OPTIMAL GROWTH SCHEDULE OF A PERENNIAL PLANT

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Deciduous plants living in a seasonal environment show a variety of leaf-expansion schedules. For example, two contrasting types (and an intermediate one) of leaf-expansion phenology (Kikuzawa 1983, 1984) have been reported for deciduous trees and shrubs. Trees of the flush type (exemplified by beech and oak) have most of their photosynthetic system established at the start of a growing season using the material produced in the preceding season. Plants of succeeding (or gradual) type (exemplified by poplar), by contrast, make a relatively small fraction of their leaves at the beginning of a season and continue to produce leaves until mid-season using the photosynthetic products of the year (T. Kozlowski 1971). Similar distinctions in phenology have been made for seasonal patterns of shoot elongation (T. Kozlowski and Clausen 1966; Maruyama 1978). A correlation between the growth phenology of a tree and its successional status has been noted (Marks 1975; Bicknell 1982; Boojh and Ramakrishnan 1982).

Which of the two types (and intermediate ones) of growth phenologies, then, is the more efficient for plants in a given environment? What is the best timing for beginning and ending leaf expansion? Of the material produced in a year, how much should be allocated to reproduction in the same year, and how much stored for the following season? How should these depend on parameters such as the length of the growing season, habitat predictability, the degree of disturbance, photosynthetic rate, and storage efficiency? How important is the stored material from the preceding years relative to the total annual production?

To answer these questions, we here develop an optimal-allocation model for a plant having two parts: a *production part*, including vegetative organs that are engaged in photosynthesis; and a *storage part*, for both stored material and the accumulated reproductive investment of the year.

The same model can also deal with the problem of annual versus perennial growth forms, which is an old question in theories of life-history strategy (Cole 1954; Charnov and Schaffer 1973) because an annual life cycle is a special case of allocation in which all the resource is used for reproduction with none saved for the following season.

We concentrate here on the phenology (seasonal pattern of growth) of photosynthetic organs, such as leaves, and the allocation of resources between repro-
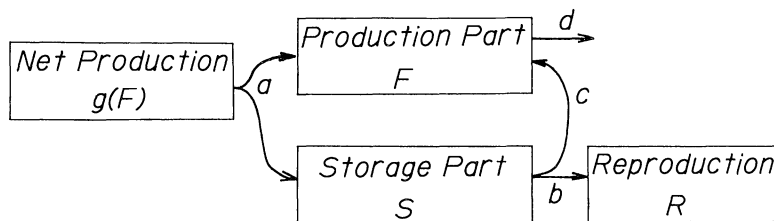
Fɪɢ. 1.—Diagram of plant parts and energy flows between them. a, Material produced by photosynthesis is allocated either to the construction of the production part or to the storage part (within-season allocation). b, The stored material is either used for reproductive activity or saved for the following season (between-season allocation). c, At the beginning of a season, the production part is reconstructed using the material stored in the preceding season. d, The production part is discarded at the end of each season.

ductive activity and storage for the following year. We do not deal with the phenology of reproductive activity, which should be affected by many complicated factors such as pollinator availability, maturation time, and seed dispersers.

Our model is similar to Schaffer's (1983), which combines continuous-time models for a within-season schedule of growth (Cohen 1971, 1976; Vincent and Pulliam 1980; King and Roughgarden 1982a,b; Schaffer et al. 1982; Chiariello and Roughgarden 1984; Iwasa and Roughgarden 1984) with discrete-time models for a between-season schedule (Cole 1954; Gadgil and Bossert 1970; Charnov and Schaffer 1973; Schaffer 1974; Taylor et al. 1974; León 1975; Schaffer and Schaffer 1977). However, in a special case that Schaffer (1983) analyzed in detail, a polycarpic perennial solution is never optimal: if the optimal growth is not annual, it must be monocarpic. This conclusion is inconsistent with the observation that the polycarpic perennial growth habit (reproducing over many years) is prevalent among terrestrial plants.

Here, we relax the assumptions made by Schaffer so that in our model (1) the net photosynthetic rate may be a nonlinear function of the size of photosynthetic organs and (2) the rate of construction of photosynthetic organs may be limited. Our model shows that perennial growth is optimal under a wide range of parameters. Furthermore, we derive several quantitative predictions of plant growth behavior, and we examine the reported patterns of leaf phenology for deciduous trees and herbs and the available data about the importance of storage in plant growth in the light of the theory.

<center>THE MODEL</center>

We consider a plant having two parts (fig. 1). The production part includes leaves for photosynthesis, stems for support and for improving the light condition of the canopy, and roots for the uptake of water and nutrients; however, it does not include trunks and large branches. The storage part includes both the investment in reproductive organs (flowers and fruits) made in the same growing season
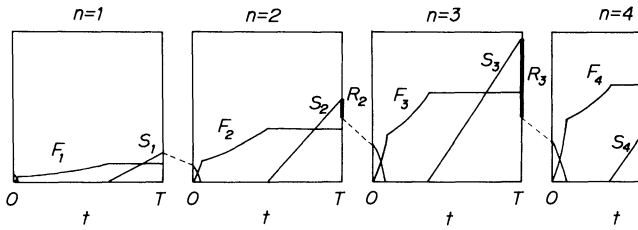
and the storage of material for constructing the photosynthetic system at the beginning of the following season. Yokoi (1976a,b) made the same distinction between the production part (P-part) and the "individual reproduction" part (R-part) when he discussed the optimal growth phenology of a perennial plant.

We indicate year by the subscript n $(n = 1, 2, 3, \ldots)$ and time within a season by a continuous parameter t $(0 \leq t \leq T)$, where the length of a growing season, T, is constrained by climatic factors. Let $F_n(t)$ be the size of the production part, and $S_n(t)$ be the size of the storage part (fig. 2; see table 1).

The daily net photosynthetic rate, denoted by $g(F)$, increases with the size of the production part, F. A typical example is

$$g(F) = fF/(1 + hF), \tag{1}$$

where f and h are constants. The net photosynthetic rate increases with F, but it becomes saturated as F becomes very large, indicated by a positive parameter h. Saturation occurs because of local resource depression, such as self-shading in the canopy and nutrient depletion in the soil, and because of the decrease in the ratio of leaf tissue to supporting stem tissue as plants grow larger. We assume that equation (1) is gross photosynthesis (CO_2 assimilation) minus respiration loss, accompanying both maintenance and construction of plant parts (McCree 1974). The maximum rate of growth per unit of biomass (the highest possible relative growth rate) is f, which is realized by a small plant with little local resource depression or stem tissue.

Photosynthetic product, defined as what remains after all respiratory costs are met, is then allocated between the production part and the storage part. The conservation of material gives

$$dF_n/dt + dS_n/dt = g[F_n(t)], \tag{2}$$

where $n = 1, 2, \ldots$ and $0 \leq t \leq T$. The material in the storage part may be transferred to the production part. In contrast, the material once used to construct the production part is assumed to be discarded. Therefore, constructing organs for production has a cost. The simplifying assumption that the material is not reused is more plausible for carbon balance than for nitrogen balance, because a significant fraction of nitrogen is known to be reallocated during reproduction (Mooney 1972).

TABLE 1

LIST OF SYMBOLS AND THEIR UNITS

Symbol	Definition	Unit
t	time parameter within season	day
n	season number	year
F	size of the production part	g
S	size of the storage part	g
$g(F)$	daily net production rate	g/day
f	maximum net production rate (maximum relative growth rate)	g/day
h	self-limiting coefficient	1/g
a	maximum exponential growth rate of the production part	1/day
b	maximum growth rate of the production part when small	g/day
T	length of growing season	day
σ	annual survival	
γ	storage efficiency	
R	annual reproductive investment	g
Φ	lifetime reproductive investment	g
x	transformed size of the production part at t_1 ($= hF[t_1]$)	1
y	transformed size of the production part at t_2 ($= hF[t_2]$)	1
S_0	initial storage-part size	g
ψ	final storage-part size as a function of initial size, assuming the optimal within-season schedule	g
s_{seed}	seed size	g
S^*	optimal storage size	g
t_1	time at which the storage part is depleted	day
t_2	time at which vegetative growth stops	day
$\hat{F}_1$	size of the production part at t_1	g
$\hat{F}_2$	size of the production part at t_2	g
$u(t)$	ratio of the growth rate of production part to the maximum rate	1
$V(S)$	reproductive value of a plant with storage-part size S at the end of a season	g
τ	productivity parameter ($= fT$)	1
α	stability parameter ($= \sigma\gamma$)	1

We assume that the production parts are lost at the end of each growing season and need to be reconstructed at the beginning of the next season: $F_n(0) = 0$, where $n = 1, 2, 3, \ldots$. The model does not apply to evergreen perennials. However, it applies to deciduous trees, because the production part, F, includes leaves, small branches, and fine roots, but not trunks.

The size of the storage part starts with a positive value if a fraction of the material produced in the preceding year is saved:

$$S_n(0) = \gamma[S_{n-1}(T) - R_{n-1}], \tag{3}$$

where $n = 2, 3, \ldots$ and R_n is the total reproductive investment made in the nth season by constructing and maintaining flowers and fruits. In fact, a considerable fraction of reproductive investment goes to maintenance costs such as making nectar. R_n satisfies the constraint $0 \leq R_n \leq S_n(T)$, because the storage part, $S_n(T)$, by definition, includes the accumulated reproductive investment made in the same year. The final storage-part size, $S_{n-1}(T)$, minus reproductive investment, R_{n-1}, is the material stored for the nth year. The *storage efficiency* γ in equation (3) is a positive constant less than or equal to one ($0 \leq \gamma \leq 1$); a fraction $1 - \gamma$ of the stored material is lost in the processes of storage and transfer through respiration,

leakage, herbivory, pathogens, etc. For the first year, the plant starts with the material stored in the seed, $S_1(0) = s_{seed}$.

The growth rate of the production part is constrained as

$$0 \leq dF_n/dt \leq aF_n + b,\tag{4}$$

where the left inequality indicates that the material for the production part is not reused, and the right inequality indicates that the growth rate of the production part has an upper limit. We also expect that the storage size ·ist be positive or zero through the growing season: $S_n(t) \geq 0$, where $0 \leq t \leq T$.

By the definition, then, the optimal growth schedule maximizes the lifetime investment in reproduction:

$$\Phi = \sum_{n=1}^{\infty} \sigma^n R_n \rightarrow \text{maximum},\tag{5}$$

where σ is the annual survival ($0 \leq \sigma \leq 1$). The strategy of a plant is to choose the schedule of material allocation within each season and the reproductive invest-ment in each season given the above constraints.

We here note that an annual life cycle is a special case of $R_1 = S_1(T)$ in which all of the material at the plant's disposal is used for reproduction in the first year, with none saved for the following seasons. If the plant is immature for several seasons and reproduces only once using all the available resource (big bang), then $R_1 = R_2 = \ldots = R_{n-1} = 0$ and $R_n = S_n(T)$. For the (polycarpic) perennial growth pattern, some resource is left for the following year and $0 < R_n < S_n(T)$ holds for many n.

This dynamic optimization problem can be solved by dividing it into two subproblems: (1) finding the optimal resource schedule within a season for a given initial storage size; and (2) deciding the optimal allocation between reproduction in that year and saving for the next year. To solve the second problem, we use the answer to the first one.

GROWTH SCHEDULE WITHIN A SEASON

To find the optimal growth schedule within a season (say, year n) when the initial storage size, $S_n(0)$, is given, we need to maximize the size of the storage part, $S_n(T)$, at the end of the season, because reproduction both in the same year and in following years is affected only by $S_n(T)$, irrespective of details of growth pattern in year n. Hence, we can concentrate on the following subproblem:

$$dF/dt = u(t)(aF + b),\tag{6a}$$

$$dS/dt = g(F) - u(t)(aF + b),\tag{6b}$$

$$F(0) = 0, \; S(0) = S_0,\tag{6c}$$

$$0 \leq u(t) \leq 1,\tag{6d}$$

$$S(t) \geq 0,\tag{6e}$$

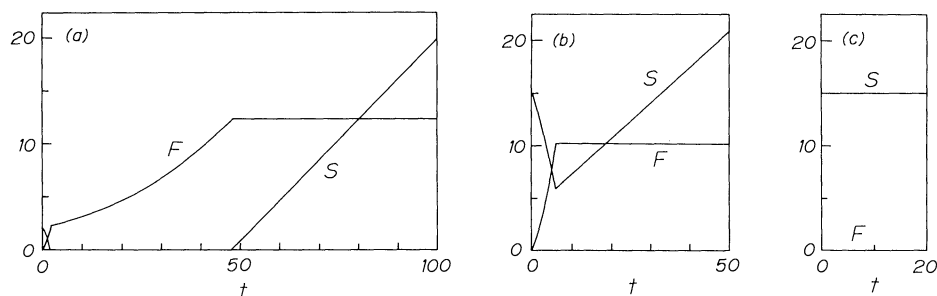$$S(T) \rightarrow \text{maximum},\tag{6f}$$

Fig. 3.—Optimal growth within a season. *a*, Three-phase growth; $S_0 = 2$, $T = 100$. *b*, Two-phase growth; $S_0 = 15$, $T = 50$. *c*, No growth; $S_0 = 15$, $T = 20$. Horizontal axis is for time t ($0 < t < T$). The pattern is generated by expressions (6) with $a = 0.2$, $b = 1$, $f = 0.05$, and $h = 0.05$.

where we deleted the suffix *n*. The control variable to choose is $u(t)$ ($0 \le t \le T$), which is the ratio of the growth rate of the production part to the maximum rate, $aF + b$. This formulation of the control variable is mathematically convenient because the control constraint (the range for the control variable), indicated in equation (6d), is then independent of the state variables.

Yokoi (1976*a*) pointed out the analogy between the optimal timing of growth within each season for a perennial and that for an annual, with storage for the perennial corresponding to reproduction for the annual. This is mathematically supported in the present model because the optimal within-season schedule for a perennial can be calculated by the reduced problem (6), which is equivalent to the optimal-growth model for an annual.

This optimal-control problem is solved in Appendix A by Pontryagin's maximum principle (Pontryagin et al. 1962), which has been used in problems of life-history evolution (León 1975; Cohen 1976; Macevicz and Oster 1976; Iwasa 1978; Vincent and Pulliam 1980; King and Roughgarden 1982*a*,*b*; Schaffer et al. 1982; Chiariello and Roughgarden 1984; Iwasa and Roughgarden 1984; J. Kozlowski and Wiegert 1986). A new point is that the state space is restricted by inequality (6e), and the co-state variable may discontinuously jump at a junction point.

For a given set of parameters from the model and the initial storage size, S_0, the optimal growth schedule is determined. A typical case is illustrated in figure 3*a*, in which the growing season is composed of three phases. Depending on the parameters, one or two of the three phases may disappear.

Three-Phase Growth

In the first phase ($0 < t < t_1$), the plant constructs the production part using both the material stored in the preceding year and that produced in the same year, at the maximum speed given by the second inequality in expression (4). At $t = t_1$, the storage organ becomes empty and the second phase ($t_1 < t < t_2$) begins, in which the plant invests all the daily net photosynthate into the construction of the production part. Then at $t = t_2$, vegetative growth stops and the plant begins to

invest all the photosynthetic products in the storage part, which includes repro-
ductive activity. This phase continues until the end of the season ($t_2 < t < T$).

The critical times (t_1 and t_2) are determined by the parameters and the initial
storage size, S_0. Let $\hat{F}_1 = F(t_1)$ and $\hat{F}_2 = F(t_2)$. The following relationships result:
the first two determine t_1, the time when the storage becomes depleted, and $\hat{F}_1$, the
size of the production part at t_1:

$$\hat{F}_1 = [\exp(at_1) - 1]b/a, \tag{7a}$$

and

$$\hat{F}_1 = S_0 + \int_0^{t_1} g\{[\exp(ax) - 1]b/a\}\,dx. \tag{7b}$$

Integrating the differential equation $dF/dt = g(F)$ for the second phase yields

$$\int_{\hat{F}_1}^{\hat{F}_2} dx/g(x) = t_2 - t_1 \tag{7c}$$

and, finally,

$$(T - t_2)\,dg(\hat{F}_2)/dF = 1, \tag{7d}$$

which gives a curve on a t-F plane separating the regions for vegetative and
reproductive growth.

Equations (7c) and (7d) determine $\hat{F}_2$ and t_2, if t_1 and $\hat{F}_1$ are given as the results
of (7a) and (7b). If the solution of these equations satisfies $0 < t_1 < t_2$, then the
above three-phase growth pattern is optimal.

Equation (7d) is derived from the condition that the marginal values of vegeta-
tive and reproductive investments are equal (Iwasa and Roughgarden 1984). Once
the plant size reaches the curve (7d), the optimal allocation strategy is to invest all
the photosynthetic product into reproductive growth, because further investment
in vegetative growth does not produce an output larger than the input.

If $g(F)$ is a linear function $g(F) = fF$, indicating the absence of self-shading ($h
= 0$), the curve of equation (7d) is a vertical line $t_2 = T - 1/f$, predicting that the
switching time from vegetative to reproductive growth phases does not change
with the plant size, as shown for annuals (Cohen 1971) and perennials (Yokoi
1976a). However, with a positive shading effect ($h > 0$), the switching time, t_2,
given by equation (7d) becomes earlier for a larger plant, as shown by Vincent and
Pulliam (1980) for the optimal schedule of an annual plant. When the solution does
not satisfy $0 < t_1 < t_2$ because of the parameters, then two other cases occur.

Two-Phase Growth

If the initial storage size, S_0, is very large, t_2 as determined by equations (7c) and
(7d) may be smaller than t_1 but still positive and the second phase in the optimal
growth disappears (fig. 3b). The optimal plant invests with maximum speed in the
production part until $F(t)$ reaches a point calculated by equations (7a) and (7d)
with $\hat{F}_1 = \hat{F}_2$ and $t_1 = t_2$. Then, the plant stops investing in the production part and
begins to accumulate all the photosynthetic products in the storage part until the
end of the season (fig. 3b). The storage part never becomes depleted during the
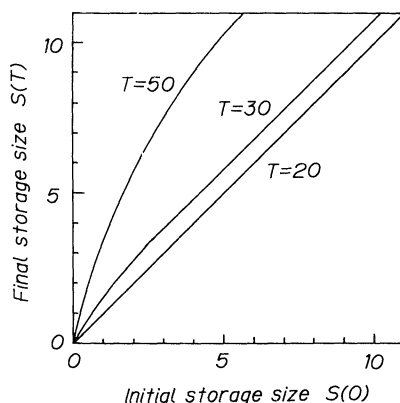growing season.

FIG. 4.—Examples of function $\psi(S_0)$, the final storage part, $S(T)$, for the optimal growth as a function of the initial size of the storage part $S(0) = S_0$, calculated for expressions (6). The three curves differ in the length of a growing season, T, as indicated. Other parameters: $a = 0.2$, $b = 1$, $f = 0.05$, and $h = 0.05$.

No Growth

Furthermore, if $T\,dg(0)/dF < 1$, no positive t_2 satisfies equation (7d). The optimal solution is then to invest nothing in the production part because the allocation to vegetative organs yields less return than the investment itself (fig. 3c). In particular, for the function described by equation (1), this phase occurs when $fT < 1$, that is, when the maximum relative growth rate multiplied by the length of a growing season is smaller than one.

Combining these, we can determine the optimal growth schedule and then calculate its performance, $S(T)$. For example, if the second phase exists, we have

$$S(T) = (T - t_2)g(\hat{F}_2) \,. \tag{8}$$

Let $\psi(S_0)$ be the size of the storage part at the end of a season as a function of the initial storage size, S_0:

$$\psi(S_0) = \max S(T) \,; \tag{9}$$

the plant follows the optimal allocation schedule during the season. Note that the function $\psi(S_0)$ depends on the parameters f, h, T, σ, γ, a, and b. Several examples are illustrated in figure 4.

ALLOCATION BETWEEN REPRODUCTION AND STORAGE

In each season, the plant must decide how much of the accumulated storage product should be allocated to reproduction and how much should be saved for the construction of the production part in the next year. The optimal allocation then depends on the loss during storage, on annual survival, and on the productivity in the next growing season, which is given by the solution obtained in the preceding section.

The problem can be solved by another technique of control theory called dynamic programming (Bellman 1957). Let $V(S)$ be the expected total reproductive investment of a plant from the nth season until its death, provided that the plant has a storage part of size S at the end of the nth season:

$$V[S_n(T)] = \max (R_n + \sigma R_{n+1} + \sigma^2 R_{n+2} + \ldots), \tag{10}$$

where the allocation schedule must be chosen optimally. The discounting factor σ is the annual survival, which is assumed to be independent of plant age and allocation strategy. Equation (10) represents the reproductive value.

The optimization of Φ, given by equation (5), is mathematically equivalent to calculating $V(S)$ in equation (10) because

$$\max \Phi = V[S_1(T)]. \tag{11}$$

Equation (10) can be rewritten as the recursive equation

$$V[S_n(T)] = \max_{0 \le R_n \le S_n(T)} \{R_n + \sigma V[S_{n+1}(T)]\}, \tag{12}$$

where the first term in the braces indicates reproduction in year n; the second, the expected sum of reproduction in the following years, expressed using definition (10) for year $n + 1$. The size of the storage part at the end of the next year, $S_{n+1}(T)$, can be related to its size at the end of the same year as

$$S_{n+1}(T) = \psi\{\gamma[S_n(T) - R_n]\}, \tag{13}$$

which is derived from equations (3) and (9). The difference between $S_n(T)$ and R_n is the amount of material to be stored for the next season. It is multiplied by the storage efficiency, γ, to produce the material for the plant's production part at the beginning of the next season. The function $\psi(S_0)$ was calculated in the preceding section.

Equation (12) combined with equation (13) is called Bellman's equation:

$$V(S) = \max_{0 \le R \le S} (R + \sigma V\{\psi[\gamma(S - R)]\}), \tag{14}$$

which is the basis for the analysis of dynamic programming (Bellman 1957). The optimal reproductive investment for $S_n(T) = S$ is the R that maximizes equation (14). Since the parameters σ, γ, and T are independent of n, the optimal reproductive investment, R_n, depends on S_n only; the problem is homogeneous with respect to the shift in n. The unknown function $V(S)$ in equation (14) can be obtained by sequential approximation as in Appendix B, with the following theorem.

Assume that $\psi(S_0) > 0$, $d\psi(S_0)/dS_0 > 0$, and $d^2\psi(S_0)/dS_0^2 \le 0$. For sufficiently large S_0, $d\psi(S_0)/dS_0 = 1$. Then, the optimal reproductive investment, R, which attains the maximum in equation (12), is

$$R_n = \begin{cases} 0 & \text{if } S_n(T) < S^*, \\ S_n(T) - S^* & \text{if } S_n(T) > S^*, \end{cases} \tag{15a}$$

where a critical storage size, S^*, satisfies

$$d\psi(\gamma S^*)/dS_0 = 1/\sigma\gamma \tag{15b}$$

if $S^* > 0$. Otherwise, $d\psi(0)/dS_0 < 1/\sigma\gamma$ and $S^* = 0$.

The optimal storage size, S^* in equation (15b), is the value of Y that maximizes $\sigma\psi(\gamma Y) - Y$, the expected gain in material from saving it for the following season. Equation (15b) implies that the optimal storage size is the horizontal coordinate of the point having slope $1/\sigma\gamma$ and tangent to the curve of function $\psi(S_0)$ versus S_0, as illustrated in figure 4. If the slope of the line is smaller than $1/\sigma\gamma$ for all $S_0 > 0$, then $S^* = 0$.

Combining this result with the results in the preceding section, the optimal growth schedule of a plant is as follows. If the optimal storage size, S^*, is zero, the plant saves nothing for the second season, and all the photosynthate in the storage part produced in the first season is allocated to reproduction; the plant has an annual life cycle. In contrast, if the optimal storage size is positive, the plant follows a perennial life cycle; for several immature years, during which $S_n(T)$ is less than the optimal storage size, S^*, the plant saves all resources for the next season. Every year, the plant starts with a larger production part using a larger amount of material stored from the preceding season and obtains a larger amount of resource $S_n(T)$, which can be used for either reproduction or storage. When $S_n(T)$ becomes greater than S^*, the plant invests the excess, $S_n(T) - S^*$, in reproductive activities and repeats the same growth schedule thereafter (at steady state).

OPTIMAL GROWTH SCHEDULE

To illustrate how the optimal growth schedule depends on various parameters, we analyze two cases, each of which considers either of the two processes (nonlinear photosynthesis and upper limit of leaf expansion rate), making the system nonlinear.

Case I: Nonlinear Photosynthetic Rate

In the first case, the rate at which the production part expands at the beginning of a growing season is sufficiently large (a and b are large) that the time period for establishing the photosynthetic system is negligible. Therefore, $t_1 = 0$, $F(t_1) = S_0$, and $S(t_1) = 0$ hold, rather than equations (6c), in the optimization of the within-season schedule.

Let $x = h\hat{F}_1$ and $y = h\hat{F}_2$, the sizes of the production part at two switching times (t_1 and t_2) in the steady-state perennial growth pattern multiplied by the self-limiting coefficient h. According to the calculation in Appendix C, the optimal levels of x and y are determined as positive solutions of the following equations:

$$3y + y^2 + \ln y = \tau - 1 + x + \ln x, \tag{16a}$$

$$y = x/[\alpha - (1 - \alpha)x], \tag{16b}$$

where the two parameters are $\alpha = \sigma\gamma$ and $\tau = fT$. If equations (16) do not have positive solutions, annual growth is optimal. If, in addition, $\tau = fT < 1$, then an
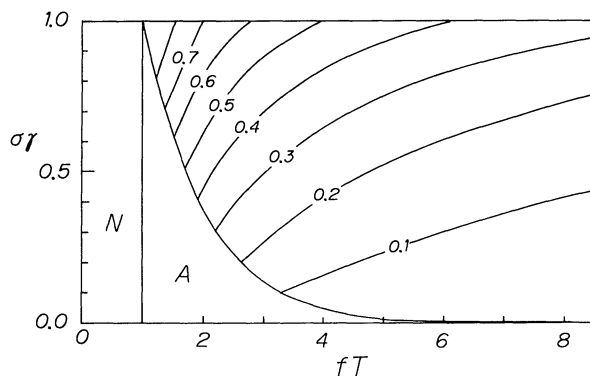
Fig. 5.—Contour map of $S(0)/S(T)$, the ratio of the initial size of the storage part to the final size at steady-state perennial growth for nonlinear photosynthesis and immediate establishment (case I). A, Parameter region where annual life cycle is optimal; N, an absence of growth is optimal.

absence of growth is optimal. Therefore, we distinguish three parameter regions, illustrated in figure 5.

1. For $\tau < 1$, a complete lack of vegetative growth is optimal. The plant must become extinct if the parameters of the environment stay in this region.

2. For $1 < \tau < 1 + \ln(1/\alpha)$, the annual life cycle is optimal; that is, the plant should allocate all the material produced in any year to reproductive activity, saving none for the following years, irrespective of the amount of resource it acquires.

3. For $\tau > 1 + \ln(1/\alpha)$, the perennial life cycle is optimal when S^* is positive. In its first years, the plant is immature, and $S(T)$ is smaller than the optimal storage size, S^*.

Parameter τ in equation (16a) represents productivity as the product of the maximum relative growth rate (or the maximum net photosynthetic rate per unit of production part) and the length of the season. In contrast, parameter α, the product of annual survival and storage efficiency, indicates the reliability of the next year's reproduction from the plant's viewpoint, because α is the chance that some biomass, if saved until the end of the following season, can contribute to reproduction; α is therefore strongly related to the stability of the habitat.

'h' as a scaling factor.—The self-limiting coefficient, h, is eliminated from equations (16), in which x and y are transformed plant sizes. Not only the steady-state relations but also the dynamics can be rewritten using the transformed variables $hF_n(t)$ and $hS_n(t)$, and then the problem no longer includes the parameter h. Therefore, h is a scaling factor, and the sizes of the production and storage parts are inversely proportional to h. Consequently, the fractions of material allocated to reproduction or to storage, the timing of reproduction within a season, and the ratio of the two parts at steady-state growth are all independent of h. Moreover, if fT and $\sigma\gamma$ are common, the same number of years are required for plants to reach maturation sizes, which may differ vastly between species.

Annual versus perennial.—The annual life cycle has an advantage over the perennial if

$$\exp(fT - 1) < 1/\sigma\gamma. \tag{17}$$

A short growing season (small T) favors an annual life cycle over a perennial. A similar result is obtained for a small net maximal photosynthetic rate per unit of biomass f because the length of a season, T, is multiplied by photosynthetic rate f in inequality (17). An annual life cycle is also favored when the habitat reliability, σ, is low, that is, when the habitat of a plant has a high chance of being destroyed before the end of the next season by such factors as herbivores, pathogens, or catastrophic physical disturbances. A low storage efficiency, γ, has a similar effect.

Equating both sides of condition (17) gives a curve on the parameter plane where perennial growth begins to be more efficient than an annual cycle; hence, we call it the "perenniality-threshold" curve.

Importance of stored material for establishing a photosynthetic system.— When an optimal perennial growth pattern is at steady state, the ratio of initial and final sizes of storage is $S(0)/S(T) = x/y(1 + y)$, and the ratio of the size of the production part just established and the maximum size is $F(t_1)/F(t_2) = x/y$. A contour map of the ratio $S(0)/S(T)$ on the parameter plane is illustrated in figure 5. Both ratios decrease monotonically with the parameter $\tau = fT$, with $\alpha = \sigma\gamma$ fixed. Therefore, the fraction of material stored for the next season by a mature plant versus that going to current reproduction is largest for a plant just above the perenniality threshold and decreases with a further increase in the length of the growing season.

Timing of storage growth.—In each year, the plant switches from the earlier phase, in which the photosynthetic products are allocated to further expansion of the production part, to the later phase, in which all the material is allocated to storage. Some fraction of the stored material may then be used for reproduction. The fraction of the period before a switch t_2 in the whole season, T, is

$$t_2/T = 1 - (1 + y)^2/\tau. \tag{18}$$

In figure 6, we plot the contour map of the ratio t_2/T. The ratio decreases with the stability of the habitat (expressed by annual survival, σ) and with the storage efficiency, γ. Although the ratio increases with the length of a growing season, T, and with the maximum relative growth rate, f, the dependence is very weak. Therefore, in a stable environment with a high σ, mature plants tend to stop leaf expansion quite early in the season, whereas plants in an unpredictable environment tend to produce leaves until much later.

In contrast to result (18) for mature perennials, for immature years in which the plant size is small, the optimal switching time depends on the productivity, rather than the stability, of the habitat; this is because, for a small plant with little resource limitation ($y \ll 1$), the optimal ratio is $t_2/T = 1 - 1/fT$, which is independent of $\sigma\gamma$. Therefore, leaf production (and growth of the whole vegetative body of the perennial) stops much later in each season in a productive environ-
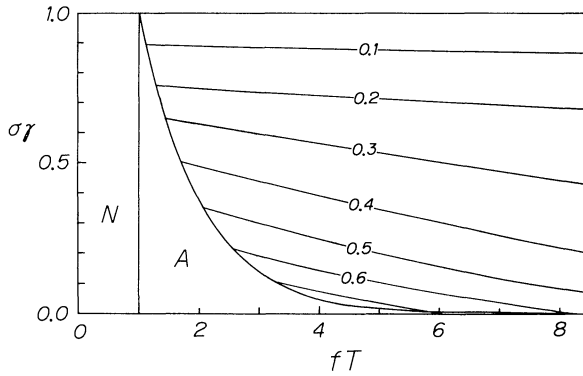
Fig. 6.—Contour map of t_2/T, the ratio of the second switching time to the total length of a growing season at steady-state perennial growth in case I. $fT = \tau$, $\sigma\gamma = \alpha$. The switching time occurs earlier for larger $\sigma\gamma$ and for larger fT. The dependence on $\sigma\gamma$ is stronger than that on fT.

ment (with higher fT), as pointed out by Yokoi (1976a) and confirmed experimentally (Hori and Oshima 1986).

As a plant grows during immature years, the period of leaf production shortens, as shown by equation (7d) for the second switching time, t_2. This is in accord with Vincent and Pulliam's (1980) derivation for annuals.

Case II: Limited Growth Rate of the Photosynthetic System

We can analyze another case in which the rate of expansion of the production system at the beginning of a season has an upper limit (a and b in inequality 4 are finite), which was neglected in the analysis in the preceding section. Instead, we assume here that the net photosynthetic rate is proportional to the size of the production part, $g(F) = fF$, that is, that the shading effect or local resource depression is negligible.

According to the calculations in Appendix D, we can prove the following results for the optimal growth schedule.

1. There are three phases in each growing season. In the first phase, the production part grows at the maximum rate, using stored material. In the second phase, all the photosynthetic product is allocated to growth of the production part. In the third phase, growth of the production part stops, and all the available resource is allocated to the storage part.

2. The annual growth pattern is optimal if inequality (17) holds. Otherwise, the perennial pattern is optimal; that is, after several immature years, a plant enters steady-state growth. Criterion (17) is independent of the constraint of finite leaf expansion rate. This result is the same as in case I.

3. The ratio $S(0)/S(T)$ decreases with the length of the growing period T and with the relative growth rate, f, if other parameters are constant (see eq. D8). However, the ratio of the production parts at the two switching times is

$$F(t_2)/F(t_1) = 1/\sigma\gamma, \tag{19}$$

which is independent of the length of a growing season, T; this differs from the preceding case of nonlinear photosynthesis.

4. The timing of the switch from the second to the third phase is $t_2 = T - 1/f$, which is independent of age or of size, making a sharp contrast to case I, in which t_2 becomes earlier as a plant grows.

DISCUSSION

Growth patterns of terrestrial plants have been successfully analyzed as the optimal strategy by which plants allocate the photosynthetic products of each day in a growing season to storage and to various organs, such as leaves, stems, roots, flowers, and fruits. The optimal timing of reproduction for an annual plant (Cohen 1971, 1976) has been developed (Vincent and Pulliam 1980; King and Roughgarden 1982a,b) and tested with comparative and experimental data (Penning de Vries et al. 1974; King and Roughgarden 1983). The schedule of allocation between roots and shoots has been modeled with multiple vegetative organs to include the effect of pruning and its dependence on age, soil moisture, and light intensity (Iwasa and Roughgarden 1984). The optimal growth of an annual plant with a storage organ was studied for the case in which the period suitable for flowering (efficient in pollination or in seed dispersal) comes considerably later than that suitable for photosynthesis (Schaffer et al. 1982; Chiariello and Roughgarden 1984). However, the allocation schedule over multiple seasons, such as the perennial-versus-annual problem, has been modeled using discrete-time optimization based on trade-offs between future and present reproduction (Gadgil and Bossert 1970; Schaffer 1974; Taylor et al. 1974; León 1975).

Schaffer (1983) developed a general formulation of the optimization model taking into account both within-season and between-season schedules of resource allocation. As an example, he then studied a simple case and observed that, if the optimal strategy for a plant is not annual, it should invest nothing in reproductive activity and continue vegetative growth indefinitely. He interpreted this result as indicating the optimality of monocarpic growth. This conclusion, however, is not very realistic because most nonannual plants show a polycarpic rather than monocarpic reproductive pattern.

Schaffer's example is a special case of our model in which neither resource limitation nor an upper limit of leaf expansion rate is assumed ($h = 0$, and $a = b = \infty$). Then, a plant starting with twice as much initial storage would have its net photosynthesis, growth rate, and reproduction all doubled without changing the timing of growth; hence, the function $\psi(S_0)$ is linear. The solution that attains the optimum in equation (14) is either $R = 0$ or $R = S$, resulting in monocarpy.

In the present model, perennial growth is optimal because of the nonlinearity of the function $\psi(S_0)$, which increases with S_0 at a decreasing rate of increase ($d\psi(S_0)/dS_0 > 0$ and $d^2\psi(S_0)/dS_0^2 < 0$, for a feasible range), as illustrated by figure 4. Processes making $\psi(S_0)$ nonlinear are (1) the nonlinearity of the daily net production rate, $g(F)$, and (2) the upper limit of growth rate of the production part of equation (4). Of these two, the former is more likely to be important, because the depression of limiting resources (e.g., light, nutrients, and moisture) is usually
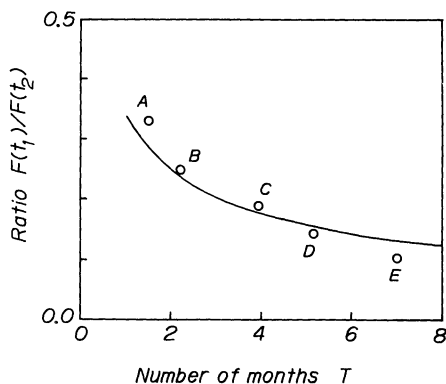
Fɪɢ. 7.—The ratio of the size of a plant just established using stored material to the maximum plant size, measured for seven deciduous perennials in northern Japan (from Yokoi 1966). A, B, *Fauria crista-galli*; C, *Aconitum chinense*; D, *Miscanthus sinensis*; E, *Miscanthus sacchariflorus*. The curve is the ratio F_1/F_2 predicted by the model with $f = 0.07$ and $\sigma\gamma = 0.33$.

very important for terrestrial plants and because allocating an increasingly larger fraction to nonphotosynthetic supporting tissues is necessary with increasing size. Laboratory measurement shows that the relative growth rate declines with size (Hunt and Lloyd 1987), supporting the nonlinear production rate. In contrast, although t_1 (the time for a photosynthetic system to establish at the beginning of a season) may be significant, if it does not increase much with the initial storage size (S_0), we may simply subtract a fixed period from the length of a growing season (T) in a model without an upper limit on leaf expansion rate.

The importance of the nonlinearity of the photosynthetic rate is supported by the comparative studies by Yokoi (1966), in which several species of perennial herbs in northern Japan were examined with respect to the ratio of $F(t_1)$, the aboveground plant size established using stored material, to $F(t_2)$, the maximum plant size. He observed that the ratio monotonically decreases with the length of a growing season, T (the circles in fig. 7), which is in accord with case I's (nonlinear photosynthesis) prediction of a decrease in the ratio with T if f, σ, and γ do not change systematically. To show that the model can explain the decrease in the ratio, we indicated the predicted ratio $F(t_1)/F(t_2)$ for various lengths of growing season, T, by a solid curve in figure 7, assuming that the maximum relative growth rate, f, is 0.07 per day and that the annual survival, σ, multiplied by the storage efficiency, γ, is 0.33. Although under optimal laboratory conditions f is about 0.20 per day (Grime and Hunt 1975), the relative growth rate for a plant in the field is much lower, and 0.07 per day is a reasonable value considering various field measurements (Hogetsu et al. 1960; Yokoi, pers. comm.). In contrast, case II, with a linear photosynthetic rate, predicts that the ratio $F(t_1)/F(t_2)$ is independent of T, as shown by equation (19), and hence is rejected.

Another line of evidence for the importance of a nonlinear production rate is provided by the observation that the same tree stops leaf expansion later in a
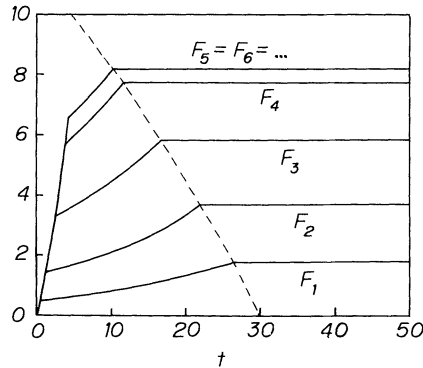
FIG. 8.—Growth in immature years. Horizontal axis is the time within a season; vertical axis, the size of the production part. The subscript indicates the year, n. Parameters: $S_1(0) = 0.5$; $a = 0.2$, $b = 1$, $f = 0.05$, $h = 0.05$, $\gamma = 0.7$, $T = 50$. The plant first reproduces in the fourth year and continues the steady-state growth thereafter. The second switching time, t_2, occurs earlier as a plant grows. The dashed line is given by equation (7d).

season when it is younger than when it is older (Kikuzawa 1981). This is again consistent with the optimal growth pattern for case I with a saturating photosynthetic function $g(F)$ ($h > 0$), predicting that the switching time t_2 decreases with plant size (fig. 8). On the contrary, case II with a linear function $g(F)$ predicts a fixed timing of the end of leaf extension.

Below, we concentrate on the situation assumed for case I.

The Scaling Factor 'h'

The resource-depression coefficient, h, is a scaling factor. If other parameters (σ, γ, f, and T) remain the same, the size of a plant is inversely proportional to h without changing the seasonal timing or the allocation fraction. For example, a larger h should cause slower growth and a smaller-sized photosynthetic organ in the mature plant but not affect the number of years until maturation. Hence, plants with very different absolute sizes can have similar growth patterns when normalized for size.

Moreover, the mature size of photosynthetic systems may be similar for two species in spite of greatly different h. The model then predicts that the plant with the larger h should have a higher annual survival (σ), a larger number of immature years, a greater importance of the stored material in establishing the photosynthetic system, and an earlier cessation of leaf production within a season. The parameter h should depend on the shape of a crown, the way leaves and branches are arranged, and the environment: a perennial growing in a dense stand should have a larger h than an isolated plant.

Equivalence Relations

An important result of the model is the equivalence of the coefficients of storage efficiency and of individual survival. Thus, a whole range of combinations of storage physiologies and ecological conditions can produce the same growth
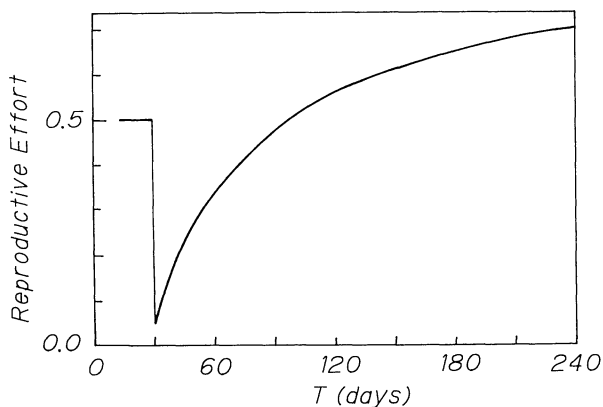
FIG. 9.—Reproductive effort, $R/[S(T) + F(t_2)]$, for mature plants. Horizontal axis is the length of a season, T. Parameters: $f = 0.07$, $\sigma = 0.9$, and $\gamma = 0.37$. For $T < 14.29$, an absence of growth is optimal; for $14.29 < T < 29.98$, an annual life cycle is optimal; and for $T \geq 29.98$, perennial growth is optimal. Note that reproductive effort depends on T nonmonotonically.

patterns. Similarly, high growth rates and a short growing season are equivalent to low growth rate and a long growing season. Thus, the effective number of parameters that determine the optimal growth pattern is smaller than in the first formulation.

Annual versus Perennial

The threshold for the perennial growth pattern is given by inequality (17) for both cases I and II. A larger reliability of habitat (σ), a higher storage efficiency (γ), a higher productivity of the environment (f), and a longer growing season (T) all tend to promote the evolution of perennial life, as suggested by previous models of life-history strategy (Stearns 1976).

Reproductive Effort

The ratio of reproductive investment to the total available resource in a year is called the reproductive effort (Abrahamson and Gadgil 1973; Pianka 1976). Figure 9 illustrates the reproductive effort for mature plants, $R/[S(T) + F(t_2)]$, for different lengths of the growing season, T. Reproductive effort is large for annual plants, which invest all the available resource in current reproduction, and may be regarded as the degree to which a plant relies on immediate rather than prospective reproduction (Harper et al. 1970; Abrahamson and Gadgil 1973). However, we should not expect reproductive effort to be smaller for a "strongly perennial" plant than for a "slightly perennial" one. Indeed, we observe the opposite in our model (see fig. 9): if the length of a season, T, increases and exceeds the threshold for the perennial life cycle, the reproductive effort is lowest for perennials with parameters just above the threshold, increases as T further increases, and becomes even larger than the level for annuals. Similarly, the model predicts that a

perennial plant in a shaded habitat with lower f and hence lower fT should allocate less to reproduction, which agrees with the observed increase in reproductive effort with increased light level (King, pers. comm.).

In accordance with this result, the importance of the stored material relative to the total production for mature plants, measured either by $S(0)/S(T)$ or by $F(t_1)/F(t_2)$, decreases with the length of a growing season, T, multiplied by the maximum relative growth rate, f (figs. 5, 7). These ratios also increase with the annual survival, σ, and with the storage efficiency, γ.

Timing of Leaf Production

Comparative studies have revealed that the phenology of leaf production and shoot elongation is correlated with the status of trees along a successional gradient and with habitat characteristics (Marks 1975; Maruyama 1978; Bicknell 1982; Kikuzawa 1983). For example, among deciduous trees, species living in forest gaps or early-successional species tend to continue to expand their leaves and shoots until mid-season, whereas climax species often produce most of their leaves at the beginning of a season. Moreover, the phenology of a species responds to the environment; for example, a perennial herb living in a productive site with higher light intensity stops leaf production later in a season (Hori and Oshima 1986).

The model predicts that the termination of leaf production within a season occurs earlier as the plant grows because of the nonlinearity of the photosynthetic-rate function. Further, it predicts that the timing of leaf production for a small immature plant and for a mature plant may be controlled by different factors. Productivity, measured by the maximum relative growth rate (f) multiplied by the length of a season (T), is the major determinant of the timing for small immature plants (causing a plant in a less productive site to stop leaf production earlier). In contrast, stability of the habitat, measured by the annual survival (σ) multiplied by the storage efficiency (γ), controls the timing for mature plants (shorter period of leaf production under a more stable environment).

However, the effects of these two factors are difficult to separate because they often go together: a higher productivity (large f) is often caused by a higher resource availability, which in turn is frequently accompanied by environmental disturbance and, hence, by low stability (small σ) (Tilman 1982). Careful examinations of comparative studies and of experiments are desired.

The model analyzed in this paper has several simplifying assumptions, some of which may be removed.

First, in the present model, a nonannual monocarpic growth schedule can never be optimal. However, monocarpy is practiced by some plants (Werner 1975; Schaffer and Schaffer 1977; Hirose and Kachi 1982), though not as often as polycarpic perennial growth (Kawano 1985). Many trees, especially climax species, fluctuate in fertility, repeating a series of very fertile years (mast years) followed by one or a few years of sterility and again a fertile one (Waller 1979; Silvertown 1980; S. Yamamoto, MS), under a relatively constant environment. Such a reproductive pattern is not optimal in the present model, in which the optimal plant should repeat the same schedule once it reaches maturity.

Fluctuating reproductive behavior can be the optimum if we change the optimization criterion (5), in which the reproductive success of a plant in a particular year is assumed to be proportional to the amount of resource invested in reproduction. We may generalize this criterion as

$$\Phi = \sum_{n=1}^{\infty} \sigma^n \phi(R_n) \rightarrow \text{maximum}, \qquad (20)$$

where $\phi(R)$ is an increasing function but could be nonlinear. Preliminary analysis suggests that, if we assume an increasing function with decreasing slope for $\phi(R)$, the optimal solution of the model with the performance function of equation (20) is either annual or a combination of several transient seasons and the steady state, that is, qualitatively similar to the result of this paper. In contrast, a temporally fluctuating solution can be optimal for a sigmoid curve, such as $\phi(R) = k_1 R^2/(1 + k_2 R^2)$, indicating that a small investment does not result in successful reproduction.

Second, if the population is either expanding or shrinking rather than remaining at steady state, then the optimal allocation strategy should be calculated with the model in which annual survival, σ, is divided by λ, the annual growth rate of the whole population (Caswell 1982; Schaffer 1983). Then, annual life and perennial life with smaller mature size would be more favored in an expanding population, where σ in equation (5) is effectively decreased, than in a shrinking population.

Third, the respiration occurring in the production part is included in the daily net production rate, $g(F)$. However, if the loss attributable to the storage part is important, the net production rate depends on both F and S. According to preliminary analysis, inclusion of a loss proportional to the size of the storage part (S) does not change the optimal growth schedule qualitatively.

Fourth, in calculating the optimal allocation for both reproduction and storage for the following season, we assumed that the allocation is made at the end of the season and that the reproductive investment is spent within that year. However, the model also applies to species that flower at the beginning of a season before leaf flush, if a large part of the reproductive organ is constructed in the preceding season, as is often the case (Yokoi, pers. comm.). Timing of reproduction (flowering and fruiting) within a season would require a separate modeling effort, considering such diverse aspects as availability of pollinators, seed dispersers, seed germination, predators, etc.

Fifth, the reproductive success of an individual plant is assumed to be measured by its lifetime seed production (and pollination success). However, plants often clone, reproducing vegetatively by runners and rhizomes. The present model may apply to those plants if we regard a patch of vegetatively reproducing clone as a single individual. However, if most seeds germinate close to their parent, the growth pattern of a parent plant in a season strongly affects the fate of its offspring produced in earlier years; thus, the model needs to be modified.

Sixth, the present model predicts that during one period of the optimal growth schedule, storage is empty. Although some plants (e.g., pseudo-annuals; Kawano 1975) fit the model, many other perennial plants retain some resource in storage during the whole season. This may be explained by its benefit for recovery after

unpredictable damage to the production part, caused by mammal or insect graz-
ing, by catastrophic physical disturbance such as fire or drought, or by trampling
by people. After damage, the plant may be able to reestablish its photosynthetic
system using the stored material (Hoefs and Shay 1981). Stochasticity in general
tends to favor the optimal mixed strategy as shown for seed germination (Cohen
1966) and for variable length of season (King and Roughgarden 1982b). (See also
the discussion by Dafni et al. [1981] about storage strategies in geophytes.)

Finally, competition between plants has been suggested as a possible key
process causing differences in leaf phenology in deciduous trees. A late-
successional tree living in a dense and crowded forest may benefit greatly from
being of the "flush type," making most leaves by stored material and thus
preempting available space at the beginning of a season (Bicknell 1982). To deal
correctly with optimization under such a competitive situation, a game model
needs to be developed instead of the simple optimization problem assumed in this
paper. Mirmirani and Oster (1978) analyzed games between perennial plants,
assuming that the vegetative organs of a plant remain intact in the nongrowing
season, and observed that in the competitive game situation the period of leaf
production within a season becomes longer than in the cooperative game (see also
Schaffer 1977; Vincent and Brown 1984). A more promising approach is modeling
the competitive process by specifying explicitly how the availability of resource
(e.g., light) is depressed. For example, we may develop a dynamic version of a
static game (Iwasa et al. 1985), in which competition for light is explicitly consid-
ered when discussing the evolution of tree height and canopy shape (see also
Mäkelä 1985). Various dynamic games on reproductive schedules are studied for
animals (Iwasa et al. 1983; Iwasa and Odendaal 1984).

In spite of these simplifications, the model is useful in combining different
problems (e.g., leaf phenology, storage size, and annual/perennial life cycle) and
in producing several testable predictions. We hope that experimental studies
designed to test the model, similar to those of King and Roughgarden (1983) for
annuals, will clarify the factors controlling the reproductive schedule of perennial
plants in light of evolutionary population ecology.

SUMMARY

The optimal growth schedule of a deciduous perennial plant is studied theoreti-
cally. We make three basic assumptions. First, the daily net photosynthetic rate of
a plant increases but saturates with the size of the production part (vegetative
organs working for photosynthesis). Second, the production part is discarded at
the end of a growing season, but it may be rebuilt at the beginning of the next
season using stored material. And finally, the plant maximizes the lifetime repro-
ductive investment by choosing both the growth schedule within each season and
the resource allocation between reproduction for the year and storage for the next
season. The model is analyzed by the combination of maximum principle and
dynamic programming.

Our analysis showed three basic results. First, the annual life cycle is optimal
under low storage efficiency, low habitat reliability, low growth rate, and a short

growing season. Second, under any other conditions, perennial growth is optimal. During years in which the final amount of resources is smaller than a critical value S^*, the plant remains immature and saves all of the resources for the next season. If it becomes larger than S^*, the plant invests the excess in reproductive activities and repeats the same growth schedule thereafter (steady state).

Finally, reproductive effort (the ratio of reproductive investment to total annual production) of a mature plant is high for an annual, is lowest for a perennial just above the threshold for the perennial growth pattern, increases as the length of the season increases, and in a very productive habitat may even exceed the level for an annual. The ratio of the plant size established by stored material to the maximum plant size decreases with the length of the growing season, which quantitatively fits the available data.

In light of the model, reported growth patterns and leaf phenology of many deciduous plants indicate that the nonlinearity of photosynthetic rate as a function of the size of the production part is important. For a case with nonlinear photosynthesis but without an upper limit to the leaf expansion rate, a plant's optimal phenology, if normalized by size, can be parameterized by two quantities: productivity (maximum relative growth rate multiplied by a season's length) and stability (annual survival multiplied by storage efficiency). The timing of the cessation of leaf production within a season by a small immature plant is determined by productivity (occurring later in a more productive habitat). Leaf production ends earlier in the season as the plant grows. The optimal time for ending leaf production in a mature plant, in contrast, is controlled mainly by stability (it ceases earlier at a more stable site) and is almost independent of productivity.

APPENDIX A

We here derive the optimal growth schedule within a season given by expressions (6) using the maximum principle (Pontryagin et al. 1962; Leitmann 1981). First, we define the Hamiltonian as

$$H(F, S, \lambda_F, \lambda_S, u) = \lambda_F u(aF + b) + \lambda_S[g(F) - u(aF + b)], \qquad (A1)$$

where λ_F and λ_S are co-state variables corresponding to F and S, respectively. Unlike other allocation models of optimal life history (León 1975; Vincent and Pulliam 1980; King and Roughgarden 1982a,b; Iwasa and Roughgarden 1984), the present model assumes that the state space is constrained by inequality (6e).

During the time interval when S is larger than zero, we have the following equations for co-state variables:

$$d\lambda_F/dt = -\partial H/\partial F = -\lambda_S dg(F)/dF + (\lambda_S - \lambda_F)ua, \tag{A2a}$$

$$d\lambda_S/dt = -\partial H/\partial S = 0. \tag{A2b}$$

A different set of equations holds during the interval when S equals zero: let $G(F, S) = -S$, so that the constraint given by inequality (6e) is $G \le 0$. Let $P(F, S, \lambda_F, \lambda_S) = (\partial G/\partial F)dF/dt + (\partial G/\partial S)dS/dt = -[g(F) - u(aF + b)]$. Then, we have

$$d\lambda_F/dt = -\partial H/\partial F + \mu\partial P/\partial F$$
$$= -\lambda_S dg(F)/dF + (\lambda_S - \lambda_F)ua - \mu[dg(F)/dF - ua], \tag{A3a}$$

$$d\lambda_S/dt = -\partial H/\partial S + \mu\partial P/\partial S = 0, \tag{A3b}$$

where μ is determined by the relation $\partial H/\partial u = \mu\partial P/\partial u$, which gives $\mu = \lambda_F - \lambda_S$ (Pontryagin et al. 1962). In addition, μ is greater than zero in this interval.

At a junction point (the boundary between the interval for $S > 0$ and that for $S = 0$), a "jump condition" holds, which says that λ_F is a continuous function of time t but λ_S may change discontinuously because G depends only on S. Combining these results with the terminal conditions $\lambda_F(T) = 0$ and $\lambda_S(T) = 1$, we have a system of equations for co-state variables.

Then, the optimal allocation $u(t)$ at each t ($0 < t < T$) is u, which maximizes H given by equation (A1) with F, S, λ_F, and λ_S fixed.

We can determine the growth schedule of a plant in which these necessary conditions for optimal growth are satisfied. An example of the optimal-growth solution is illustrated in figure 3a, in which three phases exist. In the first phase, $u = 1$; that is, F grows with the maximum speed. The co-state variable for F varies as

$$d\lambda_F/dt = -\lambda_S dg(F)/dF - (\lambda_F - \lambda_S)a, \qquad 0 < t < t_1, \tag{A4a}$$

$$\lambda_S(t) = \lambda_F(t_1), \qquad\qquad\qquad 0 < t < t_1. \tag{A4b}$$

In the second phase, $u = g(F)/(aF + b)$, and the state variable is constrained by $S = 0$. The co-state variable varies with

$$d\lambda_F/dt = -\lambda_F dg(F)/dF, \qquad t_1 < t < t_2. \tag{A5}$$

In the third phase, $u = 0$; all the products are allocated to the storage part. The co-state variable for F is

$$\lambda_F(t) = (T - t)dg(\hat{F}_2)/dF. \tag{A6}$$

$\lambda_F(t)$ is continuous. In contrast, the co-state variable for S is constant within each interval because of equations (A3b) and (A4b), but it changes discontinuously at the junction point t_1, as suggested by the jump condition (Pontryagin et al. 1962).

We note that the co-state variable in Pontryagin's maximum principle is the marginal value of each organ, the marginal increase in the objective function caused by a unit increase in the corresponding variable (Iwasa and Roughgarden 1984). Therefore, we have

$$d\psi(S_0)/dS_0 = \lambda_S(0). \tag{A7}$$

However, equation (A4b) with $t = 0$ gives $\lambda_S(0) = \lambda_F(t_1)$. Equations (7d) and (A6) with $t = t_2$ give $\lambda_F(t_2) = 1$. By integrating both equations (A5) and $dF/dt = g(F)$, we derive

$$\lambda_F(t_1)/\lambda_F(t_2) = g[F(t_2)]/g[F(t_1)]. \tag{A8}$$

Combining these, we obtain

$$d\psi(S_0)/dS_0 = g[F(t_2)]/g[F(t_1)], \tag{A9}$$

which is used to determine the optimal storage size in equation (15b). An inverse relation, similar to equation (A8), between the marginal value of the vegetative part and the net

photosynthetic rate of the whole plant is proved elsewhere (Iwasa and Roughgarden 1984, Appendix B).

APPENDIX B

We here calculate the optimal allocation between reproduction and storage. Equation (14) can be rewritten as

$$V(S) = \max_{0 \le Y \le S} \{S - Y + \sigma V[\psi(\gamma Y)]\}, \tag{B1}$$

where $S > 0$, $n = 1, 2, 3, \ldots$, and Y is the size of storage for the next season ($Y = S - R$). The unknown function $V(S)$ in equation (B1) is determined by sequential approximation as follows:

$$V_1(S) = S, \tag{B2a}$$

$$V_{n+1}(S) = \max_{0 \le Y \le S} \{S - Y + \sigma V_n[\psi(\gamma Y)]\}, \tag{B2b}$$

where $S > 0$ and $n = 1, 2, 3, \ldots$. The limit is expressed as

$$V(S) = \lim_{n \to \infty} V_n(S), \quad S > 0. \tag{B3}$$

The optimal storage size, S^*, is defined by equation (15b). Since the first derivative of $\psi(S)$ monotonically decreases, equation (15b) gives

$$1/\sigma\gamma < d\psi(\gamma Y)/dS_0 \quad \text{for } 0 < Y < S^*. \tag{B4}$$

Using Y to integrate both sides of condition (B4) from 0 to S^*, we have

$$S^* < \sigma\psi(\gamma S^*). \tag{B5}$$

Let $M = \sigma\psi(\gamma S^*) - S^*$. Using conditions (B4) and (B5) for $\psi(S)$ and S^*, we can prove the following statements by mathematical induction with respect to $n = 2, 3, 4, \ldots$:

$dV_n/dS(S) > 1$ for all $S < S^*$;

$V_n(S) = S + M(1 - \sigma^n)/(1 - \sigma)$ for $S > S^*$; and

the maximum of the right-hand side of equation (B2b) is attained when $Y = S^*$.

Since the convergence in equation (B3) is uniform with respect to S, these three statements should hold for the limit $V(S)$ as well. Thus, equation (15a) is proved.

APPENDIX C

Here we consider case I, in which nonlinear photosynthetic rate and immediate establishment of the production part are assumed. From the latter assumption, we have $t_1 = 0$. Growth during the second phase (eq. 7c) gives

$$\ln \hat{F}_2 + h\hat{F}_2 - \ln \hat{F}_1 - h\hat{F}_1 = ft_2. \tag{C1}$$

The switching time t_2 is determined by equation (7d) as

$$fT - ft_2 = (1 + h\hat{F}_2)^2. \tag{C2}$$

According to equation (15b), at steady-state perennial growth, the derivative of $S(T)$ with respect to S_0 equals $1/\sigma\gamma$. However, the final storage size is $S(T) = \hat{F}_2(1 + h\hat{F}_2)$, whose derivative with initial size S_0 is

$$dS(T)/dS_0 = (1 + h\hat{F}_1)\hat{F}_2/(1 + h\hat{F}_2)\hat{F}_1 = 1/\sigma\gamma. \tag{C3}$$

Eliminating t_2 from equations (C1), (C2), and (C3) and rewriting them using $x = h\hat{F}_1$, $y = h\hat{F}_2$, $\tau = fT$, and $\alpha = \sigma\gamma$ yields equations (16).

APPENDIX D

We here consider case II, in which the photosynthetic rate is proportional to the size of the production part, and the rate of expansion of the production part is limited.

We reasonably assume that $a > f$: the upper limit of the expansion rate is larger than the maximum net photosynthetic rate. Starting from $S(0) = S_0$, the size of the production part increases from zero at the maximum rate as $F(t) = [\exp(at) - 1]b/a$, and the storage decreases as

$$S(t) = S_0 - ftb/a - [\exp(at) - 1](1 - f/a)b/a, \tag{D1}$$

which becomes zero at $t = t_1$. Therefore, we have

$$S_0 = ft_1b/a + [\exp(at_1) - 1](1 - f/a)b/a, \tag{D2}$$

$$\hat{F}_1 = [\exp(at_1) - 1]b/a, \tag{D3}$$

where $\hat{F}_1 = F(t_1)$. For the growth between t_1 and t_2, equation (7c) becomes

$$\hat{F}_2 = \hat{F}_1\exp[f(t_2 - t_1)], \tag{D4}$$

where $\hat{F}_2 = F(t_2)$. Equation (7d) determines the second switching time as $t_2 = T - 1/f$. Then, the final storage size is

$$S(T) = f\hat{F}_2(T - t_2). \tag{D5}$$

Combining these equations, we can obtain $S(T)$ as a function of S_0 by eliminating t_1 and t_2. We also have

$$d\psi(S_0)/dS_0 = dS(T)/dS_0 = \exp(fT - 1 - ft_1). \tag{D6}$$

The steady-state perennial growth is obtained from equations (D6) and (15b), as

$$t_1 = T - (1/f)\ln(e/\sigma\gamma). \tag{D7}$$

If t_1 calculated by equation (D7) is negative, annual growth is optimal. If it is positive, perennial growth is optimal, and the ratio of initial to final storage sizes is

$$S(0)/S(T) = \sigma\gamma \{1 - f/a + ft_1/[\exp(at_1) - 1]\}. \tag{D8}$$

As the length of a growing season, T, increases, t_1 (given by eq. D7) increases linearly, and both initial and final storage sizes increase, but their ratio (eq. D8) decreases monotonically. The ratio of the production parts at the beginning and the end of the second phase for the optimal steady-state growth is given by equation (19). This ratio is independent of the length of a growing season, T, not as in case I.

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