to involve the scaling of physiological processes with size (Ryan and Yoder 1997). Possible underlying causes are the effect of plant height on hydraulic conductance (Mencuccini 2002, Ryan et al. 2006) or reallocation of growth from productive to support tissue as trees sustain greater wind loads with increasing height (King 2005).

To assess the effect of growth pattern, we examine both a power function $ds/dt = ks^q$ (Day and Taylor 1997) and the logistic function $ds/dt = ks(1 - s/s_\infty)$ (Hunt 1982) as pre-reproductive growth curves. In both equations, k is a constant representing environmental quality, with higher values corresponding to more productive microsites. The Appendix also considers the von Bertalanffy growth function, which, like the logistic, has an asymptote. It produces results similar to those obtained with the logistic. The power function has the solution

$$s(t) = \left[(1-q)kt + s_0^{1-q}\right]^{1/(1-q)} \tag{2a}$$

in which s_0 is initial size. The logistic function has the solution

$$s(t) = \frac{s_0 s_\infty}{s_0 + (s_0 - s_\infty)e^{-kt}} \tag{2b}$$

for initial size s_0 and maximum size s_∞.

Mortality rate, μ

Mortality in plants is often a function of size. For example, larger size increases the chance of surviving summer drought in *Cirsium vulgare* and *Cynoglossum officinale* (de Jong and Klinkhamer 1988, Wesselingh et al. 1997) or winter soil upheaval in *Digitalis purpurea* (Sletvold 2005). Mortality may also be related to growth rate. For example, Young (1985) found that rapidly growing plants of *Lobelia telekii* on Mt. Kenya (i.e., growing faster than the mean rate within their size class) suffered lower mortality than did slowly growing plants, across nine size classes representing approximately three orders of magnitude in total rosette leaf area.

There may be little difference between growth-dependent and size-dependent mortality on overall survivorship, because slowly growing plants also spend more time at small size and thus more time exposed to mortality factors (Landis and Peart 2005). However, a size-dependent mortality model is mathematically more complex and requires numerical methods to locate the optimal age and size at flowering, while growth-dependent mortality allows a simple analytical solution. We have used both modeling approaches to mortality and found that they produce very similar optimal norms of reaction. For simplicity, we present only a growth-dependent mortality expression in this article. Following Stearns and Koella (1986), we model instantaneous mortality, μ, as an inverse function of growth:

$$\mu = \mu_0 k^{-\gamma} \tag{3}$$

in which μ_0 is a fundamental mortality rate, k is the environmental parameter in the growth function, and γ determines the strength of the penalty for slow growth. A value of $\gamma = 0$ makes mortality identical at μ_0 for all plants, while increasing values of γ increase the mortality rate for plants with slow growth.

The mortality regime of Eq. 3 under power function growth yields the following size-specific survivorship:

$$L(s) = \exp\left[-\mu \frac{s_0^{1-q} - s^{1-q}}{k(q-1)}\right]. \tag{4a}$$

Under logistic growth, the survival function is

$$L(s) = \left[\frac{s_0(s - s_\infty)}{s(s_0 - s_\infty)}\right]^{\mu/k}. \tag{4b}$$

See the Appendix for the derivation of Eqs. 4a and 4b.

Fecundity, B(s)

Fecundity generally increases with plant size (Metcalf et al. 2003), which can be represented as

$$B = s^c \tag{5}$$

for $c > 0$ and arbitrary units of fecundity and size. (A proportionality constant would be required to equate size and fecundity measured in particular units.) The scaling exponent c is often near unity (when size is measured by mass) in herbaceous species, but may reach values around twice as large (Metcalf et al. 2003). In the tropical tree species *Bursera simaruba*, Hubbell (1980) found that a twofold increase in trunk circumference corresponded to a 50-fold increase in seed crop. If tree mass scales at the three-eighths power of trunk circumference, this relation implies an exponent of $c = 2.1$. This estimate, calculated from large trees that have flowered, might underestimate the effect of size on fecundity over a range that includes subadults in the understory that did not but might have flowered, however feebly.

Optimum size and age at flowering

From Eq. 1 and the expressions for survival and fecundity defined previously, it follows that the flowering size σ that maximizes R_0 is

$$\sigma = \left(\frac{\mu}{ck}\right)^{1/(q-1)} \tag{6a}$$

in the case of power function growth and

$$\sigma = s_\infty \frac{ck - \mu}{ck} \tag{6b}$$

in the case of logistic growth (see the derivation in the Appendix). The age at flowering, α, corresponding to the optimal size σ, is given by

$$\alpha = \frac{s_0^{1-q} - \left[\left(\frac{\mu}{ck}\right)^{1/(q-1)}\right]^{1-q}}{k(q-1)} \tag{7a}$$

for power function growth and by

$$\alpha = -\ln\left[\frac{\mu s_0}{ck(s_\infty - s_0) + \mu(s_0 - s_\infty)}\right] \Big/ k \tag{7b}$$

for logistic growth (Appendix). Eqs. 6 and 7 together specify the optimal norm of reaction for each growth pattern.

RESULTS

Power function growth

Fig. 1 shows optimal reaction norms for reproductive onset assuming different effects of growth on mortality and different scaling relations between size and fecundity. The reaction norms are superimposed on several growth trajectories representing a range of microsite quality (i.e., a range of values of k).

Each reaction norm in Fig. 1 is nearly vertical for much of its length, that is, optimal flowering is predicted to occur over a wide range of sizes but a limited range of ages. The age range shifts to later ages as the scaling exponent c increases (the fecundity payoff from large size becomes greater) or as the mortality parameter γ declines toward zero (when all individuals experience the same mortality rate regardless of their growth). Such differences in parameter values could mirror different plant architectures or environmental sources of mortality for different species. The essentially vertical form of the optimal reaction norms remains robust across a much wider range of parameter values than those depicted in Fig. 1. The wide range of optimal flowering sizes implied by vertical reaction norms corresponds qualitatively to observations of flowering in many long-lived monocarps (see *Introduction*), although the ages of reproductive plants are seldom known for such species.

Although the reaction norms in Fig. 1 are nearly vertical, they do show a positive relation between age and size at reproduction. This pattern is contrary to the behavior of facultative biennials, which delay flowering in poorer growing conditions (Silvertown 1984) and therefore present a negative relation between age and size at flowering. Although it is an interspecific rather than intraspecific comparison, the work of Poorter et al. (2005) suggests that rapid growth and early reproduction characterize a monocarpic tropical tree species relative to polycarpic competitors, consistent with a negative relation between age and size at first flowering.

Day and Rowe (2002) offered a simple life history explanation for a negative relation between age and size at metamorphosis in animals. They showed that power function growth with an "overhead threshold" yields reaction norms having the appropriate negative relation (and also an increasingly vertical form as the threshold size is lowered). An overhead threshold is a minimum size needed to undergo metamorphosis, but which does not itself contribute to size-related fecundity (i.e., fecundity scales only with the "excess" size above the threshold). Monocarpic flowering and metamorphosis may not be completely equivalent in this respect, and we consider in the *Discussion* whether similar thresholds might operate in plants.

Logistic growth

Optimal norms of reaction for logistic growth are shown in Fig. 2, superimposed on several growth trajectories for different values of k. These reaction

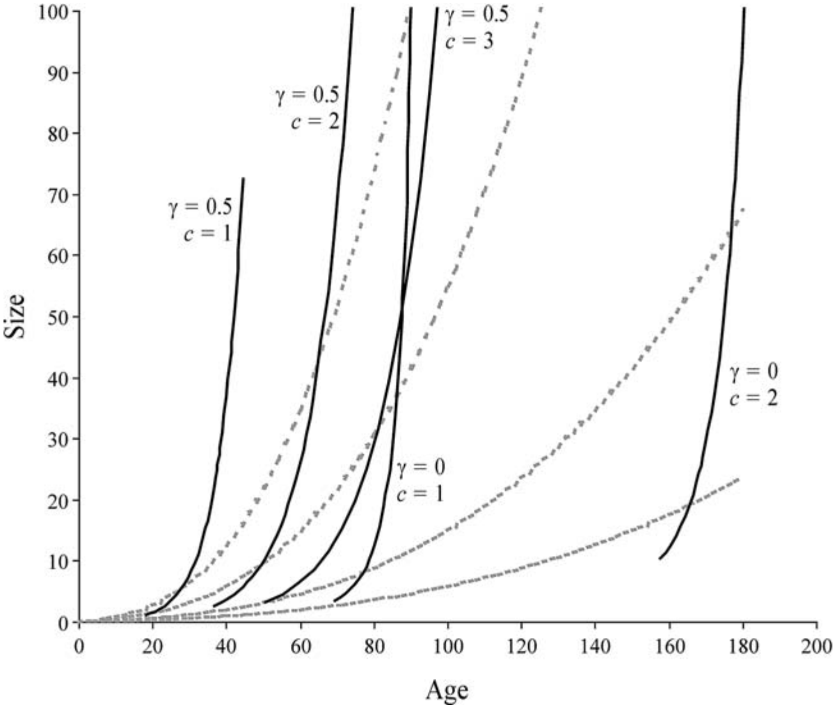

FIG. 1. Size–age reaction norms for flowering assuming power function growth trajectories. Age and size are in arbitrary units. Values of the mortality parameter γ and the fecundity scaling exponent c for each reaction norm are indicated. Values of γ between zero and 0.5 yield intermediate positions for the norms of reaction. Four growth trajectories (dotted lines) representing values of $k =$ 0.04, 0.06, 0.10, and 0.14 are shown for illustration. Other parameter values are: initial size $s_0 = 0.1$, power function exponent $q =$ 2/3, and fundamental mortality rate $\mu_0 = 0.03$.

norms are more variable in shape than those in Fig. 1, although changes in parameter values cause a qualitatively similar shift in location: greater returns to scale for fecundity (higher c) or less severe mortality penalty for slow growth (lower γ) favor a shift to the right (later flowering). The reaction norms are flatter at $\gamma = 0$ (no effect of growth on mortality) than for positive values of this parameter, i.e., reproduction occurs over a relatively limited range of sizes but with greater plasticity for age. As γ increases (the mortality penalty for slow growth increases), the optimal norms of reaction become more vertical. Higher values of γ combined with moderate values of c produce approximately vertical but curved reaction norms. Thus, a higher growth rate delays the onset of reproduction at the bottom of the reaction norm (i.e., in poorer growth environments), but accelerates reproduction at the top (among favorable environments). Comparison among the reaction norms shows that optimal flowering size and age is more strongly affected by variation in parameter values when growth trajectories are poor than when they are favorable.

So far we have assumed that all growth trajectories have the same asymptotic size, s_∞. It is possible, however, that low k would be associated with reduced potential size. For example, Ryan and Yoder (1997) suggest that slow early growth in trees brings on the development of mature vascular characteristics while a plant is small. The deleterious effects of mature vasculature on hydraulic conductance then limit future growth and potential stature of the tree. In Fig. 3, we show logistic growth trajectories in which s_∞ varies from 50 to 100 in proportion to variation in the growth parameter, k, from 0.04 to 0.14. Curves of optimal α and σ are superimposed on these trajectories. A comparison of Fig. 3 with Fig. 2 shows that growth-dependent asymptotic size shifts the reaction norms to a more vertical form, particularly for the curves corresponding to a value of $\gamma = 0$ for the mortality parameter. Although these curves are more vertical in Fig. 3 than their equivalents in Fig. 2, they nonetheless imply broad ranges of both size and age at flowering.

DISCUSSION

Size variation

We wished to understand two features of flowering in monocarpic plants: the large range of sizes at which flowering occurs and the overlap in size between flowering and nonflowering plants. Our results suggest that a large range of optimal reproductive sizes is a fairly robust prediction of simple life history models under a variety of assumptions about growth, mortality, and the scaling of fecundity. The timing of monocarpic reproduction in our models involves a gamble in which a future fitness payoff is balanced against the chance of

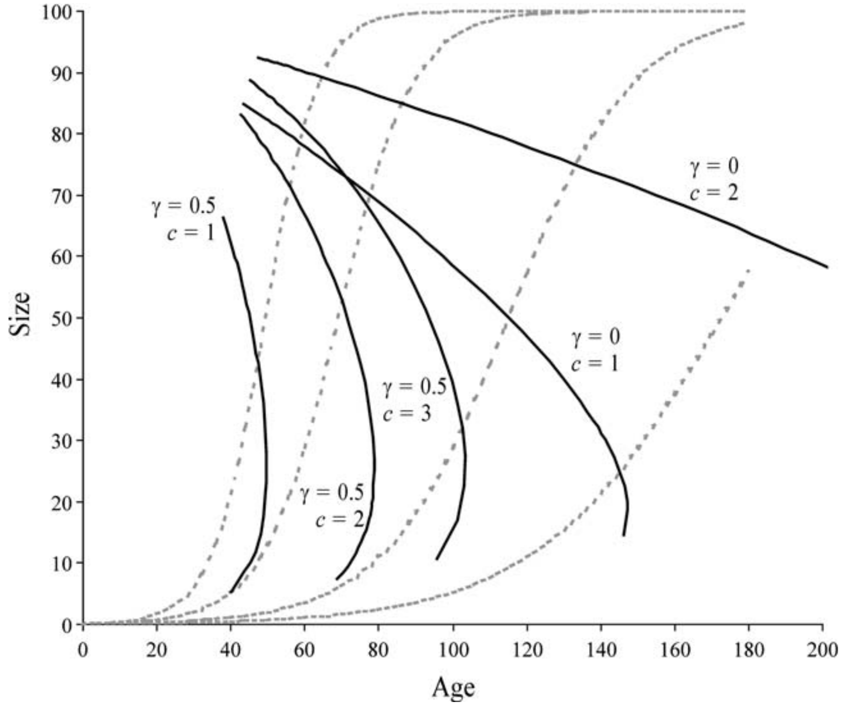

FIG. 2. Size–age reaction norms for flowering assuming logistic growth trajectories. Age and size are in arbitrary units. Values of γ and c are shown for each reaction norm and are identical to the values used to produce reaction norms in Fig. 1. Values of γ between zero and 0.5 shift the reaction norms to intermediate positions and rotate them to a more vertical form. Four growth trajectories (dotted lines) representing values of $k = 0.04$, 0.06, 0.10, and 0.14 are shown for reference. Other parameter values are: $s_0 = 0.1$, $s_\infty = 100$, and $\mu_0 = 0.03$.

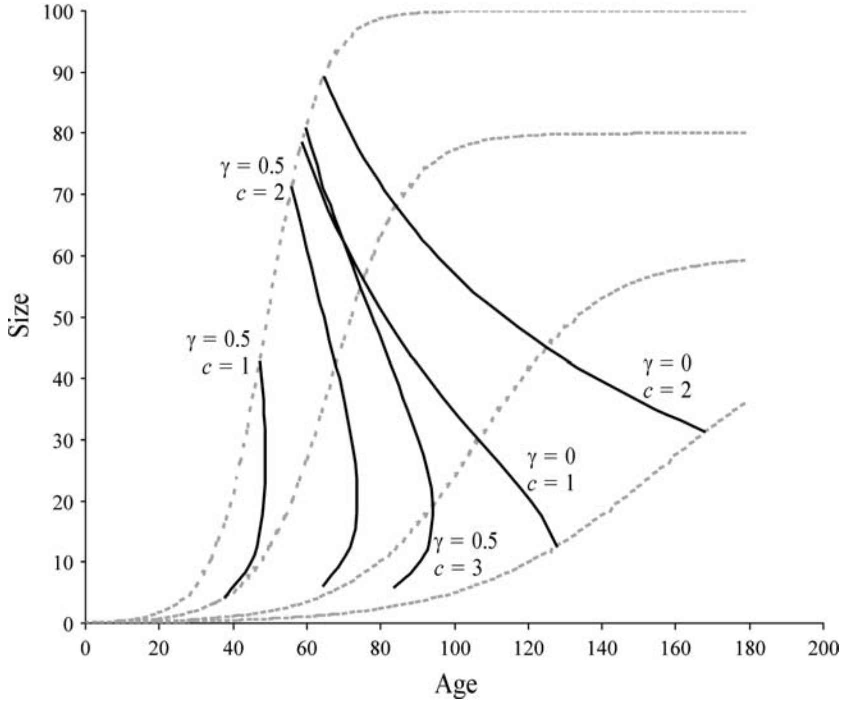

FIG. 3. Effect of growth-dependent variation in asymptotic size s_∞ on optimal reaction norms. Age and size are in arbitrary units. Four growth trajectories representing the same values of the growth parameter k used in Fig. 2 are shown for reference. All parameter values are as in Fig. 2, except that $s_\infty = 50$ for $k = 0.04$; $s_\infty = 60$ for $k = 0.06$; $s_\infty = 80$ for $k = 0.10$; and $s_\infty = 100$ for $k = 0.14$.

PLATE 1. Live trees of *Cerberiopsis candelabra* at Les bois du Sud, New Caledonia, adjacent to a tree that flowered in 2003 and subsequently died. Photo credit: G. D. Sanson.

mortality, but the quantitative structure of the bet differs within a population if the potential payoff and mortality risks vary with growing conditions. Slowly growing plants may never reach the size that will be attained by conspecifics in microsites with fewer competitors or more abundant resources, and if the mortality risk in these poor sites is higher, slowly growing plants should flower at a small size. Rapidly growing plants can "afford" to flower at a young age because they have the advantage of being large. Young (1985) hypothesized that *Lobelia telekii* responds to environmental variation in this way, and, although plant ages were unknown, growth rate, mortality, and size at flowering were consistent with the argument. The result can be a nearly vertical norm of reaction (Figs. 1–3), a pattern of plasticity that implies flowering over a large size range but limited age range. However, uniform mortality regardless of growth ($\gamma = 0$) seems to favor flatter reaction norms under logistic growth (Fig. 2). Thus, the optimal pattern of plasticity is sensitive to biological details and might vary among species.

Even with nearly vertical reaction norms, the degree of observed overlap between flowering and nonflowering plants would depend on the distribution of growth trajectories within the population. There is abundant evidence that growth conditions are often highly variable among microsites. For example, King (1993) found that the small tree *Pourouma aspera* at La Selva, Costa Rica, could take between 0.6 and 23 yr to grow from a height of 0.7 to 2.2 m. Given a large range of growth conditions and cohort ages, it is apparent that many of the reaction norms in Figs. 1, 2, or 3 would allow substantial size overlap between flowering and nonflowering plants. Indeed, large but still young plants undergoing rapid growth may not have flowered while older and small individuals suffering poorer growth have.

An interesting and analogous pattern of size overlap involving mating strategies occurs in the North American toad *Bufo woodhousii*. Males may call to attract mates or act as satellites and attempt to intercept females attracted to the calling males. Satellite males are smaller than calling males, on average, but each group displays a large range of sizes, and there is substantial size overlap between the two types. Leary et al. (2005) have shown that satellite males tend to be the ones on poorer growth trajectories, so that they adopt the satellite mating strategy even when they are the same size (but older) than calling males.

Thresholds and reaction norms

Three different meanings of "threshold" have been considered in this article. One designates a minimum vegetative size needed to create and sustain reproductive structures. This meaning corresponds to the "physical threshold" of Day and Rowe (2002), and some threshold of this type must apply to all organisms. However, simple observation of flowering sizes could be a poor estimate of this threshold, because even the smallest flowering individual in a population could have delayed reproduction past its physical threshold, if it was adaptive to do so. Experimental investigation of the

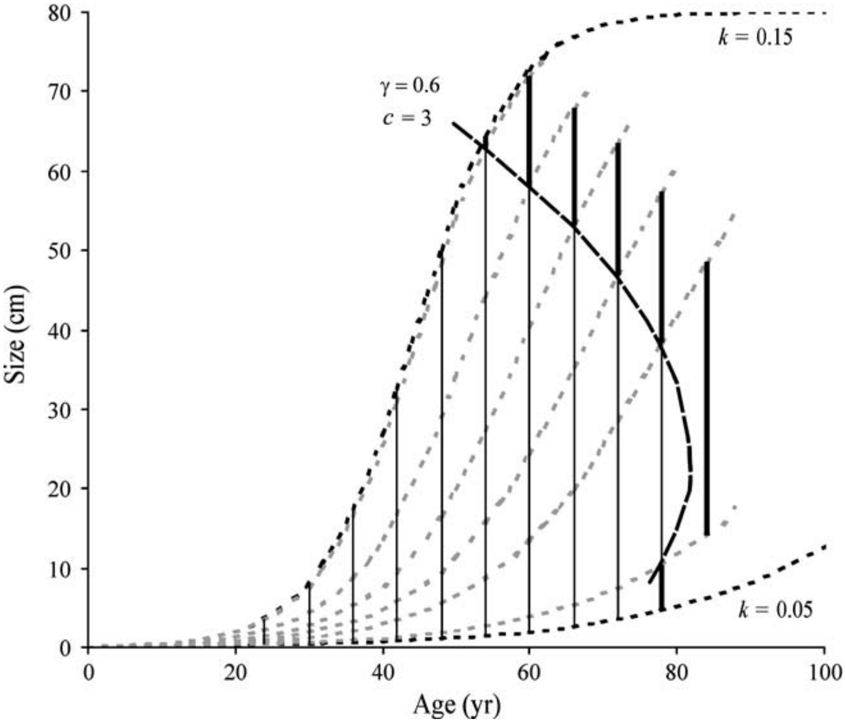

FIG. 4. Growth and flowering in a hypothetical population of *Cerberiopsis candelabra*. Size is shown in centimeters dbh, and age is shown in years. Thick dashed curves show lower and upper limits of size, assuming growth parameters in the population range from $k = 0.05$ to $k = 0.15$; thin dotted curves show growth trajectories for intermediate values of k. Pre-reproductive plant sizes are shown by thin vertical lines, and post-reproductive sizes by thick vertical lines. For parameter values and further interpretation, see *Discussion: Application to monocarpic trees*.

resource costs of flowering (e.g., Tissue and Nobel 1990) seems likely to provide better estimates of the critical size for reproduction. In any case, physical thresholds explain only why no flowering individuals occur at smaller size, not why some occur at much greater size.

A second interpretation of "threshold" relates to individual-specific effects of genetic variation, such that different individuals have different flowering thresholds (Wesselingh and de Jong 1995, Metcalf et al. 2003). We suspect that age–size reaction norms are a more likely source of flowering size variation than are idiosyncratic thresholds per se, in part because the ubiquity of environmental variation for growth over small spatial scales would seem to favor a strategy of plastic phenotypic expression of any genotype. Because reaction norms also have a genetic basis and may vary genetically among plants (de Jong 2005), considerable experimental work would be required to distinguish variable thresholds from reaction norms.

A third type of critical size is the "overhead threshold" of Day and Rowe (2002), a minimum size needed to prepare for reproduction, but which does not itself contribute to reproduction. A botanical analogy might occur in rosette plants, such as *Lobelia telekii* (Young 1985), that must invest in a large supporting stalk for the inflorescence and then need additional size-based ability to invest in flowers and fruits to gain any reproductive success. It is difficult to see that similar overhead costs would be incurred by other life forms, however. In any case, overhead costs are relevant only to the issue of the sign of the age–size relation and only in the context of power function growth. As discussed above, we expect that plant growth may often decline with increasing size apart from any effect of reproductive induction, contrary to the argument of Day and Taylor (1997) with respect to animals. Thus, the reaction norms in Figs. 2 and 3 should be most relevant to many monocarps. We note with interest, however, that nearly vertical reaction norms can occur under both growth patterns (Figs. 1 and 2), in the absence of overhead thresholds.

Application to monocarpic trees

We are now in a position to address the flowering behavior of monocarpic trees. There are few such species (Poorter et al. 2005), but they can display patterns of flowering not easily interpreted by straightforward recourse to size thresholds (Read et al. 2006). Because age is not readily determined in these tropical species, no data exist that allow us to plot the pattern of variation among individuals in both size and age at flowering. However, we can address some elements of the reproductive behavior of monocarpic trees with reference to our life history models.

Recent work by Poorter et al. (2005) on the canopy tree *Tachigali vasquezii* in the Amazon basin of Bolivia suggests that the advantage of monocarpy in this species derives from rapid growth and the relatively high survivorship to reproductive size that rapid growth provides. Median growth in stem diameter of *T. vasquezii* juveniles is about five times that of sympatric polycarpic tree species, allowing the monocarpic trees to reach reproductive maturity an average of three decades sooner than their polycarpic competitors. Although Poorter et al. (2005) addressed interspecific life history differences rather than intraspecific variation, their findings point to the central role of growth rate in the fitness of a monocarpic life history.

Cerberiopsis candelabra (see Plate 1) in New Caledonia is especially interesting because it combines monocarpy with masting (Veillon 1971). We do not yet have information on ages nor growth variation among individuals, but we know that flowering sizes vary enormously and overlap with the sizes of vegetative trees (Read et al. 2006). We therefore consider only whether these size patterns are consistent with the reaction norms in our models. Because *C. candelabra* is a canopy tree, we will assume that logistic growth is applicable, and we incorporate the masting behavior of this species by assuming that an individual tree flowers in the first masting event to occur after it reaches the optimal age–size norm of reaction for reproduction.

We suppose that the environment consists of heterogeneous microsites with variation in the logistic growth parameter from $k = 0.05$ to $k = 0.15$ (which yields realistic ages for canopy-sized trees for time measured as years). The largest *C. candelabra* tree in our sample was 79 cm dbh (Read et al. 2006), so we assign parameter $s_0 = 0.1$ cm and $s_\infty = 80$ cm to approximate seedling size and maximum size. The sizes and ages of trees in the population will then be bounded by the growth trajectories shown in Fig. 4. The vertical lines between the lower and upper growth boundaries represent the potential size range in cohorts separated by 6-yr intervals, the mean interval between masting years for *C. candelabra* (Read et al. 2006). Because we are using a linear measure of size, we set the fecundity scaling exponent at $c = 3$. For sake of demonstration, suppose the fundamental mortality rate is $\mu_0 = 0.03$ and the growth–mortality relationship is controlled by $\gamma = 0.6$. The resulting reaction norm specified by Eqs. 6b and 7b is shown as an interrupted curve in Fig. 4. Thicker segments of the vertical lines represent trees in masting years that have passed the reaction norm boundary and flowered. It is immediately apparent from this figure that the reaction norm would create flowering over a wide range of sizes, and substantial size overlap between flowering and nonflowering individuals, at approximately the sizes we observe in New Caledonia (Read et al. 2006). The gross pattern depicted in Fig. 4 could remain even with many age cohorts missing, since seedling recruitment does not occur from every masting event (Read et al. 2006).

Conclusion

The deterministic models we present here are broadly consistent with flowering patterns in at least some monocarps, and we suggest that empirical patterns of flowering in monocarps are better understood in terms of reaction norms across growth environments than as responses to size thresholds alone. Empirical testing for reaction norms will be difficult in very long-lived monocarps such as trees and alpine giant rosettes because ages will usually be unknown and unknowable. However, systematic long-term monitoring of tropical forest plots (Burslem et al. 2001) could eventually provide the required data for some monocarpic tree species (cf. Wright et al. 2005).

Some existing models of reproductive decisions in herbaceous monocarps already consider issues of environmental variation in growth rates, including stochastic temporal variation (e.g., Rees et al. 1999). We expect that unpredictability over short temporal scales would have much greater effect on flowering decisions in small, herbaceous monocarps, and stochastic models may be necessary to explain flowering patterns in such species. However, our results show that simple deterministic life history theory captures, at least qualitatively, much of the size-related flowering pattern of monocarps.

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APPENDIX

Derivation of optimal reaction norms for age and size at flowering (*Ecological Archives* E087-168-A1).