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INTERNATIONAL CENTRE FOR SCIENCE AND HIGH TECHNOLOGY
c/o INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS 34100 TRIESTE (ITALY) VIA GRIGNANO, 9 (ADRIATICO PALACE) P.O. BOX 586 TELEPHONE 040-224572 TELEFAX 040-224575 TELEX 460449 APH I

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"Optimal Patterns of Growth and Reproduction for Perennial Plants with Persisting or not Persisting Vegetative Parts"

A. Pugliese
Dipartimento di Matematica
Universita' degli Studi di Trento
38050 Povo (TN)
Italy

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Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts

ANDREA PUGLIESE
Dipartimento di Matematica, Universita degli Studi di Trento, 38050 Povo (TN) Italy

JAN KOZLOWSKI
Institute of Environmental Biology, Jagiellonian University, Oleandry 2a, 30-063, Kraków, Poland

Summary

Optimal allocation of energy to growth, reproduction and storage was considered for perennial plants differing in the proportion of vegetative structures persisting over winter and/or in the amount of resources which can be relocated to storage before abscission of some organs. It was found that for every mortality level there exists a critical proportion of persistent organs. Below this critical value it is optimal to grow without reproduction for the first years until a characteristic size is reached; afterwards, that size is maintained year after year and all extra resources are devoted to reproduction. Some storage is also necessary to maintain constant size. If the proportion of retained vegetative mass is above the critical value, the optimal strategy is gradual growth to an asymptotic size, with growth and reproduction occurring in several years following maturation. In this case real storage occurs only until maturation is reached, then storage is realized only by energy relocation from the vegetative body. Although the optimal solution changes abruptly qualitatively at a given proportion of resources saved from year to year, further growth of this proportion above the critical level brings about a greater difference between size reached at maturity and final size. The predictions of the model seem to follow the pattern of nature qualitatively.

Keywords: Optimal life histories; perennial plants; relocations.

Introduction

In most of the existing papers on optimal energy allocation to growth and reproduction annual organisms are considered (e.g. Cohen, 1971; Vincent and Pulliam, 1980; Schaffer *et al.*, 1982; King and Roughgarden, 1982a, 1982b, 1983; Ziolko and Kozlowski, 1983; Kozlowski and Wiegert, 1986). The most consistent result from the models in these papers is that in order to maximize reproductive output at the end of the growing season it is optimal to switch instantaneously from energy allocation into growth to energy allocation into reproduction. This result is unreliable only when season length is unpredictable (Cohen, 1971, King and Roughgarden, 1982b) or when the growth rate of the reproductive part is constrained by the size of this part (Kozlowski and Ziolko, 1988).

The problem becomes more complex when perennial organisms are considered. In a given season it is no longer optimal to switch from growth to reproduction at the point which maximizes reproductive yield at the end of the season. It is optimal to delay such a switch because losses

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in reproductive output in a given year can be paid back in subsequent years if an individual is lucky enough to survive. When the survival rate is high it may even be optimal to postpone reproduction for several years.

Optimal pattern of growth and reproduction in perennial organisms was considered by Kozlowski and Uchmanski (1987) under the assumption that all vegetative parts are retained over the winter. They concluded that after reaching maturity it is optimal to continue growing either asymptotically to the end of life (if life span is unlimited) or through several years (if life span is limited), which means that many years of mixed growth and reproduction should occur. In contrast, Pugliese (1987, 1988a) and, independently, Iwasa and Cohen (1989) assumed that all vegetative parts except for storage organs are lost, and an organism must regrow at the beginning of the next season using energy stored in the previous year. Results obtained with this assumption are qualitatively different; life span should be divided into two parts, with pure growth at the beginning and lack of growth (except spring regrowth) later on; only one transient year of mixed growth and reproduction can occur in this case.

In nature there is a continuum of perennial species. At one extreme some herbs lose virtually the entire vegetative body at the end of growing season; then there are other herbs keeping part of root system; suffrutescent shrubs (half-shrubs) develop herbaceous shoots which die back each year and retain perennial woody tissues only near the base of their stems; deciduous shrubs and trees accumulate ageing or dead soma and an increasing body of dependent tissue and lose only the leaves in resting seasons. At the other extreme, there are evergreen shrubs and trees whose leaves can live a few years on average. Relocation of non-structural carbohydrates from parts that are shed to storage organs can also take place; this means that resources allocated to vegetative parts are not completely lost.

In this paper we examine the optimal solution over this continuum of possibilities, when part of the vegetative body is retained into the next season (trees, shrubs, some herbs) and/or a certain proportion of energy can be relocated into storage organs from the parts that will be lost. We show analytically the qualitative characteristics of optimal solutions; using numerical examples, we examine the influence of the proportion of tissue conserved to the following year on growth pattern and size of plants. It is always assumed that there are discrete growing and resting seasons; therefore the model could not really be applied to evergreen plants. Apart from this, it is a very simple model which, at least to some extent, could be applied to most plant forms quoted above.

The model

The model describing the processes occurring in one season, denoted here by i, has been considered by several authors (see the Introduction). There are three compartments, $V_i(t)$, the vegetative parts, $R_i(t)$, the reproductive parts, and $S_i(t)$, the storage. If V is the size of the vegetative parts, resources are accumulated at the rate $f(V)$; these resources can be allocated either to vegetative parts, or to reproduction or to storage. Neglecting all other processes, we therefore have the following equations on $[0,T]$, where T is the length of the growing season:

$$\begin{cases} \frac{d}{dt} V_i = (1-u_i-v_i) f(V_i) \\ \frac{d}{dt} R_i = u_i f(V_i) \\ \frac{d}{dt} S_i = v_i f(V_i). \end{cases} \tag{1}$$

u_i and v_i are the proportion of new resources allocated to reproduction and storage, respectively. Therefore, they must be between 0 and 1, and their sum has to be lower or equal to 1.

What has to be clarified is what happens in winter. In previous work, we had assumed either that the vegetative parts are completely lost over winter and only storage persists (Pugliese, 1988a), or that the vegetative parts are completely retained (Kozlowski and Uchmanski, 1987). In general, one may assume that a fraction q_1 of the vegetative parts persists over winter and a fraction q_2 is relocated to storage at the end of the growing season. Therefore system (1) is completed by the initial conditions for season i+1.

$$\begin{cases} V_{i+1}(0) = q_1 V_i(T) \\ S_{i+1}(0) = S_i(T) + q_2 V_i(T) \\ R_{i+1}(0) = 0. \end{cases} \tag{2}$$

We may consider, within the approximations of the present model, that a large q_1 is typical of trees and shrubs, especially if evergreen, while q_1 should be close to 0 for herbaceous perennials; the magnitude of q_2 could depend on the species.

We further assume that resources are relocated from the vegetative parts to storage only, and not to reproductive parts as well. The latter process is also important in herbaceous perennials; however, as noted in Pugliese (1988a), if relocation is equally possible to storage and reproduction the qualitative conclusions of the model without relocations still hold. Therefore here we consider only the relocation process which is restricted to storage, mostly because of time constraints (reproductive allocation has to end by the time seeds are dispersed, while allocation to storage may go on after the end of the growing season).

In order to produce a more mathematically tractable model, we apply a further simplification to Equations (1) and (2). Namely, if resources are to be transferred from storage to vegetative parts, we should add a term describing this translocation to Equation (1); however, we consider that the translocation process is so fast that its dynamics can be neglected, and that all resources in the storage compartment are instantaneously transferred to the vegetative parts at the beginning of each growing season (see also Iwasa and Cohen, 1989, for a discussion of this point). All unavoidable losses of energy in this process are also neglected. Therefore, we obtain the initial conditions

$$\begin{cases} V_{i+1}(0) = q\, V_i(T) + S_i(T) \\ S_{i+1}(0) = R_{i+1}(0) = 0 \end{cases} \tag{3}$$

where $q = q_1 + q_2$. The model of resource allocation we consider consists, therefore, of Equations (1) and (3).

Mortality has also to be considered if we wish to study the maximization of fitness. Here we make the simplest assumptions, i.e. that mortality occurs only between growing seasons and that is independent of the age and size of the plant. Therefore, mortality is described in total by a single parameter, p, the survival probability between growing seasons. To consider mortality during growing seasons as well would simply make the formulae more clumsy (Kozlowski and Wiegert, 1986; Kozlowski and Uchmanski, 1987), while size-dependent mortality introduces more complications that can only be handled partially (Pugliese, 1987; Kozlowski and Wiegert, 1987).

Other simplifying assumptions have been made in order to obtain Equations (1) and (3). It has been assumed that the vegetative parts can be described by a single variable; Iwasa and Roughgarden (1984) consider roots and leaves separately for an annual plant model, and at least for trees one may have to consider a structural compartment. The ageing and herbivory of vegetative parts (described in Pugliese, 1988a as metabolic rate) are not considered here. It is

assumed that the relative cost of producing a successful seed does not change with the investment made in reproduction: the consequences of relaxing this assumption (see Schaffer and Rosenzweig, 1977; Pugliese, 1988b) will be discussed below. Constant population size is also assumed; this makes it possible to use expected (at birth) offspring number as a measure of fitness. Finally, with the exception of seasonality, environmental fluctuations in space and time are neglected, as in most allocation models.

Qualitative results

The controls $u_i(t)$ and $v_i(t)$ that maximize the expected (at birth) lifetime reproductive output are 'bang-bang', that is they are either 0 or 1, as found by several authors (see the Introduction). Therefore it is sufficient to find, for each season, the switching times τ_1 to reproduction and τ_2 to storage. For model (1) it is irrelevant whether storage occurs before reproduction or vice versa or they both occur simultaneously, as long as the proportions of the allocation to either compartment are kept fixed; to be definite, we assume that storage occurs after reproduction. We then obtain the expressions for the vegetative parts, reproductive output and storage at the end of the season as follows

$$\begin{cases} V(T) = V(\tau_1) \\ R(T) = (\tau_2 - \tau_1)f(V(\tau_1)) \\ S(T) = (T - \tau_2)f(V(\tau_1)). \end{cases} \tag{4}$$

It may well be that τ_2 is equal to τ_1 (no reproduction) or to T (no storage).

For a study of the qualitative properties of the optimal allocation, it is convenient to rephrase the whole model as a discrete problem, similar to those considered in mathematical economics (McKenzie, 1986); this is briefly described in Appendix 1.

It is found that two different kinds of optimal strategies exist. For a given function f and survival probability p, a critical value for the proportion q of vegetative parts that are kept or relocated, say q^*, exists. For q below the critical value q^*, the optimal strategy is growth without reproduction for the first years until a characteristic size is reached at the beginning of the season; afterwards, that size is maintained year after year, and extra resources are devoted to reproduction. For q above q^*, on the other hand, the optimal strategy is a few years of pure growth until maturation, followed by growth and reproduction in all subsequent years; size increases gradually towards an asymptotic size.

As for the allocations within the growing seasons, if $q>q^*$, reproduction, when it occurs, completely takes up the final part of the growing season, except possibly in the first year of reproduction. Allocation to storage then occurs only as relocation from vegetative structures after the end of the growing season. If $q<q^*$, in addition to relocation from vegetative structures, some allocation to storage always occurs during the growing season.

Numerical results

For numerical computations of the optimal strategies, we always used $f(V) = aV^b$. For that function, many expressions used in the Appendices for computation of the optimal strategy become explicit. First of all, one obtains that the critical value q^* is equal to $p^{1/b}$; the plots of q^* vs p for different values of the power b are shown in Fig. 1. As may be noted, the curves change very little for different values of b; the value of q^* depends almost only on mortality levels.

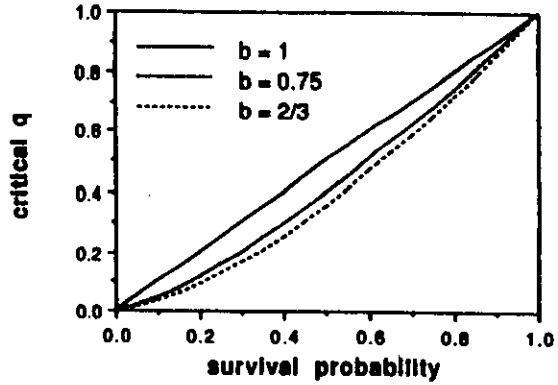

Figure 1. Plots of the threshold value q^* against survival probability p. Where the proportion of persisting structures q is less than q^*, the optimal strategy is first growth then reproduction. Where q is greater than q^*, the optimal strategy is gradual growth together with reproduction. Different curves correspond to different values of b, the exponent in the 'production' function, $f(V)$.

There are also explicit expressions for the final size x^*. If $q>q^*$, we have

$$(x^*)^{1-b} = \frac{ab(1-b)q^{1-b}T}{1-pq^{1-b}-bq^{1-b}(1-p)} \tag{5}$$

while, if $q<q^*$, we have

$$(x^*)^{1-b} = \frac{ab(1-b)p^{(1-b)/b}T}{1-q-b(p^{(1-b)/b}-q).} \tag{6}$$

Optimal switching times to reproduction and storage were found through Powell's minimization algorithm, as described in Press *et al.* (1986). We let switching times vary for the first 20 seasons, while assuming that size at the beginning of seasons had to be the same for all seasons beyond the twentieth one. This yields only an approximation for the infinite optimal sequence, but a rather close one.

In Figs 2A and B growth of vegetative parts (lines), the amount of stored energy (open squares) and relocated energy (closed squares) are shown. In Figs 2C and D reproductive output in consecutive years is also shown, both weighted by the probability of surviving to a given age (bars) and unweighted (squares). Figs 2A and C represents the case where the relocatable proportion of vegetative mass (q) is lower than $p^{1/b}$ (see figure caption for the values of parameters). Reproduction starts in the fourth year, and from the fifth year size both at the beginning of the season and at the end of the season remains constant. Reproductive output, storage and the amount of relocated energy are also constant from this year.

Figure 2B and D represents the case when q is greater than $p^{1/b}$. Reproduction starts in the fifth year, but growth still continues and brings about a gradual increase of unweighted reproductive output year after year. Storage, which is present in the initial years, disappears after maturation, and spring regrowth is possible as a result of relocated energy only.

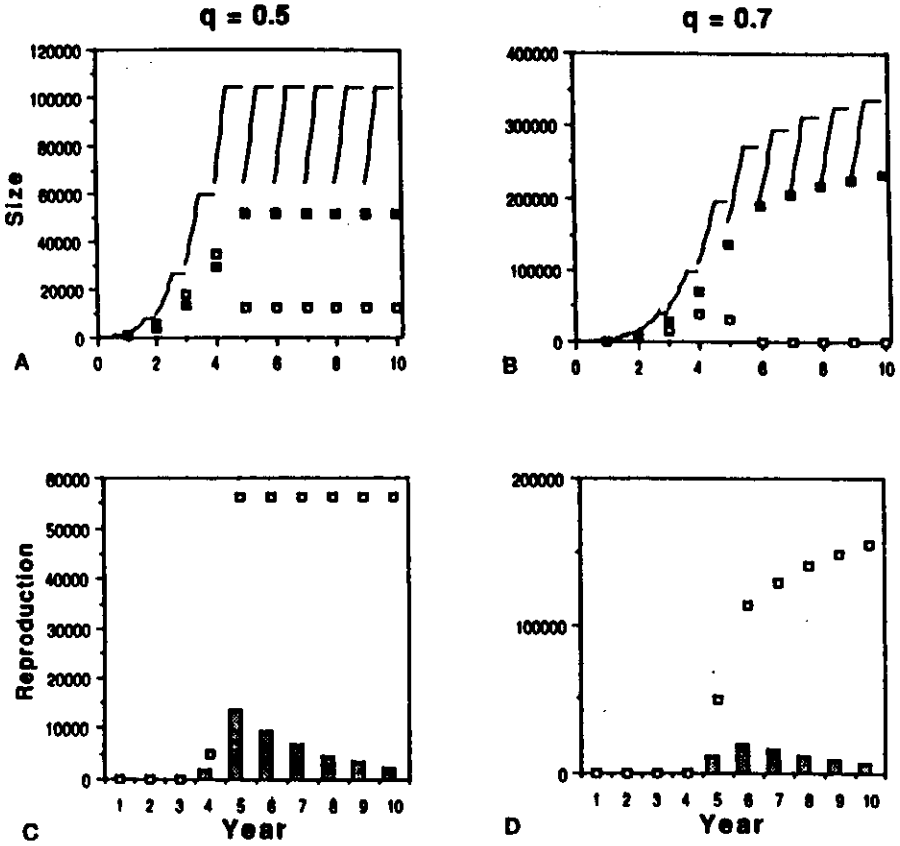

Figure 2. The optimal strategies for different values of q, the proportion of persisting tissues. In A and B the solid lines represent vegetative size over several growing seasons, the open squares the amount of storage accumulated at the end of a growing season, the black squares the amount of resources which either persist in the vegetative structures or are relocated to storage after the end of the season. In C and D the reproductive output of every season is shown; open squares represent the actual amount; bars represent that amount weighted by the survival probability (from birth) to that age. In A and C $q = 0.5$; in B and D $q = 0.7$. The production function $f(V)$ is $0.2\ V^{0.75}$. The survival probability per season p is 0.7.

In Fig. 3 the influence of q on size at maturity and on final size is shown. In Fig. 3A the solid line represents the final size (Equation (5) or (6)), and the dashed line size at maturity, which is defined as the size at the beginning of the season following the first reproductive year. Although qualitatively the optimal solution changes abruptly at a critical q, which is 0.62 in this example, an increase in the relocatable portion of energy brings about an increase in final size for values of q both below and above the critical value. An increase in q always leads to greater expected life time reproductive output. Thus a small q must either be considered to be a

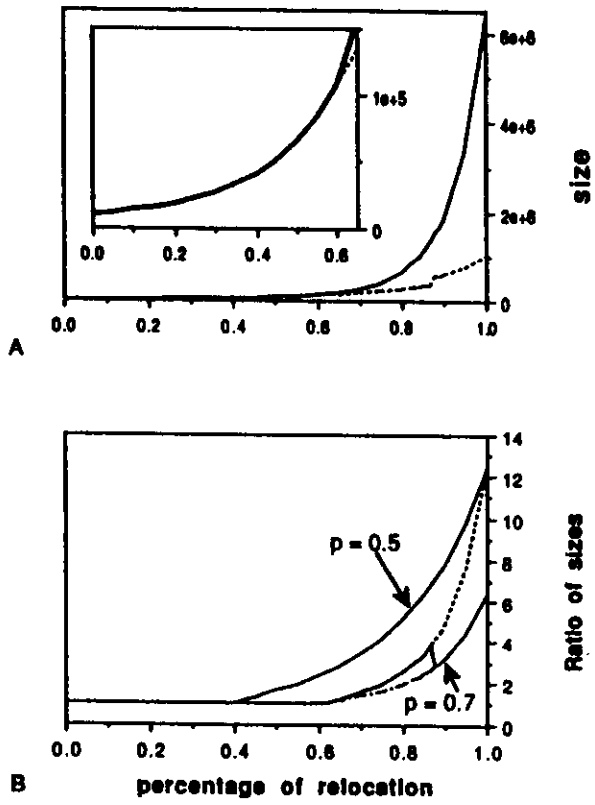

Figure 3. Final size and size at maturity for different values of q and p. In A the solid line represents fin size, the dashed line size at maturity; $p = 0.7$ and $f(V) = 0.2\ V^{0.75}$. The insert is an enlargement of th first part of the graph. In B the ratio of final size to size at maturity is shown by the solid lines for tw different values of p. The ratios of final size to size in the sixth year (dashed line) and to size at the seven year (line with dots and dashes) are also shown for $p = 0.7$. Further explanations can be found in the tex

In Fig. 3B the solid lines represent the ratio of final size to size at maturity for different value of q. This ratio is equal to 1 for q below the critical value, and increases rapidly for q above thi value. Moreover, the values of the ratio are higher when mortality is higher.

The sharp decrease (for $p = 0.7$) in the ratio when q is just below 0.9 is due to the fact tha at that value of q the first reproductive season changes from the fifth to the sixth year; this cause an abrupt increase in size at maturity, which can also be seen in Fig. 3A, and therefore a decreas in the ratio of final size to size at maturity. In the same figure, the dashed line represents fina size over size in the sixth year; the line with dots and dashes final size over size in the seven year. Both lines are smooth. However, maturity jumps suddenly from the fifth to sixth year, an then the ratio of final size to size at maturity jumps from one line to the other. On the othe

Discussion

Resource allocation models can be considered as an interface between life history optimization based on demography and the changing field of physiological ecology (Sibly and Calow, 1986). Such models make it possible to use the ultimate fitness measure, i.e. reproductive value at birth or expected offspring number at birth for constant population size, and on the other hand they incorporate some physiological and design constraints. Despite these advantages that make such models powerful predictive tools, at least potentially, they are not commonly used in evolutionary ecology. One possible reason is that they deal mainly with annual species, which are not very common in nature. Therefore, producing allocation models for perennial organisms seems very important.

The model presented in this paper can be applied to the full continuum of abilities to keep vegetative parts over winter. It is a simple model with only one compartment for all vegetative organs, and does not distinguish formally between resource relocation to storage and maintenance of parts of the vegetative body over winter. Furthermore, constant mortality is assumed as well as uniformity of the entire growing season. Vegetative reproduction is also neglected, whereas this phenomenon is common among many perennials. There are, however, several perennial plants that do not reproduce vegetatively at all or do so so infrequently that, as the first approximation, the process can be neglected. For example, most trees do not reproduce vegetatively at all.

Because of its simplicity, this model can only be considered a first approximation for any specific plant. On the other hand, it gives valuable qualitative predictions of growth patterns for different parameter values. In particular it shows the influence of the ability to maintain vegetative parts between growing seasons on growth patterns.

Perennial species differ strongly in their ability to retain their vegetative parts (or at least the energy or nutrient content of these parts) over winter. Some animals, such as molluscs, fishes, amphibians or reptiles, keep their entire vegetative parts, except the stored materials, into next year. We restrict ourselves here to the consideration of plants, but similar models can and have been applied to animals (Hom, 1987; Kozlowski and Uchmanski, 1987). As discussed in the introduction, plants range in this respect from evergreen trees and shrubs to herbs that lose their entire vegetative parts except for storage organs, which are usually in the form of bulbs or stolons (Harper, 1977). The results in this paper show that, in accordance with the value, q, of the proportion of resources allocated to vegetative parts that are either kept or relocated, optimal strategies divide in two distinct categories. When q is small (Fig. 2A), life is divided in two parts: first pure growth without any reproduction; and secondly, reproduction every year with growth occurring only in the first part of the season in order to grow back from storage to the size achieved in the previous year. There is at most one intermediate year in which there is some real growth and reproduction. On the other hand, when q is large (Fig. 2B) growth goes on after reproduction has started. Moreover, after reproduction begins, there is no more allocation to storage during growing seasons; storage occurs only as relocation after the end of the season. An increase of q beyond the threshold value causes an increase of the ratio of final size to size at maturity (Fig. 3B).

These predictions were obtained assuming constant environment. Of course, biotic and abiotic fluctuations would bring about more complicated patterns with the possibilities of decrease in size, or of seasons with low or no reproduction interspersed between highly reproductive seasons. However, the general patterns shown in Figs 2 and 3 should withstand the effect of environmental fluctuations.

Do real plants follow these predictions? We do not know of quantitative data on which to test whether the ratio of final size over size at maturity is about one for small q (the proportion of

resources in vegetative parts saved from one year to the next), and then grows with q as shown in Fig. 3B. However, we believe that this pattern is worth studying.

As for a qualitative pattern, we would generally assign a large q to trees, and a relatively small q to herbs, especially those that lose most of their vegetative tissue from one season to the next. Trees have generally long juvenile periods (Harper and White, 1974), although this is clearly dependent on the environment; nevertheless, growth seems to continue after maturation. The phenomenon of 'mast' years is also widely known. For such a phenomenon to be advantageous it has to be relatively less expensive (perhaps because of lower seed predation) to produce seeds in large numbers; this possibility is not allowed for in the present model (but see Schaffer and Rosenzweig, 1977; Kozlowski and Uchmanski, 1987; Pugliese, 1988b).

As for perennial herbs, not many data are available about growth and reproduction over various seasons, *Smilacina racemosa* individuals seem more or less not to increase in size after reproduction; actually, in some years they even decrease in size after reproduction (Pugliese and Armstrong, 1989), *Hepatica nobilis* individuals seem to have about the same number of flowers from one year to the next (Inghe and Tamm, 1988); however, it is unclear from that paper whether individuals tend on average to increase in vegetative size over the years; moreover, *H. nobilis* maintains leaves for at least one year and roots for several years (Inghe and Tamm, 1985), so probably q is relatively large. The pattern of flowering of several other perennial herbs is discussed by Inghe and Tamm (1988), but no quantitative data are given; it seems apparent that most, but not all of them reproduce almost every year after the first reproductive year. We also know of at least one herb species which apparently does not fit the scheme predicted from the model: *Corydalis cava* goes on growing after maturation despite low mortality and the loss of both stems and roots between growing seasons (D. Tumidajowicz pers. comm.).

A higher proportion of retained vegetative tissues, as shown in numerical examples, brings about larger size at maturity, more growth after the onset of maturation (Fig. 3), and higher life time reproductive output as a result. Can we conclude that inability to keep the vegetative body is a design constraint or does renewing the entire vegetative mass or part of it have some advantages? One possible advantage is escape from the problem of ageing. If all tissues are rebuilt every year, a plant stays in perpetual somatic youth except possibly for the accumulation of viruses and somatic mutants (Harper 1977). Furthermore, the overwintering parts must cope with adverse environmental conditions which require special adaptations likely to decrease some aspects of physiological performance. Summing up, it is only advantageous to keep as large a part of the vegetative body as possible from year to year if it is assumed that all other things are equal. According to the model presented, an optimal pattern of growth and reproduction is heavily dependent on survival, on the function describing the dependence of net production on body mass, and also on the season length. Adaptations to keep vegetative parts may have a negative effect on all of these.

Relocation of resources before vegetative part abscission always seems to be advantageous. The extent of this process is undoubtedly physiologically constrained and can be species dependent. There are also environmental limitations to this process. Relocation is not an instantaneous event, as is assumed in this paper, but takes some time and must occur when the temperature is not very low. Thus this process must be precisely placed in time, and must occur after it no longer pays to keep vegetative organs because of low net production but before the temperature drop is too great. This problem can be less serious for early spring herbs living under a canopy, because access to light, rather than temperature, seems to be the limiting factor on their season length. Such herbs can relocate their resources at the end of spring before shedding their leaves, and therefore can be expected to have a relatively large percentage of relocated resources. On the other hand, if fruits can ripen after the end of the growing season, resources

can also be relocated to maturing fruits. This changes the optimization results qualitatively, the solution corresponds to the case of very small q.

The function $f(w)$, which describes the dependence of net production rate on vegetative mass, is expected to be concave downward for most cases. This is because of self-shading and an increase in the proportional size of support tissues. However, it is quite possible that the function $f(w)$ has several plateaus, corresponding for example to the build up of a new stem, with a sharp rise after each of them. Clearly, the intensity of self-shading and the proportion of support tissues to 'productive' parts will depend very strongly on the shape of the plant. This in turn will be influenced by neighbouring plants, by water and light conditions, and by soil fertility. We can therefore, expect strong plasticity in patterns of growth and reproduction.

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Appendix 1. Qualitative behaviour of optimal strategies

We want to transform the problem of maximizing expected lifetime reproductive output for model (1)–(3) into a completely discrete problem. To this aim, given two positive numbers, z_i and z_{i+1}, we consider all the controls, $u_i(t)$, $v_i(t)$, such that bring the vegetative size from $V_i(0) = z_i$ to $V_{i+1}(0) = z_{i+1}$; among all these controls, assuming that at least one such control exists, we find the one that maximizes $R_i(T)$. The existence of maximizing controls is guaranteed by standard theorems (for instance, see Theorem and Corollary 5.1 in Berkovitz, 1974) and they are the only ones that need be considered; it is in fact clear that a control that takes equally from z_i to z_{i+1} and yields a lower value of $R_i(T)$ cannot be optimal.

Let $U(z_i,z_{i+1})$ be the value of $R_i(T)$ obtained through the maximizing control. The problem of finding the controls $|u_1(t), v_1(t),\ldots,u_i(t),v_i(t),\ldots|$ which maximize expected lifetime reproductive output is then reduced to

Problem 1

Find a sequence $|z_i|$ that maximizes

$$\sum_{i=1}^{\infty} p^{i-1} U(z_i,z_{i+1}) \tag{A1}$$

under the constraints that z_1 is equal to $V_1(0)$, and that z_{i+1} are reachable from z_i.

Problem 1 is typical in mathematical economics (see for example, McKenzie, 1986). In order to study it, we wish to investigate better the properties of the function $U(x,y)$.

$U(x,y)$ is precisely defined as the maximum for $R(T)$ under the constraints

$$\begin{cases} \dfrac{d}{dt} V = (1-u-v)f(V) \\ \dfrac{d}{dt} R = uf(V) \\ \dfrac{d}{dt} S = vf(V). \end{cases} \tag{A2}$$

and

$$V(0) = x,\ R(0) = S(0) = 0 \tag{A3}$$

$$S(T) + qV(T) = y. \tag{A4}$$

$U(x,y)$ is only defined when y is reachable from x.

The main assumptions we make are that $f(V)$ is increasing and concave and that $f(0)=0$. We also need the technical assumption that f is log-concave, in the sense that the function $\phi(u) = \log f(e^u)$ is concave. Graphically, this assumption means that f looks concave, when drawn in log-log paper. Finally, for the sake of simplicity, we will also assume that there exist first and second derivatives of f.

Using Pontryagin's maximum principle, one can prove the following facts:

as proved by Kozlowski and Wiegert (1986), there exists $\bar{\tau}(x)$ such that the control that maximizes $R(T) + qV(T)$ under constraints (A2)–(A3) is: u is equal to 0 on $(0,\bar{\tau})$, $u(t)=1$ on $(\bar{\tau},T)$

As for the controls $(\bar{u}(t), \bar{v}(t))$ that maximize $R(T)$ under constraints (A2)–(A4), we have:

(a) If $y \geq qV(\bar{\tau}(x))$, $\bar{u}(t) + \bar{v}(t) = 0$ on $(0,\bar{\tau}(x))$, $\bar{u}(t) + \bar{v}(t) = 1$ on $(\bar{\tau}(x),T)$. The relative allocation between storage and reproduction is then calibrated so as to have $S(T) = y - qV(\bar{\tau}(x))$.

(b) If $y < qV(\bar{\tau}(x))$, then we have $\bar{v}(t)$ identically zero, while $\bar{u}(t) = 0$ on $(0,\tau(x,y))$, $\bar{u}(t) = 1$ on $(\tau(x,y),T)$; $\tau(x,y)$ is such that $qV(\tau(x,y)) = y$. Note that $V(t)$ depends on x through the initial value $V(0)=x$.

In case (b) then there is no allocation to storage during the growing season. For ease of notation, we define the function $Q(x)=qV(\bar{\tau}(x))$; we can then say that case (a) holds when $y \geq Q(x)$, while case (b) holds when $y < Q(x)$.

Defining

$$M(x) = f(V(\bar{\tau}(x)))(T-\bar{\tau}(x)) + qV(\bar{\tau}(x)) \tag{A5}$$

which is the maximum size that can be reached in a season starting from size x, we have

$$U(x,y) = \begin{cases} M(x) - y & \text{when } y \geq Q(x) \\ f(V(\tau(x,y)))(T-\tau(x,y)) & \text{when } y < Q(x). \end{cases} \tag{A6}$$

From Equation (A6) one then obtains, through several computations similar to those performed in Appendix 2 of Pugliese (1988a), that

$$\frac{\partial}{\partial x} U(x,y) = \begin{cases} M'(x) & \text{when } y \geq Q(x); \\ \dfrac{f(y/q)}{f(x)} & \text{when } y < Q(x). \end{cases} \tag{A7}$$

$$\frac{\partial}{\partial y} U(x,y) = \begin{cases} -1 & \text{when } y \geq Q(x); \\ \dfrac{1}{q}[f'(y/q)(T-\tau(x,y)) - 1] & \text{when } y < Q(x). \end{cases} \tag{A8}$$

We summarize some properties of the above functions as

(P1) If $x_1 < x_2$ and $y_1 < y_2$, then $U(x_1,y_1) + U(x_2,y_2) > U(x_1,y_2) + U(x_2,y_1)$. A function U satisfying this property is sometimes called supermodular (Ross, 1983).

(P2) $M(x)$ is a concave function.

(P3) There exists $\hat{x} \geq 0$ such that $Q(x) > x$ on $(0,\hat{x})$, $Q(x) < x$ on $(\hat{x},+\infty)$.

(P4) $pU_x(x,x) + U_y(x,x)$ is a continuous, decreasing function of x.

The main tools in the analysis of Problem 1 are the principle of optimality and Euler's equations. We define $W(x)$ (the value of size x) as the maximum offspring number expected starting from size x,

$$W(x) = \sup \sum_{i=1}^{\infty} p^{i-1} U(z_i,z_{i+1})$$

subject to the constraints $z_1 = x$, and that z_{i+1} is reachable from z_i; for ease of notation, we define $m(z)$ as the minimum size that can be reached from z, so that z_{i+1} reachable from z_i can be written as $m(z_i) \leq z_{i+1} \leq M(z_i)$. The principle of optimality states that

$$W(x) = \max[U(x,z) + pW(z)] \tag{A9}$$

taken over all z that are reachable from x. Equation (A9) can actually be used as the definition of W through a fixed point argument. We also define the map

$$\theta(x) = \max\{z: m(x) \leq z \leq M(x),\ U(x,z) + pW(z) = W(x)\}.$$

In words, $\theta(x)$ is the first point reached from x along an optimal path (in case more than one such point exists, we choose the largest one).

Euler's equations state that small variations from an optimal path are not advantageous. Therefore we have for an optimal path $\{z_i\}$

$$U_y(z_{i-1},z_i) + pU_x(z_i,z_{i+1}) \begin{cases} \geq 0 & \text{if } z_i = M(z_{i-1}) \\ = 0 & \text{if } m(z_{i-1}) < z_i < M(z_{i-1}). \\ \leq 0 & \text{if } z_i = m(z_{i-1}). \end{cases} \tag{A10}$$

The first result is that optimal sequences do not oscillate. This follows from the fact that

$$\text{If } x < y, \text{ then } \theta(x) \leq \theta(y). \tag{A11}$$

The proof of (A11) follows from (P1), repeating step by step the proof of the analogous result in Dechert and Nishimura (1983).

Since, for an optimal path, $z_{i+1} = \theta(z_i)$, we have that either $z_i \geq z_{i-1}$ for all i, or $z_i \leq z_{i-1}$ for all i.

We have to add an assumption that avoids growth to infinite of optimal sequences, which is not very sensible biologically. Namely we assume

(P5) $\lim_{x\to\infty} pM'(x) < 1$.

(P5) is true if $\lim_{x\to\infty} f'(x) < \frac{1-q}{T}$, which seems a reasonable assumption.

Under (P1)–(P5), the optimal sequence $\{z_i\}$ is monotone and bounded; therefore it admits a limit $\hat{x} \geq 0$.

If $\hat{x} > 0$, $M(\hat{x}) > \hat{x}$. Letting i go to infinite in Equation (A10), one then obtains

$$U_y(\hat{x},\hat{x}) + pU_x(\hat{x},\hat{x}) = 0. \tag{A12}$$

From (P4), we know that there exists at most one $\hat{x}$ satisfying (A12). If $\lim_{x\to 0+} pU_x(x,x) + U_y(x,x) > 0$, let $x^* > 0$ be the solution of $pU_x(x,x) + U_y(x,x) = 0$ (there exists one such solution because of (P4) and (P5)). If $\lim_{x\to 0+} pU_x(x,x) + U_y(x,x) \leq 0$, set x^* equal to 0.

Size x^* will be the one approached by optimal paths. To distinguish between the two cases discussed in the text, we have to use also size ℓ introduced in (P3). We can now state our main result.

Theorem. All optimal paths converge to x^*. If $x^* \geq \ell$, the optimal path $\{z_i\}$ can be described for $z_1 < x^*$ as $z_{i+1} = \min\{x^*, M(z_i)\}$; i.e., the path is the quickest approach to x^*. If $x^* < \ell$, there is only asymptotic convergence to x^*; in this case, we can say that there is a finite number (possibly zero) of i's such that $z_i = M(z_{i-1})$ (no reproduction), followed by possibly one year where $M(z_{i-1}) > z_i \geq Q(z_{i-1})$, and finally by an infinite sequence of i's where $z_i < Q(z_{i-1})$ (relocation occurs only through storage); unless $z_1 = x^*$ (one starts already from the optimal size), this sequence is strictly increasing.

Proof. If $x^* \geq \ell$, consider the suggested optimal path; since $x^* \geq Q(x^*) \geq Q(z_i)$, we have $z_{i+1} \geq Q(z_i)$, for all i. Therefore

$$\sum_{i=1}^{\infty} p^{i-1}U(z_i,z_{i+1}) = \sum_{i=1}^{\infty} p^{i-1}|M(z_i)-z_{i+1}| > \sum_{i=1}^{\infty} p^{i-1}|M(z'_i)-z'_{i+1}| \geq \sum_{i=1}^{\infty} p^{i-1}U(z'_i,z'_{i+1}) \tag{A13}$$

for any feasible path $\{z'_i\}$ different from $\{z_i\}$. The strict inequality comes from the results of Spence (1973) and Pugliese (1987).

If $0 < x^* < \ell$, consider only $z_1 < x^*$. We already know that $\lim_{i\to\infty} z_i = x^*$; since $\theta(x^*) = x^*$, from Equation (A11) we know that $z_{i+1} = \theta(z_i) \leq x^*$. It is impossible to have $z_{i+1} = x^*$; in fact, if we had $z_i < x^* = z_{i+1}$, from Equation (A10) we would obtain

$$U_y(z_i,x^*) + pU_x(x^*,x^*) \geq 0 \tag{A14}$$

while by definition of x^* we have

$$U_y(x^*,x^*) + pU_x(x^*,x^*) = 0 \tag{A15}$$

and, since $x^* < \ell$, using Equation (A8), we have $U_y(x^*,x^*) > U_y(z_i,x^*)$.

Thus we have found that $z_i < x^*$; it is also true that $z_i < z_{i+1}$; in fact, if $z_{i+1} = z_i$, from $z_{i+1} = \theta(z_i)$, it would follow that $z_{i+2} = \theta(z_{i+1}) = z_i$ and so on, in contrast to $\lim_{i\to\infty} z_i = x^*$; finally $x^* < Q(x^*)$ implies that, for i large enough, $Q(z_i) > x^* \geq z_{i+1}$ (storage only from reproduction).

We now prove that

$$\text{If } z_i < M(z_{i-1}), \text{ then } z_{i+1} < Q(z_i). \tag{A16}$$

This means that if in year i there is some reproduction, from year i+1 on there will always be reproduction, and there will be no direct allocation to storage.

Suppose, on the contrary, that there exists i, such that $z_i < M(z_{i-1})$, and $z_{i+1} \geq Q(z_i)$. Using Equation (A10) for year i and year i+1, we obtain

$$pU_x(z_i,z_{i+1}) = -U_y(z_{i-1},z_i)$$
$$pU_x(z_{i+1},z_{i+2}) \geq -U_y(z_i,z_{i+1}).$$

$z_{i+1} \geq Q(z_i)$ implies that $-U_y(z_i,z_{i+1}) = 1$, $U_x(z_i,z_{i+1}) = M'(z_i)$. We also know from Equation (A8) that $-U_y(z_{i-1},z_i) \leq 1$ and $U_x(z_{i+1},z_{i+2}) \leq M'(z_{i+1})$. Putting these equalities and inequalities together, we obtain $pM'(z_{i+1}) \geq pM'(z_i)$, while the concavity of M and the fact that $z_i < z_{i+1}$ imply that $M'(z_i) > M'(z_{i+1})$. We have therefore found a contradiction, from which Equation (A16) follows.

Appendix 2. An explicit characterization of the two cases

We have seen in Appendix 1 that the important constants to characterize the strategy are x^* and ℓ; ℓ is defined in (P3), while, denoting $pU_x(x,x) + U_y(x,x)$ by $Z(x)$, we see from Equation (A15) that x^* solves $Z(x^*) = 0$. If $x^* < \ell$, we have gradual growth with reproduction; if $x^* \geq \ell$, we have first growth, then reproduction. Since $Z(x)$ is a decreasing function of x (see P4), we have

$$\text{if } Z(\ell) \geq 0, \text{ then } x^* \geq \ell; \tag{A17}$$

$$\text{if } Z(\ell) < 0, \text{ then } x^* < \ell. \tag{A18}$$

We then see from (A7)–(A8) and the expression for $M(x)$ that

$$Z(\ell) = pM'(\ell) - 1 = pf(\ell/q)/f(\ell) - 1 \tag{A19}$$

In order to see how (A17) or (A18) depend on q, one can show, using the dependence of ℓ on q and an explicit formula for $M'(x)$, that $pM'(\ell)$ is a decreasing function of q. Since it is easy to show that for $q = 0$ $Z(\ell) > 0$, while for $q = 1$ $Z(\ell) < 0$, it follows that there exists q^* such that $Z(\ell) = 0$. For $q < q^*$ (A17) holds; for $q > q^*$ (A18) holds.

If we assume that $f(V) = aV^b$, Equation (1) can be solved explicitly; then also ℓ and x^* can be computed. From Equation (A19) one sees that $Z(\ell) = pq^{-b}-1$. Therefore Equation (A17) holds when $p \geq q^b$; Equation (A18) holds for $p < q^b$. Expression (5) and (6) for x^* can then be obtained through some computations.