

Ecology and Evolution of Long-lived Semelparous Plants

Truman P. Young and Carol K. Augspurger

One of the more dramatic life histories in the natural world is that characterized by a single, massive, fatal reproductive episode ('semelparity'). A wealth of increasingly sophisticated theoretical models on differential life history evolution have been produced over the last two decades. In recent years, empirical studies of the ecology of semelparous plants (and their iteroparous relatives) have begun to address many aspects of the biology of these species, and to test the assumptions and predictions of theoretical models. Semelparity in long-lived plants is one of the few natural phenomena that has yielded specific quantitative tests of mathematical evolutionary theory.

Semelparity is a distinct life history in which a massive reproductive output is directly associated with preprogrammed whole-organism death. (The alternative – repeated reproduction – is known as iteroparity.) In plants, the syndrome of death after first reproduction can occur on several levels: (1) death of the reproductive meristem or ramet; (2) death of the physiological individual, not including disconnected ramets; and (3) death of the entire genetic individual. In this review, we restrict ourselves mainly to long-lived semelparous plant species that grow for at least five to ten years, and up to several decades, before reproduction and death of the entire individual. The botanical terms monocarpy and polycarpy are equivalent to the general terms semelparity and iteroparity, which refer to both plants and animals.

Many short-lived plants and animals are semelparous. Among long-lived organisms semelparity is relatively rare, but taxonomically diverse, including both vertebrate (salmon, alewives) and invertebrate (cicadas, squids) animals, and a wide variety of plant species in at least 20 families.

The ecological and morphological diversity of long-lived semelparous plants can be classified into two basic syndromes (Table 1). In the first are unbranched rosette plants with terminal inflorescences; these

species often occur in habitats where plants have slow growth rates, such as deserts¹, tropical alpine² and subalpine areas, bogs and epiphytic positions. In the second are highly branched woody species with strong population-level reproductive synchrony; these species occur in more mesic habitats.

The massive translocation of resources at the time of reproduction is fundamental to the biology of semelparous species. Stored resources from roots, stems and leaves are moved to reproductive structures at the time of flowering^{3–5}. It appears that in truly semelparous plants, virtually all available resources are devoted to reproduction^{3–5}. This massive and destructive reproductive effort makes plant death inevitable, but results in reproductive outputs far higher than the output per episode of closely related iteroparous species or subspecies^{3,6,7} (Table 2). This parallels similar patterns in short-lived semelparous plants and their iteroparous relatives that first flower at a similar age³. This syndrome of whole-organism death associated with high reproductive effort is a special case of the more general phenomenon of the cost of reproduction in plants and animals.

Fruit and seed production in semelparous *Yucca* and *Lobelia* are highly variable, and strongly related to resource availability^{3,8}. This is not surprising, given that there is no alternative sink for resources. On the other hand, closely related iteroparous species may keep reproductive output relatively constant with increasing resource availability, but increase allocation to vegetative structures³. Again, this parallels similar patterns in short-lived semelparous plants and their iteroparous relatives³.

By definition, long-lived semelparous plants have extended juvenile stages, from a few years to several decades. This 'delayed reproduction' in semelparous species has been the subject of considerable attention^{4,9,10}. However, closely

related iteroparous species have similarly long juvenile stages^{6,11,12}. Many iteroparous trees and shrubs and most large rosette plants have delayed reproduction. The long juvenile period is perhaps more noted among semelparous species because it is followed by only a single reproductive episode.

An additional consequence of slow growth rates and the giant rosette growth form is the extended time between the initiation of inflorescence formation at the apical meristem in the central leaf bud and final seed maturation, which can be many months to years^{4,6,9,13}. This delay means that the environmental conditions under which flowering is initiated are likely to be different from the conditions into which seeds are dispersed, making it difficult for plants effectively to track year-to-year environmental variation. Additionally, long-lived semelparous plants often exhibit little or no seed dormancy^{5,6,9,10,13–15}, putting them further at the mercy of environmental variation (but see Box 1).

There is little understanding of the genetics or the physiology of semelparity in long-lived plants. However, semelparity in long-lived plants occurs in at least 20 families (Table 1), and has apparently evolved many times. The existence of intraspecific variation in this trait^{7,16} and interspecific hybrids between iteroparous and semelparous species^{11,17} suggests that the number of mutations required to evolve semelparity is not large.

For a physiological explanation of semelparity, a source–sink model may be appropriate. In short-lived perennial species that were normally unbranched and semelparous, experimental elimination of the sink (pollinator exclusion and flower removal in *Ipomopsis*¹⁸) and supplementation of the source (high soil nutrient treatments in *Picris* and *Scabiosa*¹⁹) resulted in branching and iteroparity. Application of fertilizer to normally semelparous bamboo can also result in iteroparity¹⁰.

Truman Young is at the Center for Population Biology and Dept of Botany, University of California, Davis, CA, USA; Carol Augspurger is at the Dept of Plant Biology, University of Illinois, 505 S Goodwin Av., Urbana, IL, USA.

Table 1. Known long-lived semelparous plants

	Family
Unbranched rosette plants with hapaxanthic shoots	
Alpine	
<i>Lobelia</i> spp. (Africa)	Lobeliaceae
<i>Trematolobelia</i> spp.	Lobeliaceae
<i>Argyroxiphium</i> spp.	Compositae
<i>Espeletia floccosa</i>	Compositae
<i>Puya</i> spp. (South America)	Bromeliaceae
<i>Echium wildpretii</i>	Boraginaceae
<i>Lupinus alopecurooides</i>	Leguminosae
Subalpine	
<i>Frasera speciosa</i> (western US)	Gentianaceae
<i>Harmsioplanax ingens</i>	Araliaceae
<i>Phoenicoseris</i> spp.	Compositae
<i>Centaurodendron dracenooides</i>	Compositae
Arid and semi-arid	
<i>Agave</i> spp.	Agavaceae
(<i>Furcraea</i> spp.)	Agavaceae
<i>Yucca whipplei</i> ssp.	Agavaceae
<i>Aeonium</i> spp.	Crassulaceae
<i>Wilkesia gymnoxiphium</i>	Compositae
Bogs	
<i>Lobelia</i> spp. (Hawaii)	Lobeliaceae
<i>Puya dasylirooides</i> (Central America)	Bromeliaceae
Epiphytic	
<i>Tillandsia</i> spp.	Bromeliaceae
Other	
<i>Corypha</i> spp.	Palmae
<i>Plectocomia</i> spp.	Palmae
<i>Frasera caroliniensis</i> (Eastern US)	Gentianaceae
Insufficiently known (unbranched?) rosette plants with hapaxanthic shoots^a	
<i>Aechmanthera</i> spp.	Acanthaceae
<i>Boea</i> spp.	Gesneriaceae
<i>Brillantarsia nitens</i>	Acanthaceae
<i>Dendroseris</i> spp.	Compositae
<i>Drachophyllum verticillatum</i>	Epacridaceae
<i>Ensete</i> spp.	Musaceae
<i>Greenovia</i> spp.	Crassulaceae
<i>Heterochaenia</i> spp.	Campanulaceae
<i>Hymenoxys</i> spp.	Compositae
<i>Kalanchoe</i> spp.	Crassulaceae
<i>Orchis</i> spp.	Orchidaceae
<i>Spathelia</i> spp.	Rutaceae
<i>Sohnreyia excelsa</i>	Rutaceae
<i>Streptocarpus</i> spp.	Gesneriaceae
<i>Tauschia decipiens</i>	Umbelliferae
<i>Yunquea tenzii</i>	Compositae
Synchronously flowering branched woody plants	
Bamboo spp. (>17 genera, >150 species)	Gramineae
<i>Mimulopsis solmsii</i>	Acanthaceae
<i>Strobilanthes</i> spp.	Acanthaceae
<i>Tachigalia</i> spp.	Leguminosae
<i>Cerberiopsis candelabrum</i>	Apocynaceae
Parasite on <i>Strobilanthes</i>	
<i>Campbellia aurantiaca</i>	Orobanchaceae

^aMostly from Refs 5, 30 and 44.

Theoretical approaches to the evolution of semelparity

Numerous theoretical treatments of the differential evolution of semelparity and iteroparity have been developed over the last two decades. All assume a trade-off between present and future reproduction, i.e. that semelparity is associated with an increase in fecundity (Table 2). All of these treatments are mathematically related, but they fall into three basic types of model.

Bet-hedging models

One set of models predicts that increasing environmental variability and unpredictability favor iteroparity over semelparity^{20,21}. This formalizes the intuition that limiting reproduction to a single episode is particularly risky in an unpredictable environment (see Box 1). However, some bet-hedging analyses produce the opposite prediction²². In addition, many semelparous, and not iteroparous, plants are found in habitats likely to be more variable. Annuals and biennials are typically found in habitats that are ephemeral and unpredictable, either successional (disturbed sites) or edaphically (deserts and dunes). Long-lived semelparous rosette plants are commonly found in drought-prone habitats (Table 1), which can be highly variable with respect to rainfall and correlated demographic parameters^{3,6,9,11,17,23}. The variability of these environments is particularly difficult to track for plants without seed dormancy and with long inflorescence preformation times, as are common in long-lived semelparous plants.

Reproductive effort model

A second theoretical approach considers the relationship between present and future reproduction. In particular, Schaffer and Rosenzweig argued that selection for ever-increasing reproductive effort can lead to the evolution of semelparity²¹. One subset of that theory predicts that when the curve for the relationship between reproductive effort and reproductive success is convex, semelparity will be favored (Fig. 1a). Therefore, they predicted that when there is a positive correlation between reproductive effort and reproductive success per unit

Table 2. Estimates of relative reproductive outputs of closely related long-lived semelparous and iteroparous rosette plants

Semelparous	Iteroparous	Trait	Ratio ^a	Ref.
<i>Lobelia telekii</i>	<i>L. keniensis</i>	Inflorescence dry weight	3-4	3
		Seed set	4-5	3
<i>Espeletia floccosa</i>	<i>E. schultzii</i>	Total seed weight	3.6	6
<i>Yucca whipplei</i> ssp. <i>parishii</i>	<i>Y.w.</i> spp. <i>caespitosa</i> and <i>intermedia</i>	Panicle height times panicle diameter	~4.0	7

^aEstimates for *Yucca* and *Espeletia* are based on our calculations using published data from populations in close proximity.

reproductive effort, semelparity will be favored, but when this relationship is absent or negative, iteroparity will be favored (Fig. 1b).

Interspecific comparisons of field data from three different genera (*Yucca*, *Agave*, *Lobelia*) have all shown precisely this pattern. In the semelparous species, there were significant positive correlations between inflorescence size and relative fruit set or seed set, whereas in the iteroparous species, no such correlation was found^{1,3}. Although this represents a remarkable coherence of theoretical prediction and empirical data, so far there is no compelling evidence of a causal relationship between patterns of reproductive success in these genera and their differential life history evolution. Differential pollinator preference for larger inflorescences was initially proposed as a causal mechanism¹, but more recent experimental evidence indicates that pollinators may not limit seed set or fruit set in some of these species^{13,24,25}, and alternative, non-adaptationist explanations are possible³. In addition, some 'semelparous' *Agave* species are clonally iteroparous^{1,4,8}. Nonetheless, the theoretical basis of this model remains sound, and could potentially operate not only through pollinator preference, but also through predator satiation^{10,26} or pollination efficiency¹⁰.

Demographic models

The third theoretical approach to the evolution of semelparity considers the demographic conditions under which the loss of all future reproductive episodes is more than made up for by the increase in fecundity associated with semelparity. This approach has led to a series of increasingly complex and 'realistic' demographic models^{20,27-29} (Box 2). However, increasingly complex models^{20,27} become increasingly impractical to test. Summarized, these models predict that as repeated reproduction becomes increasingly unlikely, semelparity is more likely to evolve. One of these models has been used in conjunction with long-term demographic data to show how the decreased likelihood of repeat reproduction in drier sites can explain the evolution of semelparity in *Lobelia* spp. on Mount Kenya³.

Semelparous syndromes

The two distinct syndromes of long-lived semelparous plants shown in Table 1 differ in many aspects of their morphology and ecology. It is likely that natural selection has operated in different ways to produce semelparity among these species.

Unbranched rosette plants

In some plants with terminal inflorescences, axillary buds are produced at the bases of the inflorescences, and the reproductive shoots continue to grow after flowering. In other species, there are no distal axillary buds, and the entire shoot dies after flowering. Such shoots are called 'hapaxanthic'³⁰. Unbranched hapaxanthic plants (architecturally, labelled 'Holttum's model' by Halle³⁰) are semelparous; branched hapaxanthic plants ('Tomlinson's model') are iteroparous. All semelparous rosette plants in Table 1 are unbranched and hapaxanthic. Most have close relatives that are hapaxanthic, but branched and iteroparous^{4,8,11,12,14,17,30}. Therefore, branch pattern is intimately related to life history in this group (although there are *Agave deserti*¹⁶ and *Puya dasylirioides*¹⁷ plants that both branch and are semelparous when side rosettes flower along with the main rosette).

It appears that rosette plants with hapaxanthic shoots are predisposed to evolve semelparity. Virtually all such taxa known to us include at least one species that has evolved semelparity. This is remarkable, considering the relative rarity of semelparity among long-lived plants. In contrast, rosette taxa with terminal inflorescences that are not hapaxanthic ('Chamberlain's model' and 'Leeuwenberg's model')

Box 1. Variable generation times in semelparous plants: alternate strategies

Semelparous organisms have a particular problem when faced with environmental unpredictability. Because semelparous plants 'put all their eggs in one basket', individuals that flower in years of total reproductive failure have zero lifetime fitness, a fate iteroparous plants may avoid by flowering more than once. Any cohort of semelparous plants with invariable generation times would run the risk of extinction in environments with even rare unpredictable years of reproductive failure.

Semelparous plants appear to solve this problem in two different ways. For annual plants, in which the time between germination and flowering is largely fixed at a single growing season, strong seed dormancy provides considerable variation in generation time within each cohort⁴². In non-annual semelparous plants, seed dormancy is weak or absent. This holds for short-lived (Table 3) and long-lived^{15,6,9,10,13-15} semelparous species. In these species, however, there is considerable variation in post-germination maturation times^{6,9,11}, which has been suggested as advantageous to semelparous plants in unpredictable environments⁹. This variation could be inherent but it is more likely due to microenvironmental variation^{6,11}. Annual plants, with only minimal recourse to variable maturation rates⁴³, have evolved seed dormancy as an alternative strategy.

In long-lived semelparous species, particularly those that are synchronous^{5,10}, seed dormancy may even be selected against⁴, if suitable establishment sites are created by the deaths of adults⁴¹.

have no semelparous representatives³⁰.

Schat *et al.* found that several traits are strongly associated with semelparity in short-lived perennial plant species³¹. These include the rosette growth form, terminal inflorescences and large tap roots. The fact that these traits are overrepresented also among the iteroparous species in the same families that have many semelparous species suggests that they predispose certain taxa to evolve semelparity.

An additional predisposing factor may be indeterminate inflorescences³². A large tap root and

Table 3. Seed dormancy of eastern US herbs differing in life history^a

Life history	Dormancy none or conditional ^b	Full dormancy ^b	Total species
Annuals	43 (0.49)	45 (0.51)	88
Polycarpic perennials	32 (0.68)	15 (0.32)	47
Monocarpic perennials ^c	13 (0.81)	3 (0.19)	16

^aData summarized from Ref. 45.

^bNumbers (and proportions) of species.

^cAll of these are short lived.

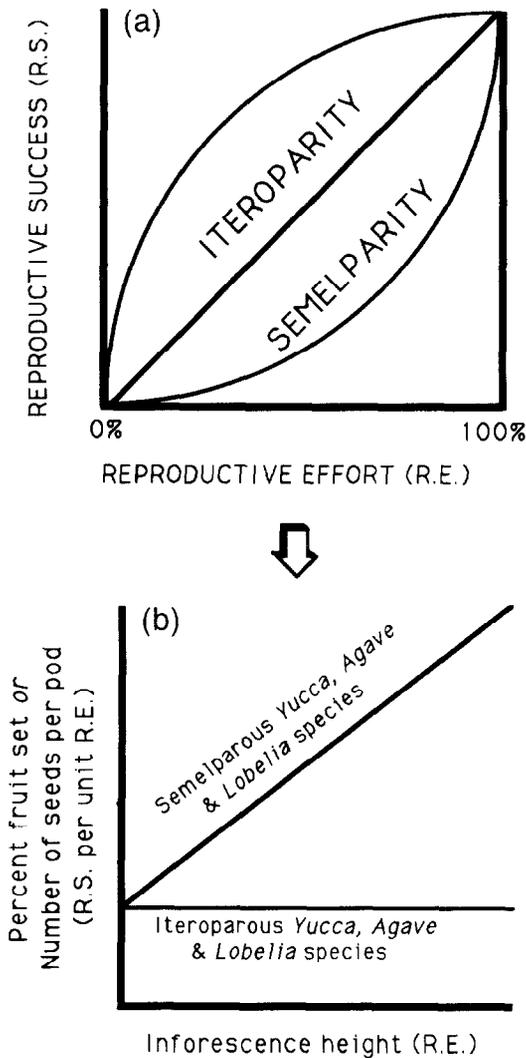


Fig. 1. (a) Putative life history consequences of alternative relationships between reproductive effort and reproductive success. (b) Observed relationships between relative reproductive success and inflorescence size in three genera of long-lived plants with both semelparous and iteroparous representatives. Redrawn from Ref. 3 with permission.

an indeterminate inflorescence provide energetic and structural potential for the large ecological and evolutionary increases in reproductive output associated with semelparity. In addition, the combination of the rosette growth form and terminal inflorescences may combine with demographic constraints to produce conditions that make the evolution of semelparity more likely. Hapaxanthic meristems die after the onset of reproduction, and rosette plants often have a limited number of active meristems. Rosette plants tend to occur in habitats where growth rates are slow, and many branched rosette plants therefore exhibit poly-annual reproduction. The mortality of any rosette is a large loss to a plant with only a few meristems, and chance mortality associated with reproduction may be high. Infrequent reproduction and high adult mortality rates may favor the evolution of semelparity in alpine lobelias³ (see Box 1). The applicability of this result to other semelparous rosette species is not known.

Branched species with strong reproductive synchrony

There are several long-lived semelparous plant species that are woody and branched (Table 1). While the previous group comprised a single growth form, this

group is morphologically more diverse, including bamboos, shrubs, trees and herbaceous parasites. Unlike most unbranched rosette species, they tend to occur in mesic, often forested, sites. All of these species exhibit strong reproductive synchrony within populations, and often over the entire species range, in which infrequent reproductive episodes are separated by long periods (up to several decades) with virtually no reproduction. Mast- ing by itself may not be uncommon³³, and occurs in several semelparous rosette plants^{6,9-11}. However, highly synchronous reproduction exhibited by entire species is rare¹⁰.

Janzen, in a review of bamboo reproductive ecology, suggests that predator satiation favors the evolution of high reproductive outputs on the level of both populations (reproductive synchrony) and individuals (semelparity)¹⁰. Reproductive synchrony also may be enforced by increased pollination efficiency^{10,33-35}. However, it is not obvious that the factors favoring strict reproductive synchrony (seed-predator satiation, pollination efficiency, seed dispersal³³) would also favor semelparity. For example, one might expect that the effects of reproductive synchrony over an entire population may often swamp the advantages of the increased fecundity of an individual plant that would be associated with semelparity. On the other hand, there may be selection for long-lived semelparous organisms to evolve reproductive synchrony^{10,36}.

Many of these highly synchronous woody species occur in low-diversity plant communities in which they are the dominant species, often forming nearly monospecific stands^{10,37}. When synchronous flowering and death occur, there are profound effects on plant³⁷ and animal¹⁰ community structure. In particular, long-lived herbivores that depend on the vegetative structures of a long-lived semelparous plant species are suddenly deprived of their main food after its synchronous flowering and death. In at least two systems [giant pandas (*Ailuropoda melanoleuca*) and bamboo^{38,39}; bongo (*Boocercus euryceros*) and *Mimulopsis*⁴⁰] this may result in herbivore population den-

Box 2. Deterministic demographic models

Demographic models of the differential evolution of iteroparity and semelparity all assume that iteroparous genotypes have less fecundity per episode than semelparous genotypes, an assumption amply supported by field data³ (Table 2). Demographic models ask: under what demographic conditions does the increase in fecundity associated with semelparity (B_s/B_i) more than make up for the loss of future reproductive episodes? These models suggest that semelparity tends to be favored by decreased adult survivorship (P), increased time between individual reproductive episodes (Z), earlier senescence (x), higher population growth rates (λ), and higher juvenile survivorship (C). Only once has any of these models (eqn 3b) been tested with empirical data. Young³ has shown that as one approaches the ecological boundary between semelparous and iteroparous *Lobelia* species, adult survivorship and frequency of reproduction decline, and suggests that at this ecological boundary, future reproduction is so unlikely that semelparity has been favored.

$$B_s - B_i = 1 \quad (1)$$

$$\uparrow P=C (=1)$$

$$B_s - B_i = P/C \quad (2a)$$

$$\uparrow \lambda = CB_s$$

$$\frac{B_s}{B_i} = \frac{1}{1 - P/\lambda} \quad (2b)$$

$$Z = 1 \quad \uparrow x \rightarrow \infty$$

$$\frac{B_s}{B_i} = \frac{1 - (P/\lambda)^{xz}}{1 - (P/\lambda)^z} \quad (3a)$$

$$\lambda = 1 \quad \downarrow x \rightarrow \infty$$

$$\frac{B_s}{B_i} = \frac{1}{1 - P^2} \quad (3b)$$

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sities above local carrying capacity as well as increased mortality and decreased reproduction. Might not these episodic herbivore population reductions be adaptive for synchronous semelparous plants? The evolutionary origin of such an adaptive behavior is not straightforward, however, and mechanisms akin to group selection might need to be invoked to explain it. On the other hand, an individual out of synchrony would pay a large price for supplying the only food available after the reproduction and death of the rest of the population, and be strongly selected against. The mortality of herbivores may be merely an added benefit of this selection.

As a semelparous plant, the tropical forest tree *Tachigalia versicolor* (along with several congeners) is anomalous^{15,41}. First, it is the only highly branched canopy tree among the species in Table 1. Second, its strong reproductive synchrony is limited to subsets of the population in a given reproductive year⁴¹. Seedlings of *T. versicolor* exhibit unusually high survivorship and physiological adjustment to varying light conditions¹⁵. It has been suggested that high juvenile survivorship can favor the evolution of semelparity²⁸, but this effect may be applicable primarily to growing populations²⁹.

The selective forces that have favored the evolution of semelparity in these reproductively synchronous species are not yet clearly understood. Empirical data are sparse, and quantitative tests of hypotheses are lacking. It is likely that different evolutionary pathways have led to semelparity among the plants that comprise the two syndromes described above.

Conclusion

The study of long-lived semelparous organisms is one of the few areas in which the marriage of theory and field studies has been fruitfully pursued. A picture of semelparity in long-lived plants that involves phylogenetic history, morphological constraints and opportunity, strong ecological and evolutionary forces, alternate evolutionary pathways and a set of well-developed mathematical theories is emerging from the literature.

Semelparity is a model system for the development of a multidisciplinary evolutionary synthesis. However, our understanding of the ecology and evolution of semelparous plants is still rudimentary. We need to know more about the phylogenetic history of the morphological traits associated with semelparity, about the physiological ecology of allocation to reproductive and vegetative meristems, and most importantly, about the population ecology of closely related semelparous and iteroparous plants. Nonetheless, the research to date on long-lived semelparous plants has stimulated some of the most interesting theory and tests of theory in evolutionary biology.

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