

Dynamic optimization of plant growth

Yoh Iwasa*

Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812-8581, Japan

ABSTRACT

The growth and reproductive schedule of terrestrial plants can be usefully studied as the dynamic optimal allocation of material between different organs. This idea, pioneered by Dan Cohen, has been formalized as an optimal control problem and analysed using Pontryagin's maximum principle or dynamic programming. Here, I review several examples of dynamic resource allocation models. First, the seasonal timing of reproduction of annuals is discussed. This can be extended to plants with multiple vegetative organs and the optimal shoot–root balance is assessed. Secondly, the growth schedule over multiple seasons is examined, and the reproductive effort, the leaf phenology of deciduous perennials, and the conditions under which perenniality is more advantageous than annuality are considered. With some modifications, the same model can handle intermittent reproduction and monocarpic perennials (one large reproduction after many years). Thirdly, growth in an unpredictably fluctuating environment is analysed for the case in which a sudden disturbance (herbivory or fire) removes the photosynthetic system altogether, followed by recovery using stored material, and for the case in which environmental productivity fluctuates in a Markovian process. Finally, the optimal level of chemical defence against herbivory is formalized and used to explain the intensity of alkaloid defence decreasing with leaf age. These examples illustrate the usefulness of dynamic resource allocation models in understanding plant life-history adaptation.

Keywords: defence against herbivory, dynamic programming, growth schedule, life-history strategy, phenology, Pontryagin's maximum principle, shoot–root balance, stochastic environment.

INTRODUCTION

Every day in a growing season, a plant obtains material by photosynthesis and allocates it to various organs, such as leaves, roots, stems, flowers and fruits. The plant may also invest in storage for the future and defence against fire or herbivory (van der Meijden *et al.*, 1988). Diverse patterns of plant growth and life history are observed in nature, and these are presumably the result of adaptation to each environment. Evolutionary outcome of plant life history can be viewed as the optimal schedule of resource allocation, chosen under physical and informational constraints.

* e-mail: yiwasscb@mbox.nc.kyushu-u.ac.jp

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However, maximizing fitness over a lifetime does not involve maximizing survivorship or fecundity at every instant in time. For example, to maximize the total lifetime reproductive success, a plant should first grow vegetatively and then switch to reproductive activity. This view was clearly stated by Dan Cohen in his seminal paper published in 1971. Later, formal calculations of dynamic optimization were introduced (Taylor *et al.*, 1974; Leon, 1976), techniques developed in engineering to calculate the optimal design and optimal schedule. They gave a clear and unified understanding of the diverse life histories of terrestrial plants. By using these models, we can study when, for example, annuals should start reproduction and whether plants should allocate all material to seed production at the end of the first year to be an annual, or save some for the following season to be a perennial.

The aims of this paper are to review several examples of dynamic resource allocation models and to illustrate how a wide variety of aspects of plant life can be usefully understood as dynamic resource allocation. Models based on dynamic optimization have also been applied to animals, including behaviour (Iwasa *et al.*, 1984; McNamara *et al.*, 1987; Mangel and Clark, 1988), sex changes in fish and shrimp (Iwasa, 1991a) and seasonal caste production in social insects (Oster and Wilson, 1978), but here I concentrate on models for terrestrial plants.

DYNAMIC RESOURCE ALLOCATION WITHIN A SEASON

Let us begin with the timing of flowering for annuals, a problem addressed by Cohen (1971, 1976). Let $F(t)$ be the size of vegetative organs, including leaves, stems and roots. Daily net production – the gain by photosynthesis minus respiration – is an increasing function of vegetative part size, such that $g(F) = aF/(1 + hF)$. This becomes saturated as F becomes very large, because of local resource depression, such as self-shading in the canopy or nutrient depletion in the soil. The new production will be allocated to growth of the vegetative part and to reproductive activity. The growth in a season ($0 < t < T$) is expressed as:

$$dF/dt = (1 - u)g(F) \quad (1a)$$

$$dR/dt = ug(F) \quad (1b)$$

with initial conditions $F(0) = F_0$ given by seed size and $R(0) = 0$. $u(t)$ is the fraction of new production allocated to reproductive activity. It may change with t , satisfying the constraint $0 \leq u(t) \leq 1$. R is the accumulated investment in reproductive activity, including the construction and maintenance of flowers and fruits made before t . The optimal schedule is the one that achieves the maximum total amount of reproductive investment made over the whole period:

$$\varphi = R(T) \rightarrow \text{maximum} \quad (2)$$

Justification of this assumption is given by natural selection. A phenotype with greater reproductive success than others would increase its frequency in the next generation and, after many generations, the population will be expected to include only those individuals realizing the maximal reproductive success under given constraints. Here, what the plant should choose among alternatives is not simply a single quantity, but a function of time $u(t)$.

Maximum principle: Dynamics of marginal values

The optimization problem as formulated above can be solved by using Pontryagin's maximum principle (Pontryagin *et al.*, 1962). The basic concept underlying the technique is marginal values of different activities (Iwasa and Roughgarden, 1984). Suppose that a vegetative part size F , such as leaf mass, increases by a unit amount at time t . Then, the enhanced photosynthetic rate produces additional photosynthate from t until the end of the season T , and it finally improves total reproduction φ . The increment of reproductive performance φ caused by the unit increase in vegetative part size F is called the marginal value of vegetative growth, $\lambda_F(t)$. It decreases with time t and becomes zero at the end of the season, because the vegetative part can contribute to the reproductive success only by improving photosynthesis until the end of the season (Fig. 1B). In contrast, the marginal value of reproductive activity, $\lambda_R(t)$, is always 1, because unit investment of reproductive activity contributes to φ by a unit amount irrespective of time. Hence, there is a switching date t_s , so that the marginal value of vegetative growth is larger than that of reproductive activity before t_s , but smaller after t_s . The optimal strategy each day in the season is to invest the photosynthate only in the organ with the highest marginal value. Hence, the model predicts a clear switch at t_s from vegetative to reproductive growth, as shown by many annuals (Cohen, 1971; Vincent and Pulliam, 1980; King and Roughgarden, 1982; Schaffer *et al.*, 1982) (Fig. 1A).

The switching occurs when the investment in vegetative growth, such as further leaf production, does not result in a sufficient return to pay back the cost because of the limited growth period remaining in the season. Hence, in a favourable environment, the switch from vegetative to reproductive growth (i.e. flowering) should occur late. In contrast, in environments less favourable for production, the plant should stop further leaf production earlier. The timing of the switch predicted by dynamic resource allocation models has been tested by comparative and experimental data (e.g. Schaffer *et al.*, 1982; King and Roughgarden, 1983).

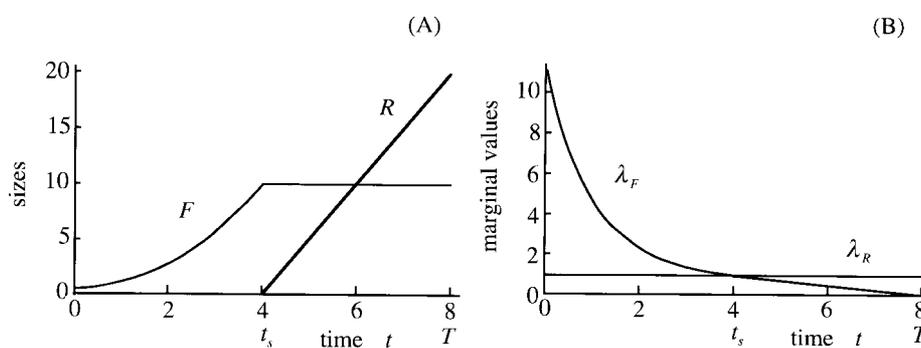


Fig. 1. Optimal growth and reproduction for an annual. (A) Before a switching date t_s , all the new product will be invested in the growth of vegetative organs; after t_s , all will be invested in reproduction. (B) Marginal value of vegetative growth λ_F decreases with time, whereas the marginal value of reproductive activity λ_R is constant. Before the switching date t_s , vegetative growth is more effective $\lambda_F > \lambda_R$; after t_s , reproductive activity is more effective $\lambda_F < \lambda_R$ in contributing to fitness φ . Parameters are: $a = 0.1$, $h = 1$, $F(T) = 10$, $t_s = 4$, $T = 8$, $F(0) = 0.5$.

Shoot–root balance

Plants show great phenotypic plasticity in growth. The numbers and relative sizes of organs often change with local environmental conditions. If a plant grows in a moist and nutrient-rich habitat, the size of roots (below-ground part) relative to shoots (above-ground part) is small, whereas in a dry and open environment, the root-to-shoot ratio of the same species is larger (Russell, 1977; see references in Iwasa and Roughgarden, 1984). To understand the observed balance of shoot and root sizes in terms of a plant's adaptation, Iwasa and Roughgarden (1984) analysed a dynamic optimization model of resource allocation.

Let X_1 , X_2 and R be the shoot size, the root size and the accumulated reproduction respectively. Daily net photosynthesis $g(X_1, X_2)$ increases with shoot size X_1 because photosynthesis occurs in leaves. However, it also increases with root size X_2 , as sufficient water intake is needed to maintain a high photosynthetic rate. A plant starts from initial sizes ($X_1(0)$, $X_2(0)$) given by the material in a seed, and grows by allocating the photosynthate to shoot growth, root growth and reproductive activity:

$$dX_1/dt = u_1(t)g(X_1, X_2) \quad (3a)$$

$$dX_2/dt = u_2(t)g(X_1, X_2) \quad (3b)$$

$$dR/dt = u_0(t)g(X_1, X_2) \quad (3c)$$

where the allocation ratios $\{u_1(t), u_2(t), u_0(t)\}$ are functions of time, satisfying constraints $u_0(t) + u_1(t) + u_2(t) = 1$ and $u_i(t) \geq 0$ ($i = 1, 2$ and 0).

The optimal growth schedule that maximizes the total reproductive activity (equation 2) is again composed of vegetative growth and a switch to reproductive growth. However, vegetative growth normally includes the simultaneous growth of multiple organs. The trajectory of shoot and root sizes during vegetative growth is illustrated in Fig. 2. We can prove that an optimally growing plant should grow along the 'balanced growth path' indicated by the bold curve in Fig. 2 (calculated by $\partial g/\partial X_1 = \partial g/\partial X_2$). Along this path, a plant has the root-to-shoot ratio that maximizes daily net photosynthesis for a given total biomass. Specifically, suppose that daily net photosynthesis is

$$g(X_1, X_2) = \frac{1}{(a_1/LX_1^{b_1}) + (a_2/WX_2^{b_2})} \quad (4)$$

where L is the intensity of light in the canopy and W is soil moisture. Then, along the balanced growth path, root and shoot sizes satisfy the following allometric relation:

$$[\text{root size}] \propto \left(\frac{[\text{light}]}{[\text{moisture}]} \right)^{1/(1+b_2)} [\text{shoot size}]^{(1+b_1)/(1+b_2)} \quad (5)$$

which shows that the root-to-shoot ratio should increase with intensity of light and decrease with moisture availability. The simple ratio of root-to-shoot sizes changes as the plant grows if $b_1 \neq b_2$.

The model also explains the way a plant grows when its shape deviates from the balanced growth path due either to pruning or to environmental changes (Russell, 1977; see references in Iwasa and Roughgarden, 1984). For example, after shoot pruning, the plant should stop root growth immediately and start investing all its photosynthate in shoot recovery. The simultaneous growth of shoots and roots occurs when their ratio returns to a balanced growth curve.

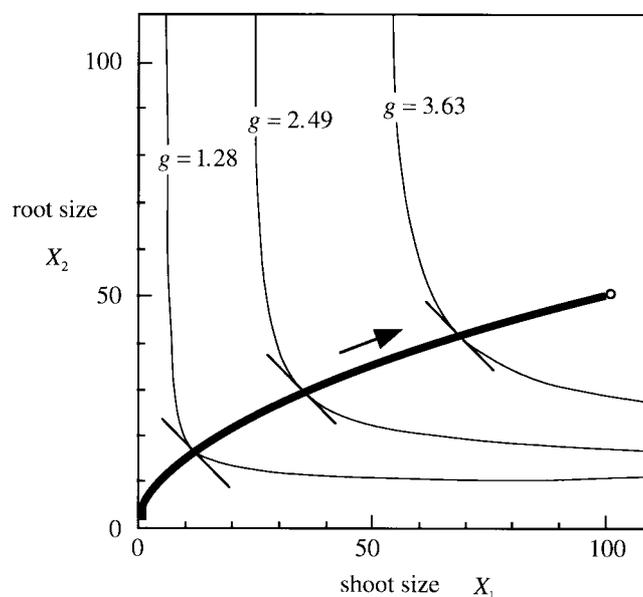


Fig. 2. Shoot–root balance for an optimally growing plant. Horizontal axis is shoot size X_1 and vertical axis is root size X_2 . A family of thin curves are contours of daily production rate $g(X_1, X_2)$ and the bold curve is the balanced growth path; the arrow indicates the direction of growth. The open circle = maturation size. Parameters are: $a_1 = 2$, $a_2 = 60$, $b_1 = 0.5$, $b_2 = 2$, $L = 1$ and $W = 1$ (modified from figure 3 in Iwasa and Roughgarden, 1984).

PERENNIALS

At the end of a growing season, a plant may save some material in storage organs, with which it reconstructs the photosynthetic system at the beginning of the next season. What are the conditions under which such a perennial life history is more advantageous than an annual one? Of the material produced in a year, how much should be allocated to reproduction in the same year and how much should be saved for the following year? How should these depend on parameters such as the length of the growing season, the stability of the habitat and the rate of photosynthesis? To address these questions, Iwasa and Cohen (1989) developed an optimal allocation model for a deciduous plant with two parts: a production part, including vegetative organs working for photosynthesis (leaves, stems and roots combined), and a storage part, including both stored material and accumulated reproductive investment for the year (see Pugliese, 1988a). The model is a combination of a continuous-time model for within-season growth schedule and a discrete-time model for between-season allocation (Gadgil and Bossert, 1970; Schaffer, 1974; Taylor *et al.*, 1974; Leon, 1976; Schaffer and Schaffer, 1977).

Growth over multiple seasons

The year is indicated by a subscript n ($= 1, 2, 3 \dots$) and the time within a season by a continuous parameter t ($0 \leq t \leq T$). Let F_n be the size of the production part and S_n be that of the storage part (Fig. 3). The daily net photosynthetic rate increases with size of

the productive part as $g(F) = aF/(1 + hF)$. Photosynthetic product is allocated between the productive part and the storage part:

$$dF_n/dt + dS_n/dt = g(F_n) \quad (n = 1, 2, 3 \dots; 0 \leq t \leq T) \quad (6)$$

The production part is lost at the end of each growing season (the plant is deciduous), and it needs to be reconstructed at the beginning of the following season: $F_n(0) = 0$ ($n = 1, 2, 3 \dots$). The production part F does not include the trunks of trees.

The size of the storage part in the $(n + 1)$ th season is:

$$S_{n+1}(0) = \gamma(S_n(T) - R_n) \quad (n = 1, 2, 3 \dots) \quad (7)$$

where R_n is the total reproductive investment made in the n th season by constructing and maintaining flowers and fruits, and satisfies the constraint $0 \leq R_n \leq S_n(T)$. Only a fraction γ of the stored material can be recovered due to loss in the storing process (Fig. 4). The initial size for the first year $S_1(0)$ is given by seed size. The growth rate of the production part may also be constrained by some upper limit.

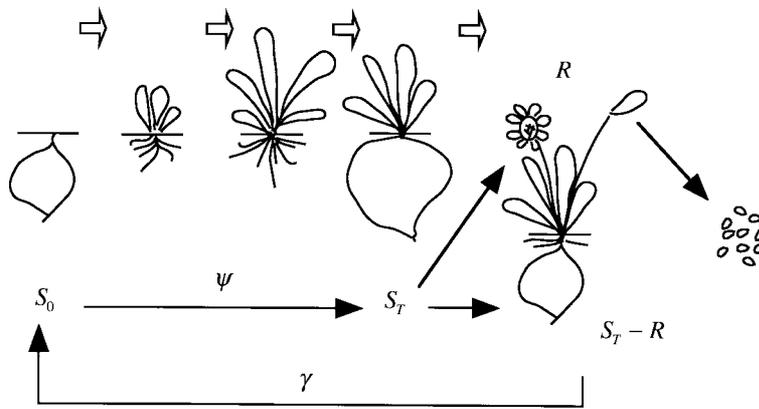


Fig. 3. Scheme of perennial growth.

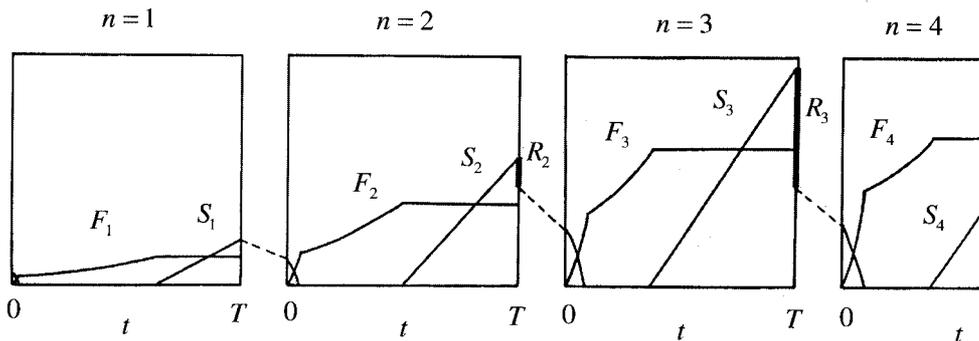


Fig. 4. An example of perennial growth. Time within a season is indicated by t ($0 < t < T$) and year by n ($n = 1, 2, 3 \dots$). For an annual plant, all material in the storage part is used for reproduction at the end of the first year (adapted from figure 2 in Iwasa and Cohen, 1989).

The optimal growth schedule is the one which maximizes the lifetime reproductive success:

$$\varphi = \sum_{n=1}^{\infty} p^n f(R_n) \rightarrow \text{maximum} \tag{8}$$

where p is the annual survivorship ($0 < p < 1$). $f(R)$ is the reproductive success in a year in which the plant invests the total resources R , and is an increasing function. The strategy that a plant chooses is its growth schedule within a season and the allocation of resources between reproductive investment and saving for the following season.

Optimal growth schedule

The optimal growth schedule within a season (say, year n), when the initial storage size $S_n(0)$ is given, is the one that maximizes the final size of the storage part $S_n(T)$, because reproduction both in the same year and in the following years is affected only by $S_n(T)$, as pointed out by Yokoi (1976). The optimal growth schedule in a season is composed of three phases. Initially, the plant constructs its production part at maximum speed, mainly using material stored in the previous year. After the storage organ becomes empty, the plant continues to grow vegetatively, using all daily net photosynthate. At a certain time, vegetative growth stops and the plant starts to accumulate photosynthetic products in the storage part. The problem can be solved by the method explained in the last section.

As a result of optimization within a season, the size of the storage part at the end of a season can be expressed as an increasing function of the initial storage size. We denote this as:

$$\psi(S(0)) = \max S(T) \tag{9}$$

where ‘max’ indicates that the plant follows the optimal allocation schedule in the season. $\psi(\cdot)$ is an increasing function but with a diminishing rate of increase because of the limited resources, such as light, soil water and nutrients.

Now we face the choice of allocation between seasons. In each year, the plant must decide how much of the accumulated storage product should be used for reproduction and how much should be saved for the construction of production parts in the following year. The problem can be solved by dynamic programming (Bellman, 1957). Let $V[S]$ be the expected total reproductive investment of a plant from the n th season until its death, provided that the plant has a storage part of size S at the end of the n th season:

$$V[S] = \max_{0 \leq R \leq S} \{f(R) + pV[\psi(\gamma(S - R))]\} \tag{10}$$

where the symbol ‘max’ indicates that the allocation schedule is chosen optimally (Iwasa and Cohen, 1989; Klinkhamer *et al.*, 1997). Equation (10) has a single unknown function $V[S]$ on both sides, but all the others are known. Starting from $V_0[S] = 0$, we apply the following recurrence formula:

$$V_{n+1}[S] = \max_{0 \leq R \leq S} \{f(R) + pV_n[\psi(\gamma(S - R))]\} \tag{11}$$

Then we have the solution of equation (10) in the limit when n is infinitely large. R attaining the maximum in equation (10) gives the optimal reproductive investment to be made in a

year when the storage part size is S . In the braces in equation (10) is the sum of two terms – the first term is the reproductive success made in the current year, and the second is that in following years. The optimal reproductive investment R_n is determined by considering the trade-off between these two (Schaffer, 1974).

When reproductive success is proportional to energy expenditure ($f(R) = R$), Iwasa and Cohen (1989) proved that the optimal solution is:

$$R_n = \begin{cases} S_n - S^* & \text{if } S_n > S^* \\ 0 & \text{if } S_n \leq S^* \end{cases} \quad (12)$$

where the critical storage size S^* is the value of $S - R$ that achieves the maximum in equation (10). If the per-year survivorship p is small, the optimal storage size S^* is zero. Then all the photosynthate in the storage part produced in the first year should be used for reproduction, indicating annual life-history. In contrast, if the optimal storage size S^* is positive, the plant should take a polycarpic perennial life-history – it experiences several immature years during which S_n is less than the optimal storage size S^* , and saves all of its resources for the following season. When S_n becomes greater than S^* , the plant invests the excess $S_n - S^*$ in reproductive activities, and repeats the same growth schedule thereafter (Fig. 5A, C).

Annuality is favoured over perenniality if the habitat reliability p is small – that is, if the habitat of a plant has a high chance of being destroyed before the end of the next season, due for example to herbivores, pathogens or catastrophic physical disturbances. A low

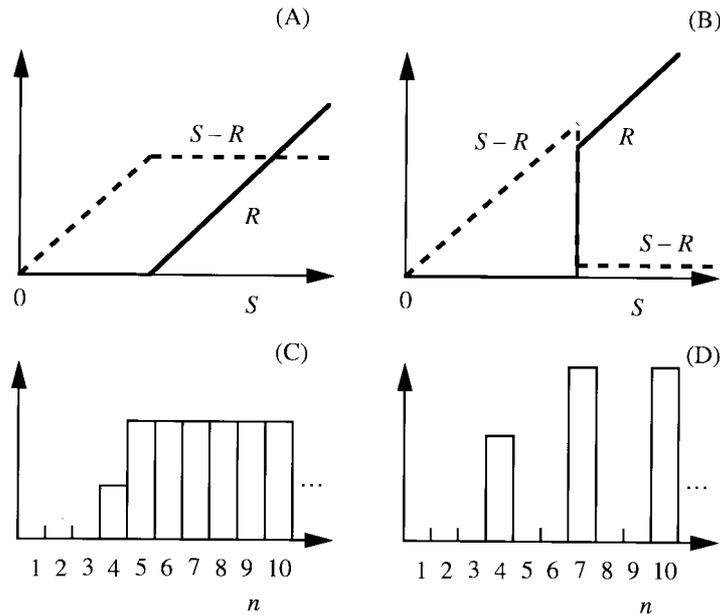


Fig. 5. Optimal allocation to the reproductive activity in the current year (solid line) and the resources saved for the following year (dotted line). Horizontal axis is storage size at the end of a season. (A) The basic model, with $f(R) = R$. (B) Reproductive success is an accelerating function of investment. (C) Optimal reproductive activity for different age n , for the basic model. (D) Optimal reproductive activity for accelerating $f(R)$. Periodic and intermittent reproduction is the optimal.

storage efficiency γ has a similar effect. A short growing season and a small net photosynthetic rate also favour annual life over a perennial one.

The model of an optimal growth schedule over multiple seasons explains many regularities of plant growth and leaf phenology that have been observed in nature, for example how reproductive effort (ratio of reproductive investment to the total annual productivity) should change with environmental parameters, or the timing of leaf production in different habitats (Iwasa and Cohen, 1989).

Masting and monocarpy

This formalism clarifies how optimization within a season and optimization over the years can be combined. However, the predicted optimal growth does not fit perfectly with the plant growth behaviour observed in nature.

First, in the basic model explained above, optimally growing plants should stop investing in growth once they reach maturity. However, many trees continue to grow after maturity. This can be considered the optimal growth behaviour if some fraction of the vegetative part remains usable in the following years, which is quite plausible for trees and animals (Pugliese and Kozłowski, 1990). Other factors favouring growth after maturity include non-linear trade-offs, variable season length, and production and mortality rates that are both increasing (or decreasing) functions of body size (Perrin and Sibly, 1993).

Secondly, the basic model suggests that perennials should reproduce every year at a constant rate once they reach maturity. However, many trees, such as beech and oak, show a large fluctuation in reproductive activity over the years. In mast years, a large number of flowers and fruits are produced, but in non-mast years tree reproductive activity is very low. The degree of fluctuation in their reproductive activity is too large to be explained by year-to-year environmental fluctuation in photosynthetic ability (Koenig *et al.*, 1994).

A still larger problem arises for monocarpic perennials, in which individuals reach maturity after a number of years (hence not annual), but once they reproduce they use all their stored materials for reproduction and die, exemplified by bamboo and many biennials common in sand dunes. Klinkhamer *et al.* (1997) studied several modifications of the model to explain intermittent reproduction (masting) and single big reproduction (monocarpy) as the optimal resource allocation.

Predators, such as rodents, can eat seeds or seedlings effectively if a tree produces a small number of them, while they may leave some uneaten if a large amount of seeds are produced. Predator satiation tends to favour trees showing masting, and is a major hypothesis explaining the adaptive significance of the intermittent reproduction of trees (or masting) and monocarpy (Koenig *et al.*, 1994; Schaffer and Schaffer, 1977).

This can be represented by the case in which reproductive success $f(R)$ in equation (10) is not a linear function of R , but an S-shaped function, such as $f(R) = aR^2/(1 + hR^2)$, or simply a power function $f(R) = aR^k$ with $k > 1$, which increases with R at an increasing rate for small R (Pugliese, 1988b). When we use these non-linear functions, the optimal reaction of the plant in equation (10) has a threshold storage size, below which no reproductive investment should be made. However, a plant with storage size larger than this threshold should invest a large amount of resources in reproductive activity, much larger than just the excess from the threshold, and this results in a very depressed level of resources in the following year (Fig. 5B, D). It may take several years before the energy reserves of the plant return to the reproductive threshold again, and the optimal reproductive pattern

is an intermittent reproduction (Yamauchi, 1996; Klinkhamer *et al.*, 1997). However, even if we choose $f(R)$ as a very sharply increasing function, it is difficult for this model to generate the optimal solution with monocarpic perennials showing a single big reproduction accompanying the ending of life.

The mortality of the parent may also be enhanced by reproduction compared to the value for a non-reproductive individual, which may be caused by the herbivores and pathogens that are attracted by reproducing plants (Klinkhamer *et al.*, 1997). This can be simply modelled by an annual survivorship $p(R)$ decreasing with reproductive activity R . Then, the optimal reproductive schedule is either intermittent and fluctuating reproduction (masting) or monocarpy (a single big reproduction followed by death).

Klinkhamer *et al.* also examined the reduction in storage efficiency depending on reproductive activity, expressed by $\gamma(R)$ as a decreasing function of R . From the above, Klinkhamer *et al.* (1997) concluded that reproduction-related mortality mediated through herbivores or pathogens may have played an important role in the evolution of semelparous perennial life-histories, such as biennials.

STOCHASTIC ENVIRONMENTS

The natural environment for plants is spatially heterogeneous and temporally fluctuating. In their choice of growth and reproduction, plants must consider the potential environmental fluctuations that are often unpredictable. Optimal growth under fluctuating environments can be handled by stochastic dynamic programming. I illustrate this using two examples.

Storage for recovery after unpredictable disturbances

Terrestrial plants often live in environments in which above-ground photosynthetic organs (production parts) are suddenly removed by unpredictable disturbances, such as fire, frost, desiccation, pathogen attack, breakage by wind and trampling, or herbivory by insects and mammals. Iwasa and Kubo (1997) studied the optimal growth schedule for a plant having a below-ground storage organ that is used for recovery (or regrowth) of photosynthetic organs after disturbances. Processes included in the model are illustrated in Fig. 6.

Let X be the total plant size, which is the sum of the production part size F and the storage size S . The daily net production rate $g(F)$ is an increasing function of F but saturates for a large F . Let u be the function of daily production allocated to reproductive activity. The rest – that is, the fraction $1 - u$ of the daily production – is allocated to the growth of the production part and storage.

Now, let τ be the time for a recoverable disturbance event that removes the above-ground production part. Then

$$X(\tau + 0) = S(\tau - 0) \quad (13)$$

which indicates that the total plant size after a disturbance event is the same as the storage size just before it. We assume that recoverable disturbances occur in Poisson processes at rate λ . In addition, fatal disturbances occur in Poisson processes at rate μ , and kill the whole plant. The average lifetime of an individual is $1/\mu$.

The optimal strategy of growth and recovery of the plant is the one that achieves the maximum expected lifetime reproductive success. The plant can choose storage size S and

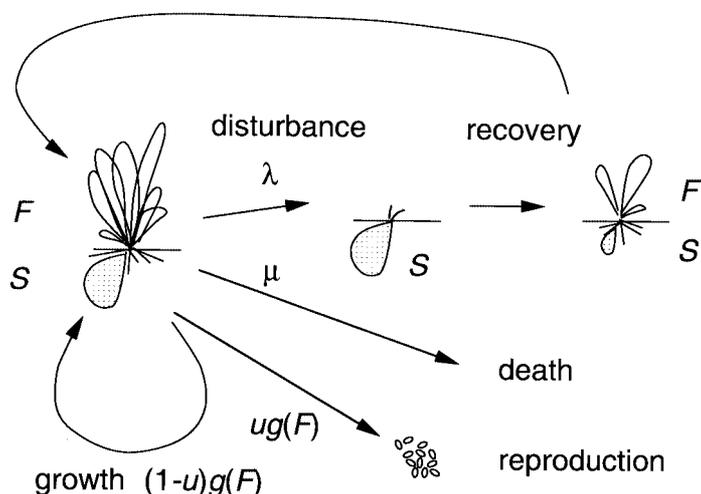


Fig. 6. Scheme of a plant under disturbance that removes the above-ground production part. The plant is composed of a production part (F) and storage part (S). Fraction u of daily photosynthesis $g(F)$ is used for reproduction and the rest is allocated to growth and storage. Recoverable disturbances occur randomly at rate λ , and remove all the production part. Then, the plant recovers quickly using the stored material (to size S), and then recovers more slowly by photosynthesis. Fatal disturbances occur randomly at rate μ . The optimal strategy of the plant is to maximize lifetime total reproductive investment (adapted from figure 1 in Iwasa and Kubo, 1997).

reproductive allocation ratio u at each time, which are given as functions of the total plant size: $S(X)$ and $u(X)$. For simplicity, we assume that recovery by reallocation of stored material occurs rather quickly.

Let us first suppose that there is a final time point T beyond which the plant cannot survive. Let $V[x, t]$ be the expected reproductive success to be made by a plant of size x at time t until its death and before the final time T provided that the plant behaves optimally. We decompose $V[x, t]$, considering the events that can occur during a short time interval of length Δt :

$$V[x, t - \Delta t] = \max_{0 \leq u \leq 1} \max_{0 \leq S \leq x} \{ug(x - S)\Delta t + \lambda\Delta t V[S, t] + \mu\Delta t \cdot 0 + (1 - (\lambda + \mu)\Delta t)V[x + (1 - u)g(x - S)\Delta t, t] + o(\Delta t)\} \quad (14)$$

where $o(\Delta t)$ is a small term that goes to zero faster than Δt . The first term within braces, $ug(x - S)\Delta t$, is the reproductive investment made in this time interval. u is the fraction of new photosynthate allocated to reproduction, and $x - S$ is the size of the production part. The second term, $\lambda\Delta t V[S, t]$, is for a recoverable disturbance. It occurs with probability $\lambda\Delta t$, and after a disturbance event the plant size becomes S , the storage size just before the disturbance. The third term indicates a fatal disturbance occurring with probability $\mu\Delta t$. The fourth term is for the event without these disturbances, in which plant size increases by $(1 - u)g(x - S)\Delta t$, where $(1 - u)$ is the fraction of daily production allocated to growth. The fraction of reproductive investment u and the storage size S are chosen optimally under constraints $0 \leq u \leq 1$ and $0 \leq S \leq x$, respectively, as indicated by the symbol

'max' in equation (14). In the limit when the interval Δt is very small, we have a partial differential equation:

$$-\frac{\partial V}{\partial t}[x, t] = \max_{0 \leq S \leq x} \left\{ \max_{0 \leq u \leq 1} \left(u + (1-u) \frac{\partial V}{\partial x} \right) g(x-S) + \lambda V[S, t] \right\} - (\lambda + \mu)V[x, t] \quad (15)$$

for $0 < t < T$, with the terminal condition $V[x, T] = 0$. The optimal storage size S and the reproductive allocation u are the values that achieve the maximum in equation (15). By solving equation (15) and then calculating the limit when T is infinitely large, we have the optimal solution for the infinite time horizon.

According to the analysis in Iwasa and Kubo (1997), an optimally growing plant shows the following pattern: The ratio of storage size to production part size (S/F ratio) is large if the longevity is large (μ is small) and if the disturbance rate λ is large but a little smaller than the productivity coefficient a . The S/F ratio of mature plants is larger than that of small immature plants. When the plant reaches a threshold size, all the material obtained by photosynthesis will go to the reproductive activity of producing flowers and fruits. After disturbances, the above-ground production part recovers quickly, but reproductive activity is depressed until storage size recovers. The storage organ works as a shock absorber that stabilizes the size of the production part F (Shiyomi *et al.*, 1986). The variations over time and between habitats differing in disturbance frequency are smaller for production part size than for storage size and for reproductive activity.

Growth under stochastic environment

In the last section, the value $V[x, t]$ in the dynamic programming depends on plant size and time, but not on the current environment. This is because the disturbance is assumed to occur completely at random. More realistically, the environment may fluctuate with autocorrelation. For example, if the air temperature today is higher than the average temperature of the season, it is likely to be higher tomorrow as well. If the fluctuation of the environmental condition is Markovian, we can handle the problem nicely. To illustrate this, we consider an annual plant with growth period of length T . Denote the vegetative part size by F . The daily production rate is

$$g(X, F) = \frac{aXF}{1 + hF} \quad (16)$$

where X is the resource availability, such as light intensity or soil moisture.

As discussed earlier, in a constant environment the optimal switch from negative growth to reproductive growth occurs later if X is larger (more favourable environment). How should the optimally growing plant behave if the environment fluctuates? In the calculation of dynamic programming, we now need to consider the current environmental state X because the optimal behaviour of the plant depends on it. The value function is $V[F, x, t]$, which is defined as the average reproductive success made by the plant with size F at time t , and the current environmental value then is $X = x$.

Iwasa (1991b) studied two cases. In a simpler model of two-state Markovian processes, the environmental resource level X jumps between high (x_1) and low (x_2) levels at random time points. Let p_1 and p_2 be the rates of transition from x_1 to x_2 and the reverse transition, respectively. The optimal allocation u depends not only on the time t but also on the size $F(t)$

and on the current resource level $X(t)$. By considering events that possibly can happen during a short time interval of length Δt , we can derive a pair of partial differential equations for $V[F, x_i, t]$ ($i = 1, 2$), and calculate the optimal allocation from these (Iwasa, 1991b).

An example of the optimal growth rule is illustrated on the F - t plane (Fig. 7A). At the beginning of a season (Region I), the plant should grow vegetatively at both resource levels. Towards the end of a season (Region III), the plant should reproduce. In Region II, which lies between the other two, the plant should use a different strategy depending on the current resource level: it should grow vegetatively ($u = 0$) if the current resource availability is high ($X = x_1$), and it should reproduce ($u = 1$) if X is low (x_2). The plant growth in Region II tracks the fluctuation of environmental resource availability.

Figure 7B illustrates the optimal growth rule if the environmental changes are more frequent than in Fig. 7A. Region II becomes narrower, and the optimal plant should follow an almost fixed schedule of phenology independent of the resource level that it experiences. If the environmental resource supply changes quickly, the current level does not give a reliable estimate of the future resource availability.

The optimal growth schedule can also be calculated for the case in which resource availability may change continuously with time, following diffusion processes, which are characterized by the standard level K and the exponential rate r of decay in autocorrelation (Iwasa, 1991b).

Plants with the same photosynthetic ability and the same resource supply will have a very different growth reaction if they differ in the adapted scheme of environmental changes. Many species of plants live under severely restricted nutrient supply. They tend to grow slowly in an experimentally given environment with high nutrient availability, and

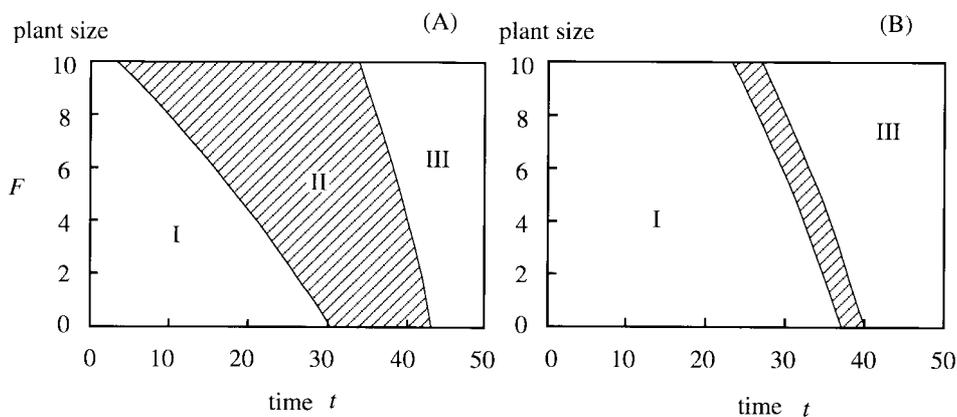


Fig. 7. The optimal growth rule for a plant in a stochastically fluctuating environment. The horizontal axis is the time of season t and the vertical axis is plant size F . Environmental value is a random jumping between high and low values. In Region I, the plant should grow vegetatively in both environments; in Region III, it should reproduce. In Region II, the plant should grow vegetatively if the current resource level X is high, and should reproduce if X is low. Region II is wider if the plant is adapted to a slowly changing environment, as in (A) ($p_1 = p_2 = 0.01$), than if it is adapted to a quickly changing environment, as in (B) ($p_1 = p_2 = 0.2$). Other parameters are: $a = 0.05$, $h = 0.05$, $T = 50$, $x_1 = 3$ and $x_2 = 0.8$ (modified from figure 1 in Iwasa, 1991b).

are called stress-tolerant plants (Grime, 1988). The apparent paradox of these plants can be understood in the light of stochastic dynamic optimization studied here. The production of large vegetative organs is accompanied by the cost of construction and maintenance, and it is beneficial to the plant only when environmental resources remain high for a sufficiently long time to pay back the investment. A pessimistic plant, adapted to the environment with a constantly low resource level and with occasional brief flushes of resources, would not respond to the high level of resources provided experimentally.

CHEMICAL DEFENCE AND LEAF AGE

Many terrestrial plants grow under strong herbivore pressure. An effective way of protection against insect herbivory is to produce a variety of secondary chemical substances for defence (Coley *et al.*, 1985). On the other hand, producing defence chemicals is accompanied by a cost of material or energy, resulting in a slower growth rate (Gulmon and Mooney, 1986). Hence, a plant should choose efficiently the level of chemical defence and how it allocates its limited defence effort to different parts of its body.

For example, in the sand dune biennial *Cynoglossum officinale*, the concentration of pyrrolizidine alkaloids tends to be higher in young leaves than in mature leaves (van Dam *et al.*, 1996). Radioactive precursors showed that pyrrolizidine alkaloids are redistributed from ageing leaves into the youngest leaves (van Dam *et al.*, 1995). This is plausible because young leaves typically have a higher photosynthetic potential than old leaves, which makes them more valuable to the plant.

Calculating the optimal level of defence chemicals contained in a leaf as a function of leaf age is again a dynamic optimization problem (Iwasa *et al.*, 1996).

Optimal defence

Consider an individual in a vegetative phase growing in a constant environment. The plant has a number of leaves with different ages and it constantly produces new leaves using the material obtained by photosynthesis. Let x be the age of a leaf, and $n(x, t)$ be the number of leaves with age x at time t . The leaf age structure follows:

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial x} - h(A(x))n \quad x > 0 \quad (17)$$

where $h(A(x))$ is the rate of loss of leaves. It is a decreasing function of the amount of defence chemical, $A(x)$, contained in the leaf. The data obtained from experiments fit well to an exponential function, $h(A) = h_0 e^{-cA}$, or to a hyperbolic function, $h(A) = h_0/(1 + cA)^k$ (with $k > 0$) (see Fig. 8B). We assume that the defence chemical is not decomposed, but that the plant can reallocate the defence chemical from old leaves to newly produced leaves without loss, as observed in *C. officinale*. Then, the following relationship indicates the conservation of energy:

$$n(+0, t)(a + bA(0)) = \int_0^{x_{\max}} f(y)n(y, t)dy + \int_0^{x_{\max}} b\left(-\frac{dA}{dy}\right)n(y, t)dy \quad (18)$$

where the left-hand side is the number of new leaves multiplied by the cost per leaf. The energetic cost of producing a new leaf is the sum of a , which is independent of the amount

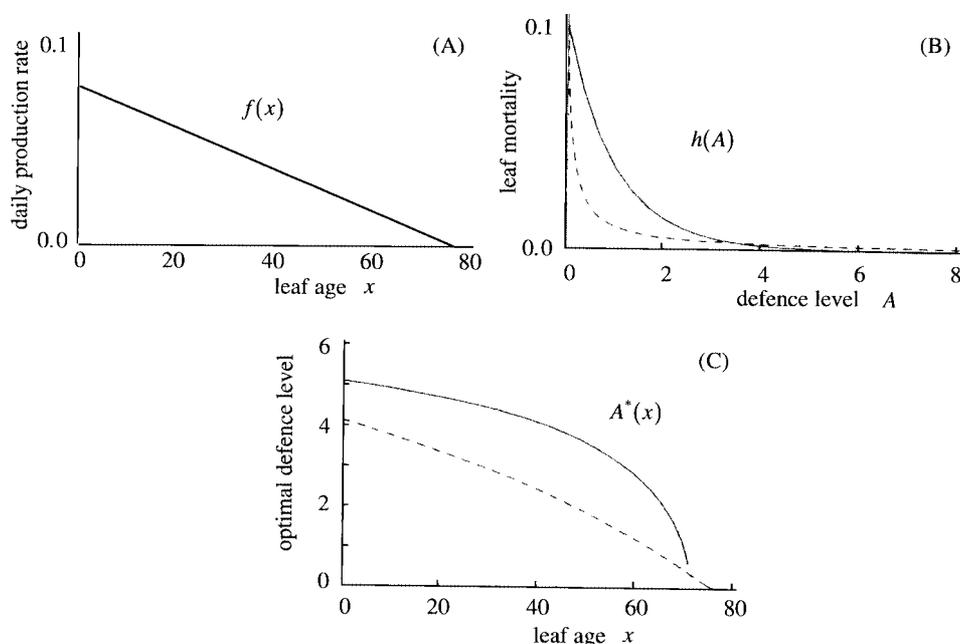


Fig. 8. An example of an optimal defence schedule. (A) Photosynthetic ability of a leaf as a function of age x . (B) Loss rate due to herbivory as a function of the alkaloid defence level A . Solid curve is an exponential function $h(A) = 0.1 \cdot \exp[-A]$; broken curve is a hyperbolic function $h(A) = 0.1/(1 + 9A)$. (C) Optimal defence level A as a function of leaf age x . Solid and broken curves correspond to the two curves in (B). Parameters are: $f_0 = 0.0875$, $x_{\max} = 77$, $a = 1$, $b = 0.00925$ (modified from figure 1 in Iwasa *et al.*, 1996).

of defence chemicals, and $bA(0)$, which is proportional to the amount of chemicals contained in a new leaf. The first term on the right-hand side of equation (18) is for the rate of energy acquisition via photosynthesis, and the second term is for the reallocation of alkaloid from old leaves measured in energetic equivalent. Both are integrals over all leaves with different ages. The rate $f(x)$ is the net photosynthetic rate of a leaf of age x that can be used for production of new leaves; hence, it is the net photosynthetic rate minus the fraction that on average goes to roots, stems or organs other than leaves (for details, see van Dam *et al.*, 1996). The daily production rate decreases with age, such that $f(x) = f_0(1 - x/x_{\max})$ for $x \leq x_{\max}$, and $f(x) = 0$ for $x \geq x_{\max}$ (see Fig. 8A).

If a plant uses a particular age-specific schedule of chemical defence $\{A(x)\}$, the leaf age structure will soon converge to a stable distribution, and then the total number of leaves will increase exponentially with time. By assuming

$$n(x, t) = e^{rt} \hat{n}(x) \quad (19)$$

in equations (17) and (18), we can derive a formula for the exponential rate of increase in r .

What is the age-specific concentration of defence chemicals in leaves $\{A(x)\}$ that realizes the fastest growth of a plant, achieving the largest r ? This problem is the same as searching for the optimal life history that attains the maximum rate of population growth (e.g.

Charlesworth, 1980), because chemical defence is used to improve leaf survivorship. To search for the optimal $A(x)$ that maximizes Malthusian parameter r is mathematically equivalent to the maximization of a leaf's lifetime reproductive success with an exponential discounting for future gain, which was proved by Taylor *et al.* (1974) and Leon (1976) in the context of general life-history optimization. The problem of the latter form is the maximization of an integral of time, and hence it can be solved by Pontryagin's maximum principle (Iwasa *et al.*, 1996).

Optimal schedule of defence chemical concentration

The curves in Fig. 8C illustrate two examples of optimal age-specific defence. The parameters are chosen to correspond approximately with a *Cynoglossum officinale* population studied by van Dam *et al.* (1996). In the optimal solution, defence chemicals decrease with leaf age, but the details of the way they decline may depend on the form of function $h(A)$. An exponential mortality-defence function $h(A)$ would maintain a high optimal level of defence more than half of the leaf's lifetime followed by a quick decrease in defence (the solid curve in Fig. 8C); in contrast, a hyperbolic $h(A)$ predicts a linear decrease in chemical defence throughout the leaf's lifetime (the dashed curve). The optimal pattern of age-specific defence $A^*(x)$ depends also on the net photosynthesis–age relationship, $f(x)$.

According to sensitivity analyses, the level of defence of new leaves, $A(0)$, increases with the cost of leaf production (a) and herbivory intensity (h_0), but decreases with the cost of defence chemicals (b), the effectiveness of the chemical (c) and productivity (f_0). These results are consistent with a simpler model of optimal levels of defence without considering leaf-age dependence (Yamamura and Tsuji, 1995).

Iwasa *et al.* (1996) applied the model of the case of *Cynoglossum officinale* (van Dam *et al.*, 1995, 1996), and found that the level of defence of real plants as a function of age can be explained relatively well. However, to explain the sharp decline with age shown by the observed plants, it was necessary to consider that older leaves tend to be shaded in the rosette.

DISCUSSION

I have illustrated the use of dynamic resource allocation in modelling plant schedules of growth and reproduction by several examples. Optimality models provide us with a useful approximation to the behaviour of well-adapted organisms and a benchmark against which the actual behaviour of plants can be compared. Identifying discrepancies makes us realize important constraints on plant life history that have yet to be appreciated fully. For plant life history, the concept of dynamic optimal allocation of material to different organs and to different activities, introduced by Dan Cohen (1971), provides us with a unifying view of plant ecology and life history, and sometimes useful ways of quantitative modelling of the diverse patterns of growth and reproductive schedule of plants. In the following, I note a few important aspects of evolutionary models that have not been mentioned in this article.

Plants must compete for environmental resources, such as light, soil moisture and nutrients, with their close neighbours. The optimal schedule of growth and reproduction is then affected by the presence of competitors. The evolutionary outcome of dynamic resource allocation is the competitive equilibrium at which an individual plant maximizes

the reproductive success of itself under the environment formed by its competitors. We cannot neglect this aspect, especially when we discuss investment in plant height. Studies of dynamic game models have shown that competition for light makes each plant produce a shoot larger than in the solitary optimal model (Mirmirani and Oster, 1978; Makela, 1985).

In analysing these competitive dynamic game models, three important aspects require careful examination. First, the competitors are often closely related individuals. Competitors may belong to the same genet with relatedness of 1. Even if they belong to different genets, they may be related because dispersal distance of pollen or seeds is often limited. In such a case, we need to maximize the inclusive fitness, rather than simple reproductive success, considering the relatedness between competitors (Mirmirani and Oster, 1978; Day and Taylor, 1997).

Secondly, many of the models studied in dynamic games assume an 'open loop' solution, in which each player (plant) can choose the allocation schedule as a function of time, and is not able to change its behaviour in response to the behaviour of its competitors. In contrast, if each plant can respond to the behaviour of its competitors, the optimal strategy of a plant will be a function of the past behaviour of its competitors, rather than just a function of time. The calculation then becomes a lot more complicated than an open loop (see Sasaki and Iwasa, 1991, for examples of differential games of pathogenic viral strains within the same host). The result of the game should critically depend on the information available when each individual plant decides its growth and reproductive schedule.

Another important point that has not been discussed in dynamic optimization games is the spatial structure formed by past reproduction. Terrestrial plants often engage in both vegetative propagation, such as by rhizomes or root budding, in addition to producing seeds. Offspring produced by vegetative propagation tend to remain in the vicinity of the parent and are more likely to compete in the near future than offspring from a seed. One area of theoretical ecology that has developed considerably in the last decade is population dynamics and evolution in spatially explicit models. Although many of these are based on direct computer simulation, several useful methods have been developed that capture the essence of spatial clumping (Harada and Iwasa, 1994, 1996; Dieckmann *et al.*, 2000). However, the dynamic optimization and resource allocation arguments have not been combined with work on studies of spatially explicit modelling. This will be one of the most fruitful areas of theoretical evolutionary plant ecology in the future.

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