Herbivores and the evolution of the semelparous perennial life-history of plants

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Abstract

The relationship between a plant and its potential enemies changes drastically after reproduction has started. Using a dynamic modelling approach we study the effects of herbivores and pathogens, that are attracted by reproducing plants, on optimal allocation of resources, and life-history strategies. We assume that the level of attack increases with the investment in reproduction, which may lead to a reduction of current years reproductive success, a reduction of storage efficiency or an increase of plant mortality. If herbivores or pathogens attracted by flowering plants mainly reduce current years reproductive success, the optimal life-history is annual or iteroparous perennial if the attack is an all or nothing event. If the level of consumption increases with the number of herbivores attracted, the optimal life-history is most likely iteroparity with or without mast years. Only under very restricted conditions this may lead to semelparity. If herbivores mainly reduce the efficiency of the resources stored for next year, the optimal life-history is iteroparity. If herbivores mainly reduce survival, the optimal solution is likely to be mast years or semelparity. For parameter values that are realistic for Cynoglossum officinale, a semelparous perennial from calcereous soils, the model predicts that reproduction should start in the third year and that 99% of the available resources at the end of season should be invested in reproduction and only 1% saved for growth next year. With such an investment only c. 1% of the plants would survive after reproduction, so the optimal life-history is close to semelparity. For the small fraction of plants that reproduce more than once, years of vegetative growth only and years with reproduction should alternate. Multiple reproduction is rare in C. officinale. However, such a life history is very common for plants known as semelparous perennial. Although the available empirical evidence is, as yet, circumstantial rather than
conclusive we propose that reproduction related mortality mediated through herbivores or pathogens may play a role in the evolution of the semelparous perennial life-history.

Introduction

The evolution of the semelparous (= monocarp) perennial life-history is still one of the unsolved questions of life-history theory. It is relatively easy to understand why the iteroparous (= polycarpic) perennial life-history, with the advantage of repeated reproduction, and the annual life-history, with the advantage of avoiding the harsh season have evolved. But why do plants, that are able to survive through all seasons, invest everything in reproduction and then die? To solve this problem two lines of research were followed: a demographic approach and an approach based on optimal allocation theory. Most of the semelparous perennial plants are relatively short-lived. They are often called “biennials” because under optimal conditions for growth they reproduce in their second year (e.g., *Verbascum thapsus*, *Senecio jacobaea*). Some other semelparous plants may need a considerable longer period for reproduction (*Bamboos*, *Agaves*).

The demographic approach goes back to Charnov and Schaffer (1973) and Hart (1977) who calculated that at the optimal ratio of juvenile and adult survival a biennial has to produce at least four times the number of seeds as a perennial to achieve a higher population growth rate. A comparison of seed production of biennial and perennial plants showed that indeed on average biennials produced about four times as many seeds as perennials (Hart, 1977). Young (1981) extended the model of Charnov and Schaffer (1973) for variable times between reproductive periods. Generally this type of demographic models predict that increasing adult survivorship and age of senescence favour iteroparity and that increasing juvenile survivorship favours semelparity. When comparing the demography of semelparous *Lobelia telekii* and the iteroparous *L. keniensis* on mount Kenya, Young (1984, 1990) convincingly showed that a simple, mathematical demographic model accurately described the conditions that favoured the semelparous species over the iteroparous species.

There is however a serious limitation to this demographic approach. While it is capable of calculating why an existing semelparous type may be selected for over an existing iteroparous type in a given environment, it can, by its nature, never explain why the optimal allocation fraction to reproduction in this environment equals one instead of some lower value. To do the latter one would need to know the demography of a whole range of (geno)types with different allocation fractions.

The evolution of semelparity is an optimal allocation problem and should be studied as such. The approach based on optimal allocation goes back to Schaffer (1974) and Schaffer and Gadgil (1975). They predicted that semelparity will be favoured when fitness increases more than proportionally with the investment made in reproduction (the “reproductive effort model”). Later models on optimal growth and reproduction schedules showed that when the reproductive effort model does
not apply, i.e., when reproductive output does not increase more than proportionally with reproductive allocation, the optimal life-history schedule is either annual or iteroparous perennial, with or without mast years, but never semelparous perennial (Iwasa and Cohen, 1989; Pugliese, 1988). If reproductive output does increase more than proportionally with reproductive allocation a semelparous perennial life-history may be optimal although often iteroparous perennial life-history with mast years appears to be superior (Pugliese, 1988). Janzen (1976) argued that saturation of seed predators can be a mechanism causing a more than proportional increase in plant fitness with increasing investment in reproduction. Long-lived semelparous bamboos flower simultaneously over very large areas with a life-span of 100 or more years. By this reproductive strategy bamboos are able to saturate seed predators and can escape from predation.

Selection for every-increasing reproductive effort has also been suggested in Yuccas and Agaves. In the semelparous species of these groups, pollinators preferentially visited larger inflorescences and percent fruit set was positively correlated with inflorescence height (Schaffer and Schaffer 1977, 1979). However, later studies indicated that fruit set was limited by resources and not by pollinators in Agave and Yucca (Udovic, 1981; Udovic and Aker, 1981; Aker, 1982). A similar situation was found for Lobelia telekii by Young (1990) and for Echium vulgare (Klinkhamer et al., 1994). Young (1990) argued that the differences in patterns of reproductive success in Mount Kenya Lobelia species do not reveal an underlying set of selective forces favouring either semelparity or iteroparity, but rather these differences are likely to be the result of the fact that taller inflorescences of the semelparous species grow on more favourable sites. The same argument may hold for Echium vulgare. Other studies on the relationship between plant size and reproductive output in semelparous species revealed that seed production increased proportionally or even less than proportional with plant mass (Klinkhamer and de Jong, 1987; Klinkhamer et al., 1992).

Iwasa et al. (1995) considered the reproductive effort model in the light of the male function of reproduction (pollen export) rather than the female function (seed production). Their model on pollen export showed however that plants with many flowers (the ones with a large investment in reproduction) are relatively bad at exporting pollen because of geitonogamy (the pollination of a flower by a flower on the same plant) (de Jong et al., 1992; de Jong and Klinkhamer, 1994; Iwasa et al., 1995). The prevailing view, at least for animal pollinated plants, on male fitness nowadays is that it is a decelerating function of investment in reproduction (Devlin et al., 1992).

The reproductive effort model for explaining semelparity so far is not supported by the available empirical evidence. Of course it might be an explanation for some species, but it does indicate that it is at least not the general cause for the evolution of semelparity. We can, therefore, conclude that in contrast to the assertion of a number of recent textbooks on population dynamics and life-history theory (e.g., Stearns, 1992) the evolution of the semelparous life-history in plants is still one of the unsolved problems of life-history theory.
In this paper we want to discuss an alternative hypothesis. We will use the model by Iwasa and Cohen (1989) to investigate the possible effects of herbivores or plant diseases on optimal allocation schedules. The empirical evidence we will discuss is circumstantial rather than conclusive. Nevertheless we hope to set out the conditions under which herbivores or plant diseases may explain the evolution of semelparity.

**Herbivores and reproducing plants**

The relationship between a plant and its potential enemies changes dramatically after reproduction has started.

1. In most plants flowering stems, flowers and seeds are attacked by a variety of herbivores. Reproduction therefore adds a whole new array of potential enemies to that already present in the vegetative state. In many species these herbivores can have severe consequences for seed production (Crawley, 1983) and may alter the relationship between reproductive investment and seed production. In addition they may also enhance plant mortality.

2. A lot of plants depend for their reproduction on insects or other animals as pollen vectors. This means that flowers of these plants inevitably are frequently visited. Pollinators may however not only transmit pollen but also be the vector of viruses or other diseases.

3. Populations of a number of insect species (e.g., thrips spp.) that can also be found on vegetative leaves develop much faster when also flowers are available (de Jager et al., 1996). Also thrips are well-known vectors of plant diseases (Peters et al., 1991). Wounds caused by herbivores make the plant much more vulnerable for infections, which may reduce growth or increase mortality.

4. During stem, flower and seed development resources are reallocated from roots and leaves to reproductive plant parts (de Jong et al., 1987). Nitrogen is then transported as free amino-acids. In this form nitrogen can easily be taken up by herbivores. This improves plant quality from the herbivores point of view after the onset of reproduction. If herbivores select high quality plants, reproduction will increase herbivore pressure which in turn will reduce plant growth and may increase plant mortality.

5. Plants become much more apparent to herbivores after the start of reproduction. This increase of apparency is most obviously in rosette plants which have only a set of leaves close to the ground when vegetative and usually produce an erect tall flowering stem. Such a growth form is characteristic for semelparous perennial plants (Schat et al., 1989). Wiklund (1984) writes: “The means by which *Palaechrysothamus* locates its host plant is particularly interesting. Although the leaves of *Rumex acetosa*, on which the larvae feed, are low and do not extend above the surrounding vegetation, the butterfly females can easily find the host plant by orientating towards the inflorescences which are some 1 m high.” Many butterflies and possibly also other herbivores are known to be able to use coloured petals for the detection of host plants. Wiklund (1984) showed that: “... it is evident that the females which never seem to have difficulty in finding their host plants...”
use plants that are quite "apparent" to the human observer, either by extending above the surrounding vegetation or by being conspicuously coloured (as with many plants when in bloom). Difficulty in finding the appropriate host plants is, on the other hand, generally exhibited by butterflies that use "unapparent hosts".

Points 1 to 5 may change the relationship between investment in reproduction and reproductive output or lead to reproduction-related mortality or a decrease of the available resources for growth next season. This effects the optimal allocation pattern.

The model and results

The basic structure of the model is the same as that in Iwasa and Cohen (1989). We consider a plant living in a seasonal environment. The plant may have a storage organ and at the end of each growing season the plant must decide which fraction of its resources can be saved for the following season and which fraction can be used for reproduction in the current year. Our question is under what conditions the iteroparous perennial strategy is optimal and under what conditions the semelparous perennial strategy is optimal.

We assume that the optimal schedule within a year has already been solved so that the plant starting with storage size $S_0$ in the beginning of a season has $\phi(S_0)$ resources available at the end of the season. $\phi(S_0)$ is a decelerating function of $S$, because of shading and other resource competition among leaves or roots of the same individuals, and hence,

$$\phi(S_0) > 0, \quad \phi'(S_0) > 0, \quad \phi''(S_0) < 0.$$

The specific function of $\phi(S)$ we will use is generated as in Iwasa and Cohen (1989) (Fig. 1, Appendix 1).

The optimal life-history is the one that is evolutionary stable, and hence it is the one that maximizes lifetime reproductive success in a population that does not increase indefinitely in time. By considering the dynamic programming formalization (Iwasa and Cohen, 1989; Pugliese, 1988; appendix 2) we have:

$$V(S) = \max \{f(R) + p(R)V(\phi)[\gamma(R)(S - R)]\}$$

where $V(S)$ is the reproductive success of a plant with storage size $S$ and hence is the same as the reproductive value under the assumed population dynamics, $f(R)$ is the reproductive success of a plant with reproductive investment $R$, $p(R)$ is the survivorship of the plant after reproduction to the following years, and $\gamma(R)$ is the efficiency of the material recovered from the storage in the following season.

In the standard model of Iwasa and Cohen (1989) in which $f(R) = R$, $p(R) = \text{constant}$ and $\gamma(R) = \text{constant}$, the optimal solution is either an annual or iteroparous perennial (Iwasa and Cohen, 1989). The optimally growing plant at some point reaches a maturation size of storage, and diverts all extra resources to reproduction. As a result it stops growing and reproduces with the same size every year afterwards. Therefore, this basic case cannot explain the evolution of semelparity. If $f(R)$ is a
nonlinear function of R other solutions may be found. For instance, if \( f(R) \) is a decelerating curve, the optimal solution often includes iteroparous perennials that keep growing after reproduction (Iwasa and Cohen, 1989). If, on the other hand, \( f(R) \) is an accelerating curve either monocarp or fluctuating reproductive activity (mast years) can be the optimal solution (Pugliese, 1988).

Herbivores affect either current year reproductive success, survival to the following year, or storage efficiency. If the level of herbivory is (partly) determined by the investment in reproduction (\( R \)) then \( f, p \) and \( \gamma \) become (non-linear) functions of \( R \). Here we want to study if herbivores can shape \( f(R), p(R) \) and \( \gamma(R) \) in such a way that semelparous perennial can be the optimal solution. The basic assumption in this paper is that the number of herbivores on a plant increases with the investment in reproduction (\( R \)).

**No effects of herbivores**

The growth function we use in this paper is one that is realistic for *Cynoglossum officinale* (this will be discussed later), and we may consider this growth function typical for short-lived monocarpic plants (Appendix 1, Fig. 1). If, as in the standard model of Iwasa and Cohen (1989), storage efficiency (\( \gamma \)) and survival \( p \) are independent of the amount of resources invested in reproduction, and seed production is a linear function of the amount of resources invested in reproduction (\( f(R) = R \)), the optimal life-history schedule is perennial. For \( \gamma = 0.5 \) and \( p = 0.8 \), the plant should grow to a size of 0.82 g and then invest all resources above that size in reproduction (Fig. 2 top, line \( R \)). As a result the resources invested in storage
Herbivores can affect current year's reproductive success ($f(R)$)

Herbivores can affect current years reproduction in two ways:

1. In the case of gregarious insects, an egg batch is laid on a plant. A single egg batch may suffice to eat the whole flowering stem. In that case, herbivore attack is an all-or-none event. The attack rate increases with reproductive investment, the chance of not being attacked can be described as $e^{-aR}$ and hence,

$$f(R) = Re^{-aR},$$

which creates a decelerating curve and hence indicates selection for polycarpy (Fig. 3). A plant should increase size after maturation. It takes three seasons
Fig. 3. A. The optimal investment in reproduction ($R$) as a function of storage size ($S$) at the end of the growing season. $S - R$ gives the amount of resources invested in storage for next year. Parameters as in Figure 2 except $f(R) = R e^{-0.2 R}$. B. The resulting optimal investment in reproduction in time.

even after maturation to reach its maximum size (Fig. 3, bottom). Reproduction should start already in the first year and the amount of resources invested in reproduction increases to a constant value of $2$, $3$ g after the fourth year.

2. In the case of e.g., solitary insects, herbivore attack will be a continuous event. We used the function $f(R) = R^z$, if $z > 1$ this means that the proportion of reproduction that is eaten by herbivores decreases with the investment of reproduction, if $z < 1$ this proportion is increasing. When $f(R)$ is a decelerating function of $R$ ($z < 1$) the optimal solution is a perennial life-history (not shown here). A situation with $z > 1$ produces an accelerating curve of $f(R)$ and is thus analogous to the “reproductive effort” model of Schaffer (1974) who predicted monocarpy. However, if we use the standard parameters, even a value as high as $z = 9$ gives mast years as the optimal life-history schedule (Fig. 4). Below $1.3$ g plants should not invest in reproduction, above $2.8$ g c. $95\%$ of all resources should be invested in reproduction (Fig. 4, top). Reproduction should start in the second year, after the third year there should be an alternating pattern of years with and without reproduction (Fig. 4, bottom). Only when the survival ($p(R) = 0.1$) and storage efficiency ($\gamma(R) = 0.1$) are very low, an accelerating function of $f(R)$ produces monocarpy (Fig. 5). The optimally reproducing plant should reproduce in its fourth year and invest all resources ($1.8$ g) in reproduction.
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Fig. 4. A. The optimal investment in reproduction ($R$) as a function of storage size ($S$) at the end of the growing season. $S - R$ gives the amount of resources invested in storage for next year. Parameters as in Figure 2 except $z = 9$. B. The resulting optimal investment in reproduction in time.

Reproduction related herbivory reduces storage efficiency $\gamma(R)$

Herbivores feeding on leaves at the end of the season effectively reduce the storage efficiency. Also larvae or pupae overwintering in or near the plant may destroy leaf material formed next growing season and reduce storage efficiency. We used the form $\gamma(R) = \gamma_0 e^{-mR}$. This herbivore mediated reduction in storage efficiency after flowering leads to a perennial life-history with mast years as the optimal solution. The optimal investment in reproduction fluctuates in time (Fig. 6). Plants should start reproducing in their second year, after than one year of reproduction should be followed by two years of vegetative growth.

Reproductive related herbivory reduces plant survival ($p(R)$)

If herbivores are attracted by large reproductive plants and such plants experience greater mortality in the future, survival ($p(R)$) is a decreasing function of $R$. We assumed that $p(R) = p_0 e^{-cR}$, where $(1 - p_0)$ is the mortality independent of the investment in reproduction and $(1 - e^{-cR})$ is the additional mortality caused by reproduction. With this survival function, the optimal strategy is not to invest.
until a minimum size is reached and to invest nearly all resources when above that size. The resulting pattern of reproductive allocation through time is that of masting if \( c = 1 \) (Fig. 7). Reproduction should start after two years, after that one year with reproduction should be followed by one year of vegetative growth. In years of reproduction 99% of all resources (3 g) should be invested in reproduction. If \( c \) is larger (\( c = 2 \)) the optimal life-history schedule is semelparous, reproduction with investment of all available resources (2.6 g) after two years (Fig. 8).

The effects of size-related mortality

In many biennial and perennial plant species, survival is related to plant size: small plants generally have lower survival probabilities. We included this in our simulations on the effects of herbivores on plant mortality. We used the following form for the survival function \( p(R) = p_0 e^{R - R_0 [1 - e^{-R_0}]} \), where \([1 - e^{-R_0}]\) denotes the size related survival. The effect of introducing size related mortality is that monocarpy is the optimal solution at lower values of \( c \), i.e., when the effects of reproductive-related mortality are smaller. Except for size related mortality,
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Fig. 6. A. The optimal investment in reproduction \( R \) as a function of storage size \( S \) at the end of the growing season. \( S - R \) gives the amount of resources invested in storage for next year. Parameters as in Figure 2 except \( m = 2.0 \). B. The resulting optimal investment in reproduction in time. Parameter values of Figure 9 are the same as in Figure 7. With size related mortality, the optimal life-history strategy changes from mast years to semelparity. Plants should not reproduce below 0.55 g and invest all resources in reproduction above 1.8 g (Fig. 9, top). The resulting optimal pattern of reproduction is: investment of all resources in reproduction after two years (Fig. 9, bottom).

Cynoglossum officinale

In the genus *Cynoglossum* life-history variation ranges from annual to herbaceous, iteroparous perennial. *Cynoglossum officinale* is a semelparous species from calcereous sandy soils. We studied this species at the sand dunes of Meijendel near the Hague, the Netherlands. In this habitat plants reproduce and die in their third year or later. The probability of flowering in spring is strongly related to plant mass in the previous autumn (de Jong et al., 1986). Occasionally individuals growing under unfavourable conditions may live for seven years or more. Under good growing conditions in an experimental garden all plants reproduced in their second year. Plants flower in spring and need wintercold for stem formation.
In the dunes of Meijendel it is extremely rare that plants survive after reproduction, although it has been observed. For plants from Holkham (England) Boorman (pers. comm.) found that 10% of all individuals reproduced more than once under good growing conditions in an experimental garden. Therefore semelparity in *C. officinale* does not seem to be the result of morphological or other types of constraints. Rather, it seems to result from selection for increasing investment in reproduction up to the point where the survival of the reproducing plant is reduced to zero.

In our simulations we assume that the decision about the division of resources over storage (growth next year) and reproduction (next spring) is made at the end of the growing season. Consequently, if plants invest resources in reproduction at the end of the second year they will flower in their third year. Seed mass, which we took as initial plant mass is c. 0.02 g (Klinkhamer and de Jong, 1987). Relative growth rate decreases with plant mass (de Jong et al., 1989). In the latter paper, that aimed at simulating the optimal size at reproduction for 'biennial plants', the relative growth rate could even become smaller than zero (negative growth). In the way we generated the growth function $\phi S_0$ this is not possible, instead $\phi S_0$ increases with $S_0$, but the rate of increase declines (Fig. 1). The parameters to

![Graph showing the optimal investment in reproduction (R) as a function of storage size (S) at the end of the growing season.](image)
generate the growth curve were chosen to match as closely as possible the growth curve and data used by the de Jong et al. (1989). In *C. officinale* seed production is proportional to plant mass and herbivores do not have much effect on seed production we therefore take \( z = 1.0 \) so that

\[ f(R) = R. \]

The most important herbivore on *C. officinale* is *Ceuthorhynchus cruciger* a weevil foraging on roots. Because plants become infected relatively late during seed set, the effect of the weevil on seed production is only small (Prins et al. 1992). The weevil destroys the root of the plant, and we assumed that the survival of infected plants is close to zero. The summer generation of this weevil almost exclusively attacks flowering plants. The proportion of flowering plants that becomes infested increases from c. 15% in small plants to 100% in large plants. We calculated that the number of uninfected plants is best described by the function \( p(R) = e^{-cR} \) with \( c = 1 \) (Prins et al., 1992). Survival of rosettes increases with plant mass \( (b - 3.6) \). Of the large rosettes c. 80% survives \( (p(0) = 0.8) \) (de Jong et al., 1989; Wesselingh, 1995). The resulting function for plant survival is given by:

\[ p(R) = 0.8e^{-R} [1 - e^{-3.6R}] \]
Fig. 9. A. The optimal investment in reproduction ($R$) as a function of storage size ($S$) at the end of the growing season. $S - R$ gives the amount of resources invested in storage for next year. Parameters as in Figure 2 except $c = 1.0$ and $h = 0.5$. B. The resulting optimal investment in reproduction in time.

Other herbivores have little effect on storage efficiency ($m = 0$). At the end of the growing season plants loose their leaves, during winter c. 50% of the root mass is lost $\gamma(0) = 0.5$ (de Jong et al., 1987) so that

$$\gamma(R) = \gamma_0 = 0.5$$

Given the parameters discussed, the optimal life-history strategy for *C. officinale* would be close to monoparctic (Fig. 10). Reproduction should be in the third spring and nearly all resources (2.30 g, 99%) should be invested in reproduction. After that, years of vegetative growth and reproduction alternate. After reproduction, storage size is reduced to only 0.02 g. This would lead to a survival probability of 0.7%, meaning that over 99% of all reproducing plants effectively reproduce only once.

**Conclusions**

Under the assumption that the level of herbivore attack increases with the investment in reproduction, the results of this paper can be summarized as follows:

1. If herbivores mainly reduce current years reproductive success the optimal solution is annual or iteroparous perennial with size increase after maturation if
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Fig. 10. A. The optimal investment in reproduction (R) as a function of storage size (S) at the end of the growing season for Cynoglossum officinale. \( S - R \) gives the amount of resources invested in storage for next year. Parameters as in Figure 2 except \( c = 1 \), \( b = 3.68 \) and initial size = 0.02 g. B. The resulting optimal investment in reproduction in time.

1. The attack is an all or nothing event. If the attack is a continuous event (the level of consumption increases with the number of herbivores attracted) the optimal solution can be either iteroparity \( (z < 1) \) or iteroparity with mast years \( (z > 1) \); \( z \) being the parameter relating herbivory to the investment in reproduction. Only in combination with very small values for storage efficiency and plant survival, \( z > 1 \) may lead to semelparity.
2. If herbivores mainly reduce storage efficiency the optimal solution is iteroparity with fluctuating seed production.
3. If herbivores mainly reduce survival the optimal solution is likely to be mast years or semelparity.

Discussion

The relationship between reproductive output and plant size played an important role in theory aiming at explaining the evolution of the semelparous life-history. The results of our model show that even if seed production is an accelerating function of plants size \( (z > 1) \), the most likely optimal solution is mast years rather
than semelparity. A similar result was found earlier by Pugliese (1988). In accordance with this prediction, Norton and Kelly (1988) argue that to explain the evolution of mast seeding in the tree *Dacrydium cupressinum* seed predator saturation or other economies of scale are the most likely explanation.

Unfortunately there are not much data on *Z*. Courtney (1985) argued that if size-differences among plants are large relative to the distance at which they can be detected by herbivores, larger reproductive stems may get disproportionately more attacks by herbivores ($z < 1$). He showed this to be the case for a number of butterfly species. On the other hand, if size differences among plants are small relative to the distance at which they can be detected by herbivores, large reproductive stems may get disproportionately fewer attacks. The fraction of seeds of *Cynoglossum chlorotome* eaten by finches declines with the number of seeds produced.

The most clear-cut result of this paper is that reproduction-related mortality can easily lead to selection for a semelparous life-history. Equivalent to herbivore-related mortality is the well-known case of anther smut fungus on species of the Caryophyllaceae. Pollinators are the vector for the fungus. In the year of infection the fungus has no effect on seed production but if it gets systemic it makes the plant sterile. For the plant this is effectively the same as being killed. Thrall et al. (1993) analyzed the relationship between plant life-history and the occurrence of *Ustilago violacea* on different species within the Caryophyllaceae. They showed that the proportion of perennial species on which anther-smuts have been reported is five times higher than the proportion of annuals. Because in populations of e.g., *Silene alba*, the majority of plants can be infected (Shykoff and Buchelli, 1995) this indicates that the chance of becoming infected after reproduction is considerable.

Similarly, if herbivores induce damage to the plant, pathogenic micro-organisms may get their chance to infect the plant which may lead to the death of an individual. For *C. officinale* we observed that, when collecting plants from the field in autumn, in many individuals with larvae of *C. cruciger* the tap-root was infected by micro-organisms that dissolved most of the tap root, that was filled with storage sugar for winter survival. We suggest that infection by micro-organisms is a general problem for species with pronounced storage organs. Interestingly, the semelparous perennial life-history is connected to compact storage roots, while in species with a more diffuse root systems this type of life-history strategy is hardly found. It is easy to imagine that herbivore induced infections by micro-organisms are an important selective force towards semelparity in species with pronounced storage organs.

For the case we studied in detail, *C. officinale*, the optimal life-history was not strictly monocarpic, instead 1% of the resources should be stored and 99% invested in reproduction, causing 1% of the reproducing plants to survive. Although multiple reproduction is extremely rare in the *C. officinale* populations we studied, such a life-history is very common for other species known as semelparous perennials. In e.g., *Senecio jacobaea*, *Oenothera* spp., *Digitalis purpurea*, *Veronica thapsus* and many others, tiny secondary rosettes are formed during or after reproduction that may survive and grow to reproduce in one of the following years. The reason that we often found that in the optimal schedule plants should put a few percent of the available resources in storage instead of being strictly semelparous,
is that plant growth rate was rather high for plants with very small storage sizes. Nevertheless we think that even for small plants our growth curve is realistic. Given an initial size of 0.03 g, plants would weigh 0.4 g at the end of the first year, which is in the upper range found in Meijendel (de Jong et al., 1989). In our simulation, plants should allocate resources to reproduction after two years of vegetative growth at a weight of c. 2.3 g, and then flower in the third spring. This is close to mass at flowering in a natural population. In Meijendel the probability of flowering increases with plant mass, up to 100% when plant mass exceeds 4 g. When plant mass is 2–3 g, 77% of the plants reproduce (de Jong et al. 1989).

Not only in *C. officinale* herbivores are mainly found on flowering plants. For *Senecio jacobaea*, it was shown that the percentage of plants with egg batches of *Tyrtaea jacobaeae* was twice as high in flowering plants compared to non-flowering plants, even when corrected for size-differences between flowering and non-flowering plants (van der Meijden, 1976). Thus in this species also reproduction-related mortality occurs. We expect that in many more cases herbivores are attracted by reproducing plants causing increased mortality.

A problem when investigating egg-laying patterns in natural systems in relation to life-history of the plants is, however, that monocarpic plants die after reproduction. Therefore food quality for larvae feeding on leaves or roots declines rapidly within species using the flowering stem to detect hosts. Once a plant species has become semelparous as a result of herbivore pressure, there can be strong selection against using the flowering stem to detect the host. Then, semelparity may result from the “ghost of evolution past”.

The processes involved in the evolution of a semelparous life-history in plants are still poorly understood. The model presented here shows that the effects of herbivores can lead to selection for semelparity. This does not mean of course that we want to claim that a single factor tells the whole story about the evolution of the semelparous life-history. Even in the case of *Cynoglossum officinale*, the empirical evidence is, as yet, circumstantial rather than conclusive. The effects of herbivores on population dynamics of plants and on the evolution of defence mechanisms are major themes of ecological literature. In contrast to this very little is known about the effects of plant size, plant phenology and plant life-history on herbivory and vice-versa.

In the light of the results presented here it seems worthwhile to pay more attention to the role of herbivory in the selective landscape of plant life-histories.

References


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Appendix I: The growth function, $\phi(S)$

Let the daily net photosynthetic rate, denoted by $g(F)$, increase with the size of the production part $F$. In the following, we use

$$g(F) = \alpha F/(1 + hF),$$

where $\alpha$ and $h$ are constant parameters. The net photosynthetic rate increases with $F$, but it becomes saturated as $F$ becomes large.

We assume that the production part is lost at the end of each growing season and need to be reconstructed at the beginning of next season. Let $S_{n(t)}$ be the storage size at time $t$ within a year $n$ ($0 \leq t \leq T$). The size of the storage parts starts with a positive value if a fraction of the material produced in the preceding year is saved;

$$S_{n + 1(0)} = \gamma(R_n)[S_{n(T)} - R_n],$$

where $R_n$ is the total reproductive investment made in the $n$-th season by constructing and maintaining flowers and seeds.

Let $\phi(S_{n(0)})$ be the size of the storage part at the end of a season as a function of the initial storage size $S_{n(0)}$:

$$\phi(S_{n(0)}) = \max S_{n(T)};$$

the plant follows the optimal allocation schedule during the season.
To find the optimal growth schedule within a season of year $n$ when the initial storage size $S_{0(n)}$ is given, we need to maximize the size of the storage part, $S_{\text{storage},n}$, at the end of the season. Hence we can concentrate on the following subproblem:

\begin{align*}
\frac{dF}{dt} &= u(n)g(F), \\
\frac{dS}{dt} &= (1 - u(n))g(F), \\
F(0) &= 0, \\
S_{0(n)} &= S_0 \text{ (given)}, \\
0 &\leq u(n) \leq 1, \\
S(n) &\geq 0, \\
S_{\text{storage},n} &\rightarrow \text{maximum},
\end{align*}

where $u(n)$ is the ratio of growth rate of the production part to the maximum rate and we deleted the suffix $n$.

We derive the optimal growth schedule within a season given by equations (A2) using the maximum principle. We define the Hamiltonian $H$ as,

\[ H = \dot{\lambda}_F(t)u(n)g(F) + \dot{\lambda}_S(t)(1 - u(n))g(F), \]

where $\lambda_F(t)$ and $\lambda_S(t)$ are co-state variables corresponding to $F$ and $S$, respectively.

We can derive an equation for $\dot{\lambda}_F(t)$ by using the results of Iwasa and Cohen (1989), that is,

\[ \dot{\lambda}_F(t) = (T - \hat{t})g(\hat{F})/dF = 1, \]  

where $\hat{F}$ is $F_{\text{opt}}$ and $\hat{t}$ is the "jump point" (Iwasa and Cohen 1989) where the optimal switching of resource allocation $(u(n))$ becomes one to zero) within a year occurs. To calculate $\hat{t}$ and $\hat{F}$, the following equation is also required,

\[ \ln(\hat{F}) + h\hat{F} = \ln(S_0) + hS_0 + at, \]

that we derived from the integration of $dF/dt$ of $t$ from 0 to $\hat{t}$. We can obtain the numerical solutions of $\hat{t}$ and $\hat{F}$ by using the eqs. (A3) and (A4).

Then the maximized $S_{\text{storage},n}$ or $\phi(S_0)$ becomes,

\[ \phi(S_0) = (T - \hat{t})g(\hat{F}), \]

\[ = (1 + h\hat{F})\hat{F}, \]

which is derived by using eqs. (A1) and (A3).

**Appendix 2. The dynamic programming formalization**

The optimal level of the reproductive investment to be made by a plant can be determined by considering the trade-offs between the current year’s reproduction and the future reproduction.
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The basic argument used here is the same as in Iwasa and Cohen (1989) but the formulations here are more general concerning the functional form of reproductive success, survivorship of the parent, and storage efficiency.

Let $\gamma(R)$ be the storage efficiency, the fraction of material recovered in the beginning of a season from the material saved at the end of the previous year. Let $p(R)$ be the annual survivorship. In Iwasa and Cohen, both $\gamma(R)$ and $p(R)$ are assumed constant ($\gamma(R) = \gamma$, and $p(R) = \sigma$). Let $f(R)$ be the reproductive success of a plant in a year if it invests $R$ resources in reproduction. In Iwasa and Cohen (1989), $f(R)$ is assumed to be proportional to $R$ ($f(R) = R$). Following the arguments in Iwasa and Cohen (1989), we can prove that for the life history strategy that maximizes lifetime reproductive success:

\[
\text{Fitness} = \sum_{n} p(R_n) p(R_{n+1}) \ldots p(R_{n+1}) f(R_{n+1}) \rightarrow \text{maximum}
\]

The derivation is based on dynamic programming, which starts with a plant’s decision about which fraction of its resources is invested in reproduction in the current year. Storage efficiency and growth within each season together give the relation between investment in current year’s reproduction $R_n$ and reproduction in order years, $R_{n+1}$, $R_{n+2}$, etc.

First we consider an individual growing in a stable population in which the population size is constant. Then the fitness of a genotype is simply the expected total number of offspring to be produced in a lifetime.

\[
V(S) = \max \{\text{expected total of the current year’s reproductive success and future reproductive success until the death of the individual}\}
\]

Let $S_n$ be the storage size at the end of the season

\[
V(S_n) = \max_{0 < R_n < S_n} \{f(R_n) + p(R_n) f(R_{n+1}) + p(R_n) p(R_{n+1}) f(R_{n+2}) \ldots \}.
\]

Considering the definition of $V(S)$, we note that this can be rewritten as follows:

\[
V(S_n) = \max_{0 \leq R_n \leq S_n} \{f(R_n) + p(R_n) V(S_{n+1})\},
\]

where $V(S_{n+1})$ is the reproductive value of the plant in the next season, i.e. the expected reproductive success in the $n+1$th year and thereafter. It is a function of the storage size at the end of the $n+1$th year. This depends on the amount of resources saved in the $n$th year, the loss during storage, and the photosynthesis in the $n+1$th year, as follows:

\[
S_{n+1} = \phi[\gamma(R_n)(S_n - R_n)]
\]

$S_n - R_n$ is the amount of resources saved for the following season at the end of the $n$th year. $\gamma(R_n)$ is the fraction of stored products that can be recovered in the beginning of the following season and can be used for reconstruction of photosynthetic organs. Iwasa and Cohen assumed this storage efficiency as a constant, but we here assume that it decreases with the reproductive success of the individual at the end of the $n$th year.
If we combine Eq. (B2) and (B3), and write $R = R_n$ and $S = S_n$,

$$V(S) = \max_{0 \leq R \leq S} \{f(R) + p(R)\phi[R(R)(S - R)]\}$$

which is the equation given in the text.

In a population growing exponentially, at an annual rate of $\lambda$, we simply divide $p(R)$ by this factor, so that $p(R)$ is multiplied by $1/\lambda$. This implies discounting of future reproduction. All other computations remain the same (see Iwasa and Cohen 1989).

If the functions $f(R)$, $\gamma(R)$, and $\phi(S)$ are given, then we can compute the unknown function $V(R)$ so as to satisfy Eq. (A4), this gives the optimum reproductive effort $R^*$ as a function of storage size $S$ ($R^*$ is the value of $R$ that achieves the maximum in Eq. (B4)). To compute the unknown function $V(R)$, we use the following iterative method:

$$V_0(S) = S$$

$$V_{k+1}(S) = \max \{f(R) + p(R)\phi[R(R)(S - R)]\}$$

for $k = 0, 1, 2, 3, \ldots$

$V_k(S)$ converges when $k$ becomes larger, and the limit $V(S) = \lim_{k \to \infty} V_k(S)$ is the function to be used.