

the trimerophytes could elevate their sporangia further above the substrates upon which they grew. This relative increase in vertical stature could confer a greater spore dispersion radius, resulting in an increased potential to colonize new sites and a reduction in the local intraspecific competition among juvenile sporophytes. Significantly, the morphological changes seen in the transition from a rhyniophyte ancestor to a trimerophyte descendant confer advantages to sexual reproduction, as well as an increased tolerance to mutual shading by neighboring plants. Therefore, the trajectory predicted by computer analysis of branching patterns maximizes the relative success of vegetative structures and confers a potential increase in reproductive success.

Conclusion

The application of biomechanical analyses may be viewed as an extremely reductionist approach to organismic biology. But the appropriate transcription of form into quantitative descriptions of function can nevertheless reveal inherent limits on form-function

correlates and may be used to explain why plant morphology does not vary continuously throughout the domain of all possible shapes, but rather shows discretely nested expressions within the domain. The use of biomechanical approaches to identify the biologically 'possible' from the biologically 'impossible' may not have been what Sir Arthur Conan Doyle had in mind when he wrote 'when you have eliminated the impossible, whatever remains, however improbable, must be true', but the research agenda that this philosophy brings to mind is none the less full of promise.

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Onset of Reproduction in Plants: Size- versus Age-dependency

Elizabeth P. Lacey

Understanding the roles of age and size in the timing of first reproduction or flowering in plants has become a goal for those investigating the evolution of life cycle patterns in general. Here I review the studies that are helping to clarify these roles, and indicate some directions for future research.

In plants, the critical life cycle phases are embryo development on the maternal parent, seed growth (or dormancy) independent of the parent, vegetative growth and reproduction (Fig. 1). Each phase is characterized by a particular rate of resource acquisition and

pattern of resource allocation, e.g. to vegetative versus reproductive structures. The time of transition from one phase to the next marks the time when one set of phase-specific acquisition and allocation patterns switches to another set. A plant's zygotic life begins at fertilization. Its vegetative life begins at germination.

Time of transition from vegetative growth to reproduction (time of first flowering) has recently received much attention from evolutionary ecologists. This interest began in earnest in the early 1970s at the time that Harper and White¹ published a paper on the demography of plants, which showed that age at first reproduction is delayed as 'lifespan' (really, vegetative life-

span) lengthens (Fig. 2). The correlation was clear; the causes of the correlation, however, were not. Because plants often grow indeterminate, vegetative age and size can be strongly correlated. Thus, is time of first reproduction determined by age or size?

Size-dependency

Size is a good predictor of the onset of flowering in short-lived (mostly biennial) monocarps²⁻⁶, long-lived monocarps⁷⁻⁹, polycarps with long-lived monocarpic ramets^{9,10}, other polycarps¹¹, and monocarps that sometimes become polycarpic¹². Size-dependency of onset of reproduction, however, varies greatly among species.

Annuals are notably absent from this list. Natural populations of many annuals, even of wild progenitors of crop species, show great variation in the density and size at which they flower^{13,14}. In many of these plants, flowering is initiated by an external environmental cue like photoperiod, and individuals

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respond to the cue independently of size (and independently of density, which strongly determines size).

Three factors have probably led to this size-independent behavior in annuals. First, the length of the growing season is usually unpredictable, whether the limiting environmental variable be drought, heat, cold, etc. Second, the quality of the growing season often varies. Third, and most important, annuals by definition lack the ability to survive the period between growing seasons; what is predictable is their death within a year after germination. For all these reasons selection should strongly reduce size-dependency, i.e. reduce the threshold size for flowering such that it seldom determines onset of flowering. This reduction ensures that some seed is set every season, irrespective of the length and quality of the season. Variable seed dormancy, which prevents all offspring from germinating in any one year, and a predictable length of growing season could allow size-dependency to develop.

In non-annual plants, environments should select for size-dependency of the onset of flowering in cases where size influences fecundity or risk of mortality. In many monocarps and polycarps, mortality declines^{2,3,9,10,12,15-18} and fecundity rises with increasing size^{5,6,8-10,12,15,18}. A correlation between size and the onset of flowering has been found in many of these same species^{2,3,5,6,8-10,12,18}.

If size alone influences the evolution of time of first flowering, then the environment should favor an onset of reproduction when the size (X) maximizing net reproductive rate (R_0) is reached (Fig. 3). (R_0 estimates fitness independently of age at first reproduction.) No one has yet described the relationship between size at first reproduction and R_0 for any species, and only now are studies beginning to describe the effects of size on mortality and fecundity, which are the determinants of R_0 . Risk of mortality declines exponentially with increasing size of the vegetative plant in several monocarpic and polycarpic species^{3,17,18}. In some cases, however, mortality begins to increase if plants become 'too' large; for example, rock hyraxes

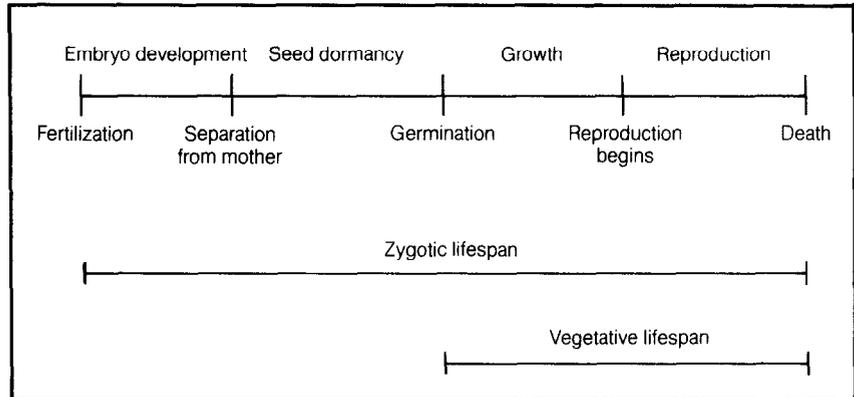


Fig. 1. Phases in the life cycle of a plant.

prefer to eat large rather than small rosettes of *Lobelia telekii*⁹. Seed set increases linearly with size in some species^{5,6} but exponentially in others^{10,12,18}. Eventually, fecundity should approach some asymptote, as in *Oenothera glazioviana*¹⁸, when morphology and physiology constrain further growth.

Several studies suggest that fecundity in monocarps should initially increase exponentially. First, many monocarpic species produce a large flowering stalk from a basal rosette. The initial cost of this stalk is high, but once the stalk is produced, a plant can produce more flowers with little additional expense^{5,19}. Also, the more flowers per stalk, the higher is a flower's probability of being pollinated, at least in monocarpic species of *Agave*⁷. Alternatively, fecundity may

increase with size if, by delaying flowering until a larger size is reached, a plant produces enough seeds to satiate seed predators²⁰ or grows sufficiently large to garner more space for the establishment of its offspring²¹.

Age-dependency

Given the wealth of empirical studies showing the effect of size on mortality and fecundity, and the theoretical arguments for the evolution of size-dependency, one wonders if the onset of flowering could be determined by anything other than size. Because size and vegetative age are often strongly correlated, most discussions have centered on vegetative age. Does flowering ever begin at a given age independently of size? Do environments ever favor flowering

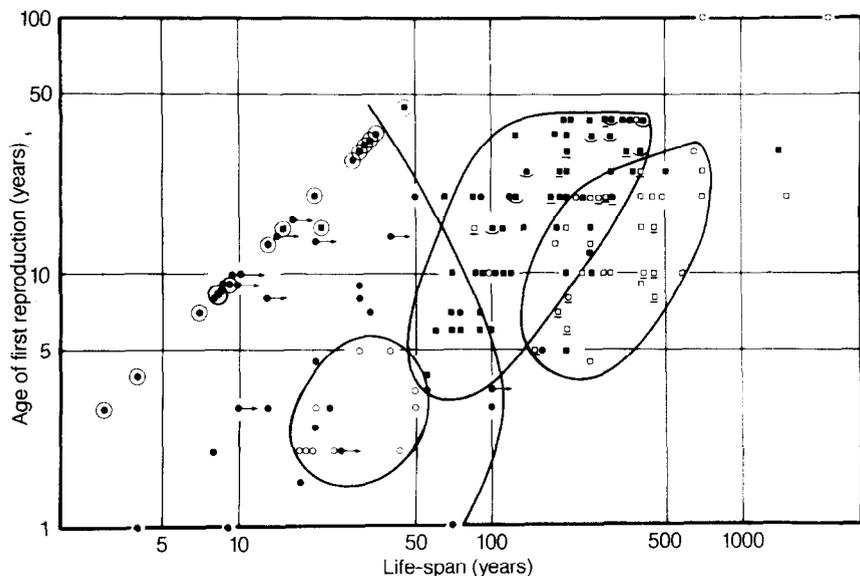


Fig. 2. The relationship between prereproductive life (or juvenile period) and total lifespan for perennial plants. The data give known normal life spans and not exceptional examples of great longevity. Key: ● herbs; ○ shrubs; ■ trees (angiosperms); □ trees (conifers); ○ monocarpic; ■ *Quercus* spp.; ■ *Carya* spp.; □ *Pinus* spp. The heavy lines roughly delineate each group of species. Redrawn from Ref. 1, with permission from Annual Reviews Inc.

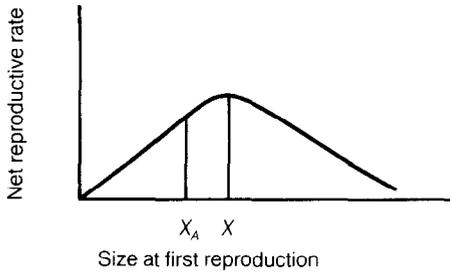


Fig. 3. Net reproductive rate (R_0) expressed as a hypothetical function of plant size.

at a given age independently of size? Recent life-history studies of monocarps show that size-related transition matrices are better than age-related transition matrices at predicting population growth²⁻⁴. Unfortunately these studies do not test the predictive capabilities of a matrix combining both age and size transition probabilities, and therefore do not show whether age as well as size influences the year of flowering. Experiments with *Verbascum thapsis*⁵ and *Daucus carota*²², however, show that the year of flowering is influenced by both population and maternal year of flowering even when size is held constant. Also, cuttings of bamboo genets bloom in a specific year, e.g. after 120 years, regardless of whether they occupy several hectares in India or are confined to a small section of a botanical garden²⁰. When biologists have looked for a genetic component to age of flowering, they have found one. Thus, one must conclude that age influences onset of reproduction in at least some species.

There are several possible reasons why flowering time might depend on age. First, earlier onset

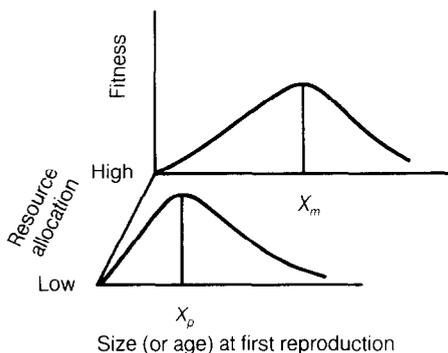


Fig. 4. Fitness expressed as a hypothetical function of size (or age) and allocation of resources to a reproductive event.

of flowering should be favored over delayed flowering because reproducing early enhances an individual's relative fitness more effectively than does reproducing late, even when the delay augments seed production²³. Delaying flowering until the second year for a monocarpic plant pays only if the plant grows sufficiently large in the second year to produce the square of the number of seeds it would have produced the first year¹³. For a monocarp producing 100 000 seeds in the 50th year, delaying flowering for one year pays only if it can produce 25 000 additional seeds in the 51st year. Fitness depends on both size and age, and onset of flowering may begin at a size that does not necessarily maximize R_0 (e.g. X_A in Fig. 3). In this case population growth rate (r) estimates fitness better than does R_0 .

One must be cautious, however, with this explanation for the evolution of age-dependency. The time from fertilization to first flowering does not often equal the length of the vegetative phase of the life cycle (Fig. 1). For example, many annuals and some 'short-lived' species have a short vegetative phase but a long seed phase, often enforced by the environment. Accelerating reproduction does not benefit these species, because their seeds can lie dormant for years^{5,13,19,24}. Instead, delaying reproduction allows a plant to augment its contribution to the seed pool even if only by a small amount. High seed mortality relative to vegetative mortality also favors delayed reproduction²⁴. In general, the effect of accelerating reproduction on relative fitness helps to explain the presence of age-dependency only in species having a short seed phase, for example sand dune species like *Oenothera glazioviana*¹⁸ whose germination is not restricted to recently disturbed sites.

A second and more pervasive factor favoring age-dependent onset of flowering is probably variation in time-dependent mortality and fecundity²³. Studies of several short-lived monocarpic species show that mortality increases after the fourth year irrespective of size²⁻⁴. Thus, flowering occurs on average after 2-3 years in these species not just because 2-3-year-

olds may produce more seeds than 1-year-olds but also because individuals that do not flower by this time do not flower at all. Time-dependent forces might also affect fecundity. For example, late successional plants (species or individuals) could limit growth of early successional plants. Second and third cohorts of *Verbascum thapsis*²⁵ and *Viola fimbriatula*¹⁵ both grow more slowly and suffer higher mortality than does the first cohort.

Size- versus age-dependency

Size and vegetative age are strongly correlated early in the vegetative phase of the life cycle. Thus, if flowering begins early in the vegetative phase, both can be used to predict the time of first flowering. The primary factor determining time of first flowering in plants is probably the amount of resources accumulated^{13,14}.

As a vegetative plant ages, however, the correlations among size, age and resource accumulation change. The correlation between size and age weakens¹³. Size becomes the better predictor of accumulated resources. For this reason alone, one would predict that as the vegetative lifespan increases, the time of first flowering should become increasingly size-dependent and less age-dependent.

Schaffer and Rosenzweig²⁶ argued that environmental variance or unpredictability should favor size-dependent over age-dependent onset of reproduction. Whether or not this proves to be true may rest on the time in the life cycle when variance is greatest. Variance in mortality during the early vegetative phase or in growth itself, which affects seed set, should favor delayed reproduction^{23,27,28}. The delay could intensify either size- or age-dependency. One study suggests that size-dependency intensifies. In *Daucus carota*, the size at time of flower induction and the growth rate just prior to the time of flower induction both predict the year of flowering²². Plants growing slowly just prior to induction are more likely to flower than are those growing quickly. This result suggests that flowering can be affected by even temporary environmental changes that affect relative changes in size. Such flexibil-

ity could be highly advantageous for individuals with a short zygotic lifespan.

By contrast, environmentally induced variance in length of the seed phase could intensify age-dependency. Delaying reproduction can enhance fitness for a plant that spends more of its time in the vegetative and reproductive phases combined^{5,13,19,24}. If a fluctuating environment causes variations in the length of the seed phase, however, then a plant reproducing early is favored^{24,29}. Earlier reproduction probably occurs by intensifying age-dependency.

Effects of resource allocation

Resource allocation may also influence both time of first reproduction and the degree of size- and age-dependency. At the proximate level, the ability of a plant to move resources among its modules determines the independence of the modules³⁰. (Here a module is an iterative unit that can both grow vegetatively and produce flowers.) Rapid resource translocation should facilitate reproduction because materials needed for successful flowering and seed packaging can converge more quickly. Limited translocation should delay the onset of reproduction.

Increasing the independence of modules should intensify selection of size-dependency of flowering. A hypothetical example is a genet periodically producing ramets that separate from each other immediately after production. Flowering linked to genet age would cause all existing ramets to flower at the same time; many ramets could die before that time is reached, and some ramets will be too small to set seed successfully. Only if flowering is delayed to a very old age, as in bamboo²⁰, might flowering linked to genet age be successful. More often flowering is probably linked to ramet size, as in *Puya dasyliriodes*¹⁰ and two species of *Lobelia*⁹.

A change in the proportion of resources devoted to reproduction once it has begun within a module may also alter the time of first flowering and age- and size-dependency. Perennial monocarpic species begin flowering later than

do perennial polycarpic species with the same vegetative lifespan (Fig. 2). Because monocarps shunt all their resources into one reproductive event, the environment may more strongly favor growth to a size large enough to ensure adequate seed set. Polycarps initially commit only a small proportion of resources to reproduction. Thus, early onset of reproduction should be favored more in polycarps than in monocarps having the same zygotic and vegetative lifespans ($X_m > X_p$ in Fig. 4). Schaffer and Schaffer⁷ argue that size-dependency should develop more strongly than age-dependency in monocarps. In *Agave*, for instance, size influences pollinator attraction more in monocarpic than in polycarpic species⁷.

Conclusions

It is clear that size and age can both influence time of first reproduction in plants. To understand more about their relative importance, and to determine some of the evolutionary mechanisms underlying the timing of the onset of reproduction, tests of the following hypotheses are needed.

- (1) As vegetative lifespan lengthens, age at first reproduction becomes more size-dependent and less age-dependent.
- (2) Onset of flowering in perennial monocarps is more size-dependent and occurs later than in polycarps having the same zygotic and vegetative lifespans.
- (3) Temporary reductions in quality of the environment accelerate flowering in monocarps but delay flowering in polycarps. Short-lived species respond to temporary changes in environmental quality more than do long-lived species.
- (4) Onset of flowering in genets composed of physiologically independent modules is more size-dependent and occurs later than in genets having physiologically integrated modules.

Few empirical studies have examined the relationship between resource allocation and year of first reproduction, and consequently there are few data to test the above hypotheses. Studying the effect of resource allocation on age at first flowering in polycarps is difficult

because it requires monitoring individuals from the seedling stage into the reproductive phase. Measuring the effect of age or size at first reproduction on fitness requires following individuals over their vegetative lifespan. This should be possible at least for short-lived polycarps.

Acknowledgements

I thank J. Antonovics and D. Simberloff for their comments on an earlier draft of this article.

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