



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

The Optimal Timing of Reproduction

Author(s): Dan Cohen

Source: *The American Naturalist*, Sep. - Oct., 1976, Vol. 110, No. 975 (Sep. - Oct., 1976), pp. 801-807

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2460084>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

The American Society of Naturalists and *The University of Chicago Press* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

THE OPTIMAL TIMING OF REPRODUCTION

DAN COHEN

Department of Botany, The Hebrew University, Jerusalem

The partition of resources between somatic growth and reproduction is one of the most important problems which a developing organism has to face. Analytical studies by Taylor et al. (1974) and computer simulation by Gadgil and Bossert (1970) have recently contributed to the study of this problem. Essentially, the problem is to choose between early reproduction with less growth and later reproduction after more growth has taken place, which allows a higher rate of reproduction.

A simple model has been discussed by Cohen (1971). In this paper further models and predictions for optimal strategies for reproduction and growth are presented, taking into account the decrease in relative growth rate with size and the decreased survival of the plants with time. Recently, Paltridge and Denholm (1974) have further developed a model for optimal switching from vegetative to reproductive growth.

THE BASIC MODEL

In general, the growth of the somatic or vegetative biomass of most organisms, in the absence of any reproductive growth, can be described by a sigmoid curve, that is, a continuously decreasing relative growth rate. This is caused by a continuously decreasing efficiency per unit biomass in gathering resources and by a continuously increasing cost of maintenance per unit biomass.

Consider, for example, annual plants growing from seeds with nonoverlapping generations. Let us call the net rate of dry-matter production by a single plant $G(M)$, where M is the vegetative biomass. Our only assumption about $G(M)$ is that it increases at low M , becomes maximal at \hat{M} , and decreases at high M , finally becoming zero at some high value of M . We also assume that this production may be partitioned between the production of vegetative biomass, M , and reproductive biomass, S , with $0 \leq F_t \leq 1$ being the fraction which at any moment goes to reproductive biomass, and $(1 - F_t)$ being the fraction which goes to vegetative biomass. Thus, for a single plant,

$$\frac{dS}{dt} = \alpha F_t G(M_t), \quad (1)$$

$$\frac{dM}{dt} = \alpha'(1 - F_t)G(M_t), \quad (2)$$

where a and a' are the corresponding conversion coefficients of dry matter to S and M .

We also assume a survival function $V(t)$, which is the fraction of the population which survives up to time t . For simplicity, we assume that $V(t)$ depends only on t . The optimal strategy is defined, therefore, as the function $F(t)$, which maximizes the expectation or the average reproductive biomass per germinating plant at the end of the growing season. At this stage we assume that $V(t)$ itself is a constant function every year.

Since $G(M)$ decreases at $M > \hat{M}$, the optimal strategy cannot allow M to increase above \hat{M} ; that is, $F(t \geq \hat{t}) = 1$. Optimal $F(t)$ at $t < \hat{t}$ can be shown to be a step function, $F(t < t^*) = 0$, $F(t > t^*) = 1$, under some well-defined conditions.

PROOF

For any given $F(t)$ function, synthesizing reproductive biomass for a short interval Δt at $t_1 < \hat{t}$ results in an average small gain per germinating plant,

$$\Delta S_1 = \Delta t a G[M(t_1)] V(t_1). \tag{3}$$

When t_1 increases at the range $t < \hat{t}$, $(\Delta S_1)/(\Delta t)$ always increases if $G[M(t_1)] V(t_1)$ is an increasing function of t_1 .

If this condition holds, total average S per plant will increase if the production of reproductive biomass during a given short time interval takes place at the latest possible time. Since this is true for any $F(t)$ function, it is also true for the optimal $F(t)$. Optimal $F(t)$ is thus a step function, $F(t < t^*) = 0$ and $F(t > t^*) = 1$, under this condition.

Since $G[M(t)]$ and therefore $(dM)/(dt)$ increases at $t < \hat{t}$ and $V(t)$ decreases with time, ΔS_1 increases over a small time interval if

$$\frac{(d^2M)/(dt^2)}{(dM)/(dt)} > \frac{-[dV(t)]/(dt)}{V(t)}. \tag{4}$$

Over a finite time interval (t_1, t_2) , the condition is

$$\frac{(dM)/(dt_1)}{(dM)/(dt_2)} < \frac{V(t_2)}{V(t_1)}. \tag{5}$$

When $V(t)$ is a step function, $V(t < T) = 1$, $V(t \geq T) = 0$, inequalities (4) and (5) are always satisfied at $t < \hat{t}$. In this case, optimal $F(t)$ is a step function at $t = t^*$, and

$$S_T = \frac{a}{a'} \frac{dM}{dt^*} (T - t^*) + r M^*, \tag{6}$$

where r is the reutilization conversion factor of vegetative to reproductive biomass; $r < a$.

$$\frac{\partial S_T}{\partial t^*} = \frac{a}{a'} \left[\frac{d^2M}{dt^{*2}} (T - t^*) - \frac{dM}{dt^*} \right] + r \frac{dM}{dt^*}. \tag{7}$$

Optimal t^* is at T if $(\partial S_T)/(\partial t^*) \geq 0$ at $t^* = T$, but this is impossible, since it would require that $r > a/a'$, which we had assumed is never the case. Optimal t^* equals 0 if $[(\partial S_T)/(\partial t^*)](t^* = 0) \leq 0$, that is, when

$$\frac{a}{a'} \frac{d^2 M}{dt^2}(t=0) \cdot T < \left(\frac{a}{a'} - r\right) \frac{dM}{dt}(t=0). \quad (7.1)$$

This would become possible when $[(d^2 M)/(dt^2)](t=0)$ is very small and would always be the case when $[(d^2 M)/(dt^2)](t=0) < 0$, that is, when $M_0 > \bar{M}$. At small M , $M_t = M_0 \cdot e^{gt}$, $(dM)/(dt) = M_0 g e^{gt}$, $(d^2 M)/(dt^2) = M_0 g^2 e^{gt}$, and $[(dM)/(dt)]/[(d^2 M)/(dt^2)] = 1/g$. Thus, at small M , inequality (7.1) becomes $(a/a')gT < (a/a') - r$, which holds when $g \cdot T < 1 - [(r \cdot a)/a']$, which is possible only under a combination of a very short growing period and a low specific growth rate.

When optimal t^* is between 0 and T , it is the solution to $(dS_T)/(dt^*) = 0$; that is,

$$t^* = T - \left(1 - \frac{ra'}{a}\right) \frac{(dM)/(dt^*)}{(d^2 M)/(dt^{*2})}. \quad (8)$$

Thus, for any given growth function, t^* is an increasing function of r , and so is M^* .

Early growth of individual plants is approximately exponential; $(dM)/(dt) = gM$, $M(t) = M_0 e^{gt}$. At this stage, $V(t)$ is often an exponentially decreasing function e^{-kt} . Thus $[(dM)/(dt)] \cdot V(t) = M_0 e^{(g-k)t}$, which is an increasing function of t when $g > k$. This is usually the case, except perhaps at very early stages of seedling mortality.

When M increases, $(dM)/(dt)$ increases at a slower rate, so that eventually $[(dM)/(dt)]V(t)$, which is the average production per initial plant, starts to decrease at some $t \leq \hat{t}$. Final average reproductive production per initial plant, \bar{S}_T , decreases if switching is delayed beyond this point.

For a step function $F(t)$, mean final S is given by:

$$\bar{S}_T = \frac{a}{a'} \frac{dM}{dt^*} \cdot \int_{t^*}^T V(t) dt, \quad (9)$$

where T satisfies $V(T) = 0$. We ignore the reutilization of vegetative biomass, assuming that in this case there is no prior signal for death for an individual plant. To find optimal t^* , we take the derivative:

$$\frac{\partial \bar{S}_T}{\partial t^*} = \frac{a}{a'} \left[\frac{d^2 M}{dt^{*2}} \int_{t^*}^T V(t) dt - \frac{dM}{dt^*} V(t^*) \right]. \quad (10)$$

Optimal $0 < t^* < T$ satisfies the equation

$$\frac{(d^2 M)/(dt^{*2})}{(dM)/(dt^*)} = \frac{V(t^*)}{\int_{t^*}^T V(t) dt}. \quad (11)$$

If $V(t) = e^{-kt}$, then optimal t^* satisfies the equation

$$\frac{(d^2 M)/(dt^{*2})}{(dM)/(dt^*)} = k. \quad (12)$$

Since $[(d^2M)/(dt^2)]/[(dM)/(dt)]$ continuously decreases, optimal t^* increases when k decreases; that is, better survival delays optimal switching time to reproductive growth. If $V(t)$ is a linear function, $V(t) = 1 - (t/T)$, optimal t^* satisfies

$$\frac{V(t^*)}{\int_{t^*}^T V(t) dt} = \frac{2}{T - t^*}. \quad (13)$$

This becomes smaller as T increases. Thus optimal t^* increases when the survival time increases.

In general, a plant may have the choice of either continuing to synthesize reproductive biomass until it dies or responding to an approaching termination of its growing period by a reutilization of its vegetative biomass to produce more reproductive biomass at once and terminating its productive life at an appropriate moment before its previously expected time of death.

If a plant can get a reliable signal about the termination of its growth period such as, for example, the increasing depletion of water in the soil, the plant is expected to reutilize optimally its vegetative biomass at the smallest possible time interval before termination time.

If, on the other hand, a plant has no prior information about the time of its death, then the average gain in reproductive biomass by termination and reutilization at time t' is

$$\Delta S_r(t') = rM^*V(t'). \quad (14)$$

If the plants continue to produce, the average gain is given by:

$$\Delta S(t') = a \cdot G(M^*) \int_{t'}^T V(t) dt. \quad (15)$$

Thus the optimal policy is to continue to produce as long as

$$\Delta S(t') > \Delta S_r(t'); \quad (16)$$

that is,

$$\frac{a \cdot G(M^*)}{r \cdot M^*} > \frac{V(t')}{\int_{t'}^T V(t) dt}.$$

When $V(t)$ is an exponentially decreasing function e^{-kt} ,

$$\frac{V(t')}{\int_{t'}^T V(t) dt} = \frac{k \cdot e^{-kt'}}{e^{-kt'} - e^{-kT}}. \quad (17)$$

Because e^{-kT} is by definition close to zero, the ratio is simply k . The inequality $\Delta S(t') > \Delta S_r(t')$ is in this case independent of t' and will be immediately satisfied at t^* or not at all.

For $V(t)$ functions less concave than the declining exponential and for all convex functions,

$$\frac{V(t')}{\int_{t'}^T V(t) dt}$$

is an increasing function of t^* , since the integral decreases more strongly than $V(t)$ itself. In all these cases,

$$\frac{V(t^*)}{\int_{t^*}^T V(t) dt}$$

increases as a function of t^* , so that reutilization becomes optimal at some $t^* < T$ except when $r = 0$. For example, in the linear case, $V(t) = 1 - (t/T)$,

$$\int_{t^*}^T V(t) dt = \frac{1}{2}(T - t^*) \left(1 - \frac{t^*}{T}\right),$$

and

$$\frac{V(t^*)}{\int_{t^*}^T V(t) dt} = \frac{2}{T - t^*},$$

which becomes infinitely large as t^* approaches T . In this case, termination will maximize S_T when $[aG(M^*)]/(rM^*) = 2/(T - t^*)$, that is, when

$$t^* = T - 2 \cdot \frac{rM^*}{aG(M^*)}, \quad (18)$$

t^* decreases when r increases and a decreases.

DISCUSSION

In an environment maintained constant between years, the optimal strategy for partitioning production between vegetative and reproductive growth, which maximizes the mean reproductive production per plant, is a step change from 0 to 1 of the fraction of reproductive growth at a time t^* , which is earlier than the time \hat{t} at which the vegetative growth rate would be maximal, and at a mass M^* , which is smaller than the mass \hat{M} at which the vegetative growth rate is maximal. The M^* is much less than the maximally obtainable somatic mass, at which $(dM)/(dt)$ becomes close to zero.

This type of optimal strategy would be selected for under the conditions where the reproductive success is strictly *proportional* to the total production of reproductive biomass. We may include the feeding of young dependent offspring in the production of reproductive biomass, since this is essentially a process which demands an excess of food gathering or food intake over the requirements for maintenance and is expected, therefore, to depend on the somatic biomass in a similar way.

An important exception to this prediction is expected to occur when somatic biomass has an added advantage for reproduction or survival. An extreme case is of polygamous males, who invest very little in strictly reproductive biomass. Their success in reproduction depends on their ability to fight with other males over mating with females. Since success in fighting probably increases with somatic size, such males are expected to grow to the maximum attainable size, which is much larger than that of the females, which have to maximize the production of reproductive biomass. Similarly caused differences in size between

males and females are expected when the reproductive success of males depends on their ability to hold and defend a territory against other males. Such differences in size are, indeed, commonly observed.

When males and females have an equal share in feeding the young, they are both adapted to maximize food gathering, and this should result in their having the same size if they utilize the same resources.

Another advantage caused by large size may be an increase in survival. This would tend to make optimal M^* larger than it would be if survival were independent of size. Such an effect may be expected in many plants and animals.

Some structures may serve both somatic and reproductive functions, for example, green photosynthesizing inflorescence parts, which later become a part of the mechanism for protection or dispersal of seeds. Thus, instead of switching from purely vegetative to purely reproductive production, it is possible in such cases to have an optimal first switch at M_1^* from purely vegetative to dual-purpose production, and an optimal second switch at M_2^* from dual-purpose to purely reproductive production. In general, the dual-purpose organs would be less efficient in each one of the specialized functions. Thus it would be expected that $M_1^* < M_0^* < M_2^*$, when M_0^* is the optimal transition size without dual-purpose organs.

Another factor which affects the optimal transition is the ability of organisms—for example, many plants—to reutilize a fraction of the biomass invested in the vegetative biomass for reproduction when approaching the termination time (see Cohen 1971). In general, this would postpone the optimal transition time and increase the optimal transition mass, as in equation (8).

In a step function $V(t)$, complete reutilization is optimal during the shortest possible time interval before T . In most other forms of $V(t)$, reutilization leading to termination of photosynthesis is often optimal before the externally imposed complete extinction of the population. Thus plants are expected to liquidate their photosynthetic machinery in response to environmental signals, such as the photoperiod, which are correlated with the approaching termination of the growing period. This will be more pronounced in real situations, where we have to assume that reutilization takes some time, so that the initiation of reutilization must start considerably earlier. In fact, much of the so-called senescence of leaves of a maturing annual plant is most probably the result of the optimal reutilization process (Paltridge and Denholm 1974). In this case, inequality (16) may be applied to each leaf in succession. For the same given termination time, leaves are utilized according to their age, which reduces their photosynthetic production relative to their reutilization value.

In a spatially heterogeneous environment, the survival function and termination time may vary considerably in different sites. If the plants are not able to get information about the local variation of the survival function, then this variation is included in the survival function of the population as a whole. If local information is available to the plants, then transition time will be locally optimized.

For example, when water shortage limits the growing period, local variation in the amounts of available water will cause local variation in the survival func-

tion. It is expected that plants would be able to respond optimally to such variations in availability of water by appropriate changes in the transition times. It has been reported in several cases that water shortage induces an earlier beginning of flowering. It is an even much more common observation that water shortage causes a much earlier complete cessation of vegetative growth (Newman 1965).

Many annual plants have a fairly sharp transition between vegetative and reproductive phases, including many crop plants such as wheat, maize, soybeans, etc. On the other hand, many wild plants and also some crop plants have a prolonged period of both vegetative and reproductive growth. I shall show in a subsequent paper that such a behavior is optimal when the survival function or the growth rate of the plants, or both, vary randomly between different years.

The derivation by Paltridge and Denholm (1974) is correct only when their senescence function, $S(t)$, is the same every year.

The present results are similar to a specific case in the very general paper by Taylor et al. (1974), although the specific assumptions are somewhat different in their model.

SUMMARY

The optimal timing of reproductive effort is determined in a model which takes into account (a) the physiological limits on the growth and biomass production of the individuals, (b) the survival function of the population, and (c) the reutilization of somatic biomass for reproduction at the end of the season.

Total reproductive biomass is maximized by a step transition from somatic growth to reproductive production. Optimal transition is at a biomass which is much less than the maximally attainable biomass. Optimal transition time is an increasing function of the survival and of the reutilization conversion factor. Much higher optimal transition biomass is expected where reproductive success depends not only on the production of reproductive biomass but is an increasing function of somatic biomass as well.

LITERATURE CITED

- Cohen, D. 1971. Maximizing final yield when growth is limited by time or by limiting resources. *J. Theoret. Biol.* 33:299-307.
- Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. *Amer. Natur.* 104:1-24.
- Newman, E. I. 1965. Factors affecting the seed production of *Teesdalia nudicaulis*. II. Soil moisture in spring. *J. Ecol.* 53:211.
- Paltridge, G. W., and J. V. Denholm. 1974. Plant yield and the switch from vegetative to reproductive growth. *J. Theoret. Biol.* 44:23-24.
- Taylor, H. M., R. S. Gourby, C. E. Lawrence, and R. S. Kaplan. 1974. Natural selection of life history attributes: an analytical approach. *Theoret. Pop. Biol.* 5:104-122.