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Optimal Level of Chemical Defense Decreasing with Leaf Age

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A recent study on a biennial plant demonstrated that pyrrolizidine alkaloids decrease with the age of leaves due to reallocation from old leaves to new leaves. Here we study the optimal age-specific pattern of defense chemical concentration in leaves that achieves the maximum growth rate of the plant. We consider a plant growing exponentially in a constant environment. Assumptions are the following: (1) The loss of leaves due to herbivory decreases with defense chemical concentration (2) The daily net photosynthesis of a leaf decreases with its age. (3) Using photosynthetic products, the plant produces new leaves that may contain defense chemicals. (4) Although there is a cost to producing new defense chemicals, such chemicals can be reallocated without cost. In the optimal schedule calculated using Pontryagin's maximum principle, the chemical defense level decreases with leaf age. The optimal level of chemical defense increases with the cost of leaf production and herbivory intensity but decreases with the cost of defense chemical production, effectiveness of the defense chemical, net productivity, and growth rate of the plant. If both generalist and specialist herbivores attack the same plant, the optimal defense level is dependent only on the generalists' abundance and sensitivity, but is independent of the specialists that are unaffected by the defense chemical. © 1996

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INTRODUCTION

Many terrestrial plants grow under strong herbivore pressure (e.g., Coley and Aide, 1991). One effective way of protection against insect herbivory

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is to produce a variety of secondary chemical substances for defense (Rosenthal and Berenbaum, 1991). On the other hand, producing defense chemicals is accompanied by the cost of material or energy, causing a slower growth rate (Gulmon and Mooney, 1986). The economically profitable level of chemical defense therefore depends on many factors, e.g., the intensity of herbivory in the habitat, the cost of producing the chemical, and the rate of plant growth (Coley *et al.*, 1985).

Chemical defenses are not evenly distributed over the plants. For example, alkaloid levels tend to be higher in young leaves than in mature leaves (listed in McKey, 1979). In some cases, as in *Coffea* spp. (Weevers, 1930; Frischknecht *et al.*, 1986) and *Cynoglossum officinale* (van Dam *et al.*, 1994), the alkaloid levels in the youngest leaf are even 75–190 times higher than in the oldest leaf. Recently studies with radioactive precursors showed that alkaloids have low turnover rates (for tobacco Baldwin *et al.*, 1994, for *C. officinale* van Dam *et al.*, 1995). Also pyrrolizidine alkaloids (PAs) are redistributed from the ageing leaves into the youngest leaves (van Dam and Hartmann, 1993). This has implications for optimal defense theory as plants can reuse defenses, which reduces the physiological costs of maintaining a high concentration.

It is thought that this skewed distribution of alkaloids is a strategy to protect the youngest leaves against herbivores (Frischknecht *et al.*, 1986; Zangerl and Bazzaz, 1992). In particular, small herbivores, such as insects, feed from plant parts rather than from the whole plant. Young leaves typically have a higher photosynthetic potential than old leaves, which makes them more valuable to the plant (Mooney and Gulmon, 1982; Bazzaz, 1984; Harper, 1989). In order to optimize its fitness, the plant thus should allocate its defenses in the most valuable parts, i.e., the youngest leaves (McKey, 1974). Yet, as Zangerl and Bazzaz (1992) emphasized, the mainstream of papers on optimal defense theory deals with the average concentration of defense chemicals in the plant as a whole and neglects different plant parts.

In this paper, we study the optimal level of defense chemicals contained in a leaf as a function of leaf age. The assumptions are as follows. The loss of leaves due to herbivory decreases with the defense chemical concentration, indicating the protecting effect of the chemical. The daily net photosynthesis of a leaf decreases with its age. Using newly acquired photosynthetic products, the plant produces new leaves that may contain defense chemicals. The defense chemical contained in old leaves may also be reallocated to new leaves. To make the argument simple, we here consider a plant in a vegetative phase growing exponentially in a constant environment, constantly producing new leaves. We examine the optimal age-specific pattern of defense chemical in leaves that realize the maximum growth rate of leaves. This optimality criterion is supported by the result

by Iwasa and Roughgarden (1984), who demonstrated, using a dynamic optimization model including multiple vegetative organs and reproductive activity, that the optimal balance between different parts of a vegetatively growing plant is in fact given by the one that achieves the fastest growth rate of the individual.

The optimal concentration of defense chemical over leaf age is the one that achieves the maximum Malthusian parameter for an exponentially growing leaf population. Hence we can follow the same logic as the one underlying general life history evolution theory (Taylor *et al.*, 1974; Leon, 1976): Since maximizing the Malthusian parameter is shown to be mathematically equivalent to the maximization of the expected lifetime production with an exponential discounting, the problem is rewritten as maximization of an integral over age, which can be analyzed by dynamic optimization techniques, such as Pontryagin's maximum principle.

In the model, the new production and redistribution of defense chemicals between leaves are postulated to be chosen adaptively. In physiological terms, the redistribution is realized by continuous processes from sources to sinks, i.e., roots to shoot, old leaves to young leaves, and young leaves to reproductive tissues, and the regulation of material flows is postulated to be designed adaptive although the physiological mechanisms are not specified in the model.

In another paper (van Dam *et al.*, 1996), all the parameters and functions included in the model are measured or estimated by experimental and field studies of a biennial rosette plant *C. officinale* in Dutch sand dune, and the quantitative predictions of the model on optimal chemical defense (pyrrolizidine alkaloids concentration) are tested. In the present paper we analyze the general behavior of the model. Many of the model's assumptions are made considering that particular plant population although we expect the basic aspects of the model's behavior to be useful in the understanding of other plant-herbivore systems also.

MODEL

We consider here a plant individual in a vegetative phase growing in a constant environment. We assume that the plant has a number of leaves with different ages and it constantly produces new leaves using the material (or energy) obtained by the photosynthesis.

Let x be the age of a leaf, and $n(x, t)$ be the number of leaves with age x at time t . We have the equation

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial x} - h(A(x))n, \quad x > 0, \quad (1)$$

for age structure of leaves, where $h(A(x))$ is the instantaneous mortality of a leaf of age x , and it is assumed decreasing function of the amount of defense chemical, $A(x)$, contained in the leaf. In addition the second derivative is positive; i.e., the effect of additional defense chemical in reducing mortality decreases for large A . Two examples are

$$[\text{exponential}] \quad h(A) = h_0 e^{-cA}, \quad (2a)$$

$$[\text{hyperbolic}] \quad h(A) = \frac{h_0}{(1 + cA)^k}, \quad (k > 0) \quad (2b)$$

where h_0 is the maximum mortality due to herbivory, indicating the intensity of herbivory pressure in the habitat. c is the effectiveness of defense chemical. Equation (2a) was used in a model of optimal seasonal schedule of defense chemical production for the whole plant (Yamamura and Tsuji, 1995). Although we use Eq. (2) for numerical analyses, most analyses in this paper are presented without specifying $h(A)$. Both Eq. (2a) and Eq. (2b) are decreasing functions, but their tails differ quantitatively. Compared with the exponential function Eq. (2a), the hyperbolic function Eq. (2b) tends to decline faster for small A and slower for large A , implying that, the defense by a low concentration of chemicals is already very effective but further increase in the level is not. This difference in the tail of the graph may give significant differences in the pattern of optimal defense level, as shown later.

To produce leaves with a high level of defense chemical is profitable because it reduces the risk of being removed by herbivory. On the other hand producing defense chemical is costly. We assume that the defense chemical is not decomposed and that the plant can reallocate the defense chemical from old leaves to newly produced leaves without loss, as is observed for *C. officinale* (van Dam and Hartmann, 1993; van Dam *et al.*, 1994). In addition, we assume for simplicity that this reallocation process is costless. Then the following relationship indicates the conservation of energy:

$$n(+0, t)(a + bA(0)) = \int_0^{x_{\max}} f(y) n(y, t) dy + \int_0^{x_{\max}} b \left(-\frac{dA}{dy} \right) n(y, t) dy; \quad (3)$$

where the left-hand side is the number of leaves multiplied by the cost of producing a new leaf. The energetic cost of producing a new leaf is the sum of a , which is independent of the amount defense chemical concentration, and $bA(0)$, a part proportional to the amount of chemical contained in a new leaf. The right-hand side of Eq. (3) is the sum of two terms: the first term is for the rate of acquisition via photosynthesis and the second is for

the reallocation of alkaloid from old leaves measured in energetic equivalent; both are integral over all the leaves with different age. The rate $f(x)$ is the net photosynthetic rate of a leaf of age x that can be used for production of new leaves, and hence it is the net photosynthetic rate minus the fraction that on average goes to root, stems, or organs other than leaves (for details, see van Dam *et al.*, 1996). In the following we call $f(x)$ simply the net production rate, the photosynthetic product that can be used for production of leaves. Let x_{\max} be the maximum age of leaves after which a leaf has no ability of photosynthesis: $f(x) > 0$ for $x < x_{\max}$ but $f(x) = 0$ for $x \geq x_{\max}$. An example of the daily production rate as a function of leaf age is

$$f(x) = \begin{cases} f_0 \left(1 - \frac{x}{x_{\max}}\right), & \text{for } x < x_{\max} \\ 0, & \text{for } x \geq x_{\max}. \end{cases} \quad (4)$$

In general, x_{\max} can be infinitely large. But if it is finite, the plant should not protect leaves older than x_{\max} . As shown below, it may be profitable for a plant to stop protecting its leaves sometime before the maximum age x_{\max} . Later we examine the case with different functional forms of $f(x)$, such as a curve with a nonlinear decrease with x or a curve initially increasing and then decreasing with x having the peak photosynthetic ability two weeks old, instead of the youngest leaves.

The second term on the right-hand side of Eq. (3) is for the reallocation of defense chemicals from old leaves, where $(-dA/dx)$ is the rate of reallocation from a leaf of age x per unit time, and a factor b is multiplied as it converts the amount of chemicals to its energetic equivalent. The rate of reallocation is expressed in Eq. (3) in terms of the amount of energetic cost saved by not producing the same amount of chemicals for new leaves.

If a plant uses a particular age-specific schedule of chemical defense $\{A(x)\}$, the age structure of leaves will soon converge to a stable distribution, and then the total number of leaves will increase exponentially with time. To make the analysis simple, we first study the case in which no cost accompanies the reallocation processes. Later we examine the effect of a very large transportation cost. Let r be the rate of exponential growth of leaves. According to calculations given in Appendix A, we can derive the following equation for r :

$$a + bA(0) = \int_0^{x_{\max}} \left(f(y) - b \frac{dA}{dy} \right) \exp \left[-ry - \int_0^y h(A(z)) dz \right] dy. \quad (5)$$

Exponential rate of leaf growth, or Malthusian parameter, r is determined implicitly as a real solution of Eq. (5). A clear analogy exists between Eq. (5) and the characteristic equation for Malthusian parameter for

demographic model of age-structured population (Roughgarden, 1979; Charlesworth, 1980). The terms $(f(x) - b dA/dx)$ in Eq. (5) indicate the amount of energy obtained from leaf of age x per unit time that can be used for production of new leaves. The energy comes either from production (minus the fraction going to organs other than leaves) or from the redistribution of alkaloid from old leaves. In fact $(f(x) - b dA/dx)$ divided by the cost of production of a new leaf $(a + bA(0))$, the left-hand side of Eq. (5), is equal to fertility, the rate of producing of new leaves from a leaf of age x . Through integration by part, Eq. (5) is rewritten as

$$a = \int_0^{x_{\max}} \{f(y) - bA(y)(r + h(A(y)))\} \exp \left[-ry - \int_0^y h(A(z)) dz \right] dy. \quad (6)$$

We ask, What is the age-specific concentration of defense chemicals in leaves $\{A(x)\}$ that realizes the fastest growth of a plant. Malthusian parameter is adopted as remeasure of adaptation of the chemical defense schedule. This problem is mathematically equivalent to the optimal life history pattern that attain the maximum rate of population growth (e.g., Charlesworth, 1980), because chemical defense is the effort of increasing survivorship. Since Malthusian parameter r is determined by $A(x)$ implicitly from Eq. (6), it is technically difficult to search for the optimal $A(x)$. However, the following theorem, first proved by Taylor *et al.* (1974) and Leon (1976) in the context of general life history optimization, shows the equivalence of the maximization of r and the maximization of the lifetime reproductive success with exponential discounting for future gain. We state this here in the context of our model (see Appendix B):

PROPOSITION. *Consider the following quantity computed from $A(x)$ and r :*

$$G(A(\cdot), r) = \int_0^{x_{\max}} \{f(y) - bA(r + h(A))\} \exp \left[-ry - \int_0^y h(A(z)) dz \right] dy. \quad (7a)$$

Let r^ be the maximum possible value of Malthusian parameter and $A^*(x)$ be the optimal schedule of chemical defense that attains the maximum r^* . Then for any defense schedule $A(\cdot)$, we have (see Appendix B) for derivation*

$$G(A(\cdot), r^*) \leq G(A^*(\cdot), r^*), \quad (7b)$$

which implies that the optimal schedule of defense $A^(x)$ is the one that attains the maximum of $G(A(x), r^*)$ in which r^* is fixed to be the optimal value.*

This states that we can search for the optimal solution $A(x)$ that maximizes r , by considering the optimal $A(x)$ that maximizes $G(A(\cdot), r^*)$. The

latter problem is the optimization of schedule $A(x)$ with r fixed to the optimal value r^* , which works as an exponential rate of discounting future benefit. Equation (7b) is rewritten as

$$a = \max_{A(\cdot)} \int_0^{x_{\max}} \{f(y) - bA(r^* + h(A))\} \exp \left[-r^*y - \int_0^y h(A(z)) dz \right] dy. \quad (8)$$

Equation (8) is a problem much simpler than the original problem because the function to be maximized in (8) is an integral with respect to time x , which can be solved by dynamic optimization techniques, such as Pontryagin's maximum principle (Pontryagin *et al.*, 1962) and dynamic programming (Bellman, 1957).

OPTIMAL SCHEDULE OF DEFENSE CHEMICAL CONCENTRATION

We consider the max in Eq. (8) to be a problem of searching for the optimal pattern of age-specific chemical concentration $\{A(x)\}$. We here use Pontryagin's maximum principle to solve the optimization of Eq. (8) (Pontryagin *et al.*, 1962). This technique has been used successfully to understand plant life history, such as reproductive timing of annuals (Cohen, 1967), shoot/root dynamic balance of a growing plant (Iwasa and Roughgarden, 1984), advantage of perennial versus annual (Iwasa and Cohen, 1989; Pugliese, 1988). In these models, dynamic optimization is used to calculate the optimization over time t , but here we compute the dynamic optimization over age x , instead of real physical time.

Let $S(x)$ be an exponential function within the integral in Eq. (8). Then we have

$$\frac{dS}{dx} = -(r^* + h(A)) S. \quad (9)$$

The initial value is $S(0) = 1$. Note that $S(x)$ is the stable age structure of leaves. Using this symbol, the objective function to maximize in the right-hand side of Eq. (8) is the integral of $\{f(x) - bA(r^* + h(A))\} S$ over x from 0 to x_{\max} . Hence the Hamiltonian is

$$H = (f(x) - bA(r^* + h(A))) S - (r^* + h(A)) S \lambda, \quad (10)$$

where the variable x in A , S , λ is abbreviated. The time change of costate variable $\lambda(x)$ is

$$\frac{d\lambda}{dx} = -\frac{\partial H}{\partial S} = -f(x) + bA(r^* + h(A)) + (r^* + h(A)) \lambda, \quad (11)$$

and its terminal conditions is

$$\lambda(x_{\max}) = 0 \quad (12)$$

because objective function (8) does not include $S(x_{\max})$ explicitly. Costate variables $\lambda(x)$ can be calculated from differential equation (11) with terminal condition (12) as explained in Appendix C. We place an additional constraint

$$A(x) \geq 0, \quad (13)$$

implying that the defense chemical concentration is either positive or zero. Pontryagin's maximum principle states that the optimal control $A^*(x)$ is the one that maximizes Hamiltonian, Eq. (10), at each age x for given state and costate variables (S, λ, x) (Pontryagin *et al.*, 1962). Hamiltonian depends on A as follows:

$$H = -bS(r^* + h(A)) \left(A + \frac{\lambda(x)}{b} \right) + [\text{terms without } A]. \quad (14)$$

Hamiltonian H as a function of A may in general have more than one local optima. Then we need to be cautious in choosing the optimal solution among these local optima.

The Optimal Solution

According to the analysis in Appendix C, the optimal solution may include two intervals, separated by a critical age x_e . Before the critical age, a leaf contains a positive amount of defense chemical ($A(x) > 0$, for $0 < x < x_e$). This implies that an optimally growing plant invests a positive amount of defense, but the level of defense chemical decreases with leaf age x . After the critical age, however, the optimally growing plant invests no defense ($A(x) = 0$, for $x_e < x < x_{\max}$). At this age, there can be a jump from a positive defense level to zero.

The optimal solution in such a form can be constructed as follows: First, note that the chemical defense level at a critical age, $\hat{A} = A(x_e)$, and the critical level of costate variable $\lambda(x_e)$ satisfy the two equalities

$$\frac{\lambda(x_e)}{b} = \frac{\hat{A}(r^* + h(\hat{A}))}{h(0) - h(\hat{A})} = \frac{r^* + \hat{A}h'(\hat{A}) + h(\hat{A})}{-h'(\hat{A})}, \quad (15)$$

which is derived from $H(0) = H(\hat{A})$ and $(\partial H / \partial A)(\hat{A}) = 0$.

The second equality of Eqs. (15) always has a trivial solution $\hat{A} = 0$. But it may also have a positive solution. If it exists, we set $A(x_e) = \hat{A}$ a positive solution in the following computation. Then we can compute x_e , the leaf

age of ending of chemical protection, from the first equality of Eq. (15) and the following equation:

$$\lambda(x_e) = \int_{x_e}^{x_{\max}} f(y) \exp[-(r^* + h(0))(y - x_e)] dy. \quad (16)$$

Second, the defense chemical level $A(x)$ before the critical age satisfies the differential equation

$$\left[\frac{d}{dA} \left\{ \frac{r^* + h(A(x))}{-h'(A(x))} \right\} - 1 \right] \frac{dA}{dx} = \frac{(r^* + h(A(x)))^2}{-h'(A(x))} - \frac{f(x)}{b}. \quad (17)$$

The optimal level of defense chemical $A(x)$ can be calculated by integrating differential equation (17) from $x = x_e$ backward using the terminal condition of $A(x_e) = \hat{A}$. Once we know $A(x)$, we can compute the stable leaf age distribution $S(x) = \exp[-r^*x - \int_0^x h(A(z)) dz]$. If Eq. (16) is smaller than the value required by Eq. (15) for any $x_e \geq 0$, then $A(x) = 0$ for all x , indicating that the optimal strategy of the plant is not to produce defense chemicals.

Depending on the form of $h(A)$, chemical defense just before the critical age can be zero ($\hat{A} = 0$), which is the case if the second equality of Eq. (15) has no positive solution. $A(x)$ does not jump at the critical age as $A(x_e) = 0$. See Appendix C for the derivation of these results. Note that the optimal age-specific defense is computed by the method described in this section for a given r^* . However, in the original problem presented in Eq. (8), r^* should be determined for given functions ($h(A)$ and $f(x)$) and parameters (a and b) so as to satisfy the equality of Eq. (8). Hence the optimal solution is obtained by the following procedures: First we choose a trial value of r^* and construct the optimal age-specific defense as described above using this r^* and functions ($h(A)$ and $f(x)$) and a parameter b , but not a . Then we estimate the right-hand side of Eq. (8) and see whether it is larger or smaller than the left-hand side, a . If it is larger (smaller) than a , then we use a larger (smaller) r^* and repeat the Verne procedure again. By trial errors, we finally obtain suitable r^* , which satisfies Eq. (8) with sufficient accuracy.

NUMERICAL EXAMPLES

Exponential Function for $h(A)$

For further analyses, we need to specify $h(A)$, the leaf mortality as a function of defense chemical concentration A and $f(x)$, age-specific rate of

net photosynthesis. We first examine the case in which $h(A)$ is given by Eq. (2a) and $f(x)$ is given by Eq. (4). The second equality in Eq. (15) gives the condition for critical alkaloid concentration \hat{A} . Let $z = c\hat{A}$; then we can rewrite Eq. (15) as

$$\frac{r}{H} = \frac{e^{-z} - 1 + z}{e^z - 1 - z}, \quad (18)$$

The right-hand side is 1 for $z = 0$, decreases monotonically with z , and converges to 0 for very large z .

Suppose that growth rate is larger than the maximum rate of herbivory ($r > h_0$), there is no solution satisfying Eq. (18). Hence no protection is to be made for any x (i.e., $A(x) = 0$, for all x). On the other hand, herbivory is sufficiently strong compared with growth rate, so that $r < h_0$, there is a positive solution of Eq. (18). By using this, we can determine the critical A , as $\hat{A} = z/c$, and then the critical level of λ from Eq. (15). Finally, we can determine then the critical age x_e from Eq. (16).

A subarc with positive chemical defense level can be calculated by using differential equation Eq. (17) for $0 \leq x \leq x_e$, starting from $A(x_e) = \hat{A}$.

A solid curve in Fig. 1B illustrates an example of the optimal age-specific defense. The parameters are chosen to approximately correspond to the situation for a *C. officinale* population studied by van Dam *et al.* (1995a). Both energetic costs and the daily net photosynthesis per leaf are measured in units of gram dry weight of new leaf; the defense chemical (PA) is measured in units of milligrams and the time in units of days. Then from experimental measurements, we have the following estimates: the cost of leaf production is $a = 1.0$ gram leaf fresh weight (gFW) by definition; the cost of alkaloid production is $b = 0.00925$ (gFW/mg); the maximum leaf age is $x_{\max} = 77$ days; the peak net productivity considering the fraction allocated to new leaf production is $f_0 = 0.0875$ (gFW/day); the leaf mortality due to herbivory in the absence of protection is $h_0 = 0.1 \text{ day}^{-1}$; and the effectiveness of defense chemicals is $c = 1.0 \text{ mg}^{-1}$. In this paper we will not describe how to obtain the parameters, see van Dam *et al.* (1996) for details.

In Fig. 1B, defense chemical level stays high until the middle of leaf lifetime and then decreases rather quickly. At a critical agent which is before the final time, there is a sudden drop of defense chemical concentration from a positive value to zero.

Hyperbolic Function for $h(A)$

We consider the case in which $h(A)$ is a hyperbolic function, as given by Eq. (2b) with $h_0 = 0.1$, $c = 9.0$, and $k = 1$, instead of exponential function Eq. (2a). Compared with an exponential $h(A)$, a hyperbolic $h(A)$ decreases

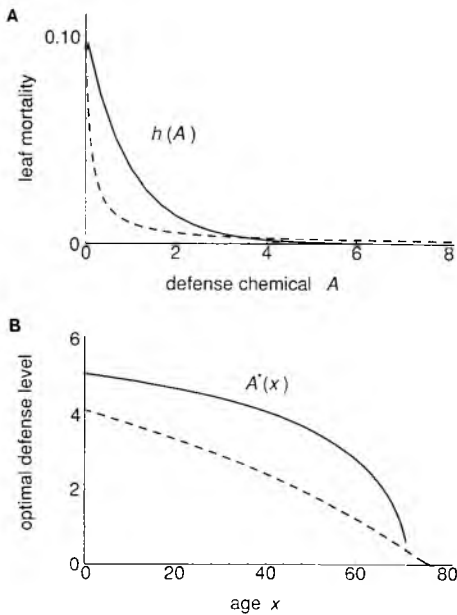


FIG. 1. The optimal age-specific defense level $A(x)$ for different mortality functions $h(A)$. (A) Vertical axis is the leaf mortality and the horizontal axis is the defense chemical concentration. Solid curve is an exponential function, Eq. (2a) with $h_0=0.1$ and $c=1.0$. Broken curve is a hyperbolic function, Eq. (2b) with $h_0=0.1$, $c=9.0$, and $k=1$. (B) Vertical axis is optimal chemical concentration computed by the model. Horizontal axis is leaf age x . Solid broken curves correspond to $h(A)$ in (A). Production rate is given by Eq. (4) with $f_0=0.0875$ and $x_{\max}=77$. Costs are $a=1.0$, $b=0.00925$.

more sharply for small A and then more slowly for large A . The net production rate is the same as in Eq. (4). By examining Eq. (15), we can show that there is no jump of defense level at the critical age ($\hat{A}=0$) but the critical time is before the final time ($x_e < x_{\max}$ if $k \leq 1$). In contrast, if $k > 1$, there is a jump similar to the case with hyperbolic $h(A)$. The broken curve in Fig. 1B indicates the optimal defense level as a function of leaf age. $A(x)$ decreases approximately linearly and smoothly connected to zero.

Effect of Different $f(x)$

Figures 2 and 3 illustrate the results for different net production rate $f(x)$ as a function of leaf age. In Fig. 2A, instead of a linear decrease in Eq. (4), consider the case with an *S*-shaped function $f(x)$ that stays high for some period and then quickly decreases. Solid and broken curves in Fig. 2B correspond to the same two mortality-defense function $h(A)$. The optimal age-specific defense level is also initially high and then becomes lower for the latter half of the leaf lifetime.

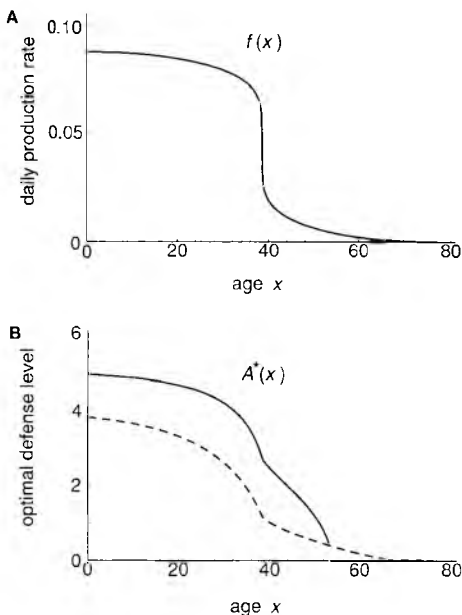


FIG. 2. The optimal age-specific defense level $A(x)$ for a different net production function $f(x)$. (A) The net production $f(x)$, which stays high until the middle of the leaf lifetime and then drops. The area under the curve $f(x)$ is the same as in Fig. 1. (B) The optimal chemical concentration computed by the model. Solid curve for exponential mortality function $h(A)$ (the same as the solid curve in Fig. 1A), and broken curve is for hyperbolic $h(A)$.

In Fig. 3, low photosynthetic ability of young leaves is considered; $f(x)$ increases with x until a certain age (about 16 days) and then decreases linearly. The same computation method explained above applies to the case with a nondecreasing $f(x)$.

These cases correspond approximately to the situation in which $h(A)$ and $f(x)$ imitate the experimental data for *C. officinale* reported in van Dam *et al.* (1996). In all of these cases, the optimal defense level smoothly decreases with leaf age, as is observed in the *C. officinale* population (see van Dam *et al.*, 1996). The amount of jump \hat{A} at the critical age if it exists at all was not very large. The overall shape of the optimal $A(x)$ is not very different, although the shape and the curvature of the graph of $A(x)$ may depend on $f(x)$ and $h(A)$ assumed.

Figure 3 shows the case in which the net photosynthetic rate $f(x)$ increases with x for small x , has a peak, and then decreases with x , as illustrated in Fig. 3A. This initial increase in photosynthetic activity indicates the time needed for expansion of leaves—it takes about 16 days ($=x_1$) to reach the maximum photosynthetic ability, and after the peak, $f(x)$ decreases linearly and becomes zero at $x = x_{\max}$. The optimal chemical

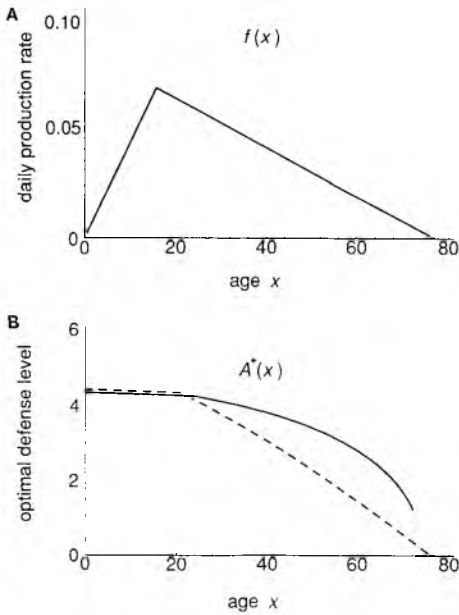


FIG. 3. The optimal age-specific defense level $A(x)$ for a production function $f(x)$ with initial increase with age. (A) The net production function $f(x) = f_{\max}x/x_1$ for $x < x_1$, $f(x) = f_{\max}(x_{\max} - x)/(x_{\max} - x_1)$ for $x_1 \leq x < x_{\max}$, and $f(x) = 0$ $x \geq x_{\max}$, where $f_{\max} = 0.0685$, $x_1 = 15.7$, and $x_{\max} = 77$. The area under the curve $f(x)$ is the same as in Fig. 1. (B) The optimal chemical concentration computed by the model. Solid curve is for exponential mortality function $h(A)$ (the same as the solid curve in Fig. 1A), and broken curve is for hyperbolic $h(A)$.

defense can be calculated using the same procedure as above and is shown in Fig. 3B. Solid and broken curves are for exponential and herperbolic $h(A)$. The overall shape of the curve $A(x)$ is not very different from the case with linearly decreasing $f(x)$.

In van Dam *et al.* (1996) we also examine $f(x)$ of curved decline, instead of a linear decrease with x , causing earlier decrease in the optimal chemical protection $A(x)$.

Parameter Dependence

Sensitivity analyses are illustrated in Figs. 4A through 4F. We examined the optimal solution by modifying the parameters (a , b , c , h_0 , f_0 , and x_{\max}) one by one from the standard case given by a solid curve in Fig. 1B. Since the general shape of the $A(x)$ did not change much, we examine the defense chemical concentration included in a new leaf. Each of Figs. 4A through 4F is composed of three graphs; the defense level for new leaves $A(0)$ is illustrated in the top graphs, the relative cost of defense among total cost

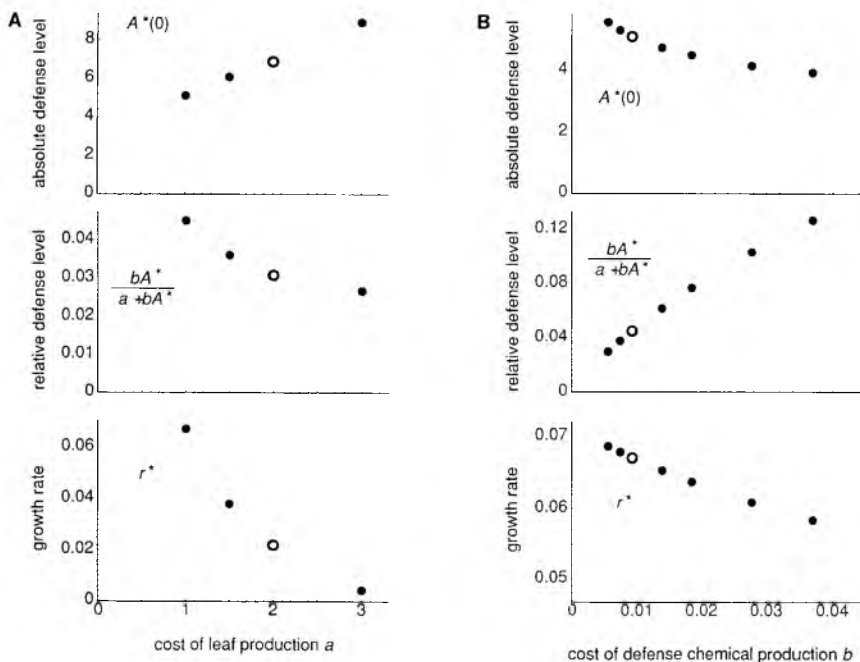


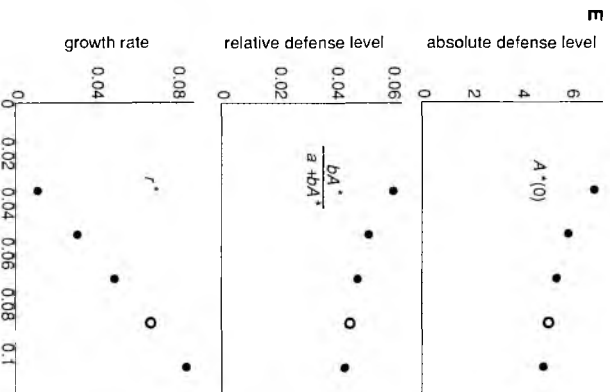
FIG. 4. Sensitivity analysis. We examined the model by modifying each of six parameters (a, b, c, h_0, f_0 , and x_{\max}) one by one from the standard given by the solid curve in Fig. 2B. Top panels indicate the defense level for new leaves $A(0)$; middle panels indicate relative cost of defense among total new leaf production $bA(0)/(a+bA(0))$; and bottom panels indicate the exponential growth rate r^* . Open circles indicate the result for the standard parameter set, and filled circles represent the results corresponding modified parameter sets. Horizontal axis is the cost of leaf production a , the cost of defense chemical production b , the effectiveness of chemical defense c , the dependency on herbivory intensity h_0 , the productivity of the habitat f_0 , and the lifetime of leaves x_{\max} .

of leaf production ($bA(0)/(a+bA(0))$) is illustrated in the middle graphs, and the growth rate r^* is illustrated in the bottom graphs.

Figure 4A illustrates the model's dependency on the cost of leaf production a . Open circles indicates the standard parameter set, and solid circles are for the results with a modified parameter. As a increases, the absolute defense level, indicated by $A(0)$, increases, but the relative defense level, $bA(0)/(a+bA(0))$ decreases, and the growth rate r^* decreases sharply.

Figure 4B shows the sensitivity to b , the cost of defense chemical production. Absolute defense level decreases with the cost b but rather slowly. The relative energetic fraction invested to defense in new leaves increases almost linearly with b . The growth rate r^* decreases with b but more slowly than r^* decreases with a , probably because the cost of producing defense chemical is itself not a large fraction of energetic investment for the plant.

effectiveness of chemical defense c



dependency to herbivory intensity h_0

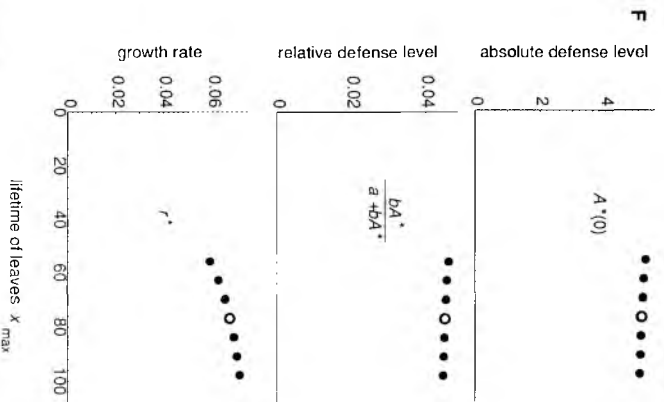


FIG. 4—Continued

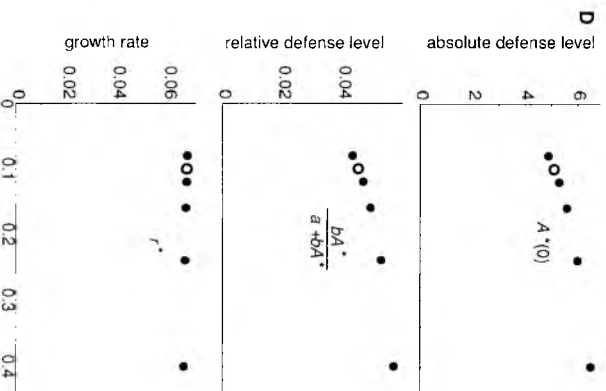
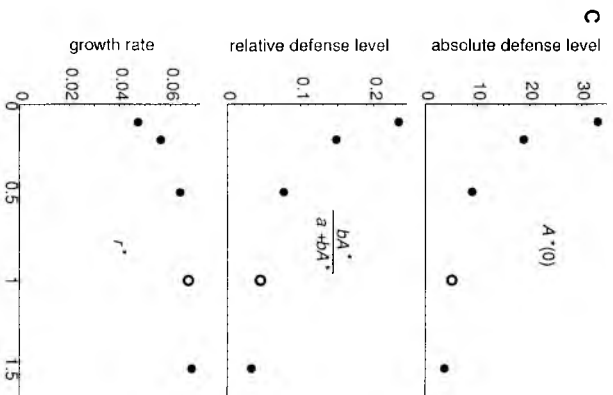


Figure 4C illustrates the sensitivity to c , the effectiveness of chemical defense. The effort of chemical defense, both absolute and relative measures, sharply declines with c . The plant growth rate increases with c . The plant need not invest a lot to defense if it is very effective.

Figure 4D indicates the dependency on herbivory intensity h_0 . It is rather surprising to see that both absolute and relative measures of defense effort are relatively insensitive to the increase in herbivore intensity, although both decrease with h_0 . An increase in the herbivory level of about five times results in about a 25% increase in the defense level. The growth rate r^* also decreases slowly with h_0 .

Figure 4E illustrates the sensitivity to the productivity of the habitat f_0 . As f_0 increases, both absolute and relative defense effort decrease, which is probably caused by the quick increase in the plant growth rate r^* with f_0 . Coley *et al.* (1985) suggest that the optimal defense level for a growing plant should be inversely proportional to the growth rate or the productivity of the habitat. Slow growing plants tend to invest more effort to protection than fast growing plants.

Figure 4F is for the sensitivity to the lifetime of leaves, x_{\max} . Defense level is rather insensitive to x_{\max} but decreases very slowly with it. Naturally, the growth rate r^* certainly increases with x_{\max} .

Fitness Effect of Defense

We may compare two plants with and without defense and discuss the cost and benefit of defense chemical in terms of the fitness effects. In the case illustrated in Table I, the standard case corresponding to the solid line in Fig. 1, the exponential rate of growth is $r^* = 0.0671$ for the optimal defense schedule under the given herbivory pressure. The growth rate of the

TABLE I

	No herbivory	With herbivory
No defense	0.0717	-0.0283
Optimal defense	0.0692	0.0671

Note. The exponential rate of growth is $r^* = 0.0671$ for the optimal defense schedule under a certain herbivory pressure, which is the same as the case generating the solid curve in Fig. 1. The growth rate of the same plant in the absence of herbivory can be computed by Eq. (6) with $h(A) = 0$, and $r = 0.0692$. In contrast the growth rate of a plant without defense, is calculated from Eq. (6) with $A(0) = 0$ and using the same $h(A)$, and the growth rate is negative $r = -0.0283$. In the absence of herbivory, the growth rate of a plant without defense is $r = 0.0717$, which is higher than the plant with defense ($r = 0.0692$).

same plant in the absence of herbivory can be computed by Eq. (6) with $h(A) = 0$, and we have $r = 0.0692$. In contrast, the growth rate of a plant without defense is calculated from Eq. (6) with $A(0) = 0$ and the same $h(A)$, which results in a negative growth rate: $r = -0.0283$ due to severe herbivory. In the absence of herbivory, however, the growth rate of a plant without defense is $r = 0.0717$, which is higher than the plant with defense ($r = 0.0692$). The difference between these two can be regarded as the cost of producing defense chemicals in the absence of herbivory, but it is only about 3.6% of the growth rate. In contrast the difference in the growth rate of plants with and without defense in the presence of herbivory gives the benefit of the protection, and it is so large that the plant without defense cannot grow under the herbivory pressure (a negative r).

THE CASE WITHOUT REALLOCATION

An important assumption of the present model is free reallocation of defense chemical from old to new leaves. The effect of this assumption can be examined by comparing the results with the case in which defense chemical concentration does not change throughout the lifetime of leaves. Then we can treat the chemical concentration $A(x)$ in Eq. (5) as a constant. We have

$$a + bA = \int_0^{x_{\max}} f(x) \exp[-(r + h(A))x] dx. \quad (19)$$

We can regard r in Eq. (19) as a function of A . Then taking derivative of Eq. (19) with respect to A and putting $dr/dA = 0$, we have

$$b = -h'(A) \int_0^{x_{\max}} xf(x) \exp[-(r + h(A))x] dx. \quad (20)$$

By using particular functional forms, we can solve A and r from Eqs. (19) and (20). For example, the optimal defense level constrained to a constant calculated from Eq. (20) is $A^* = 4.856$ for the case corresponding to the solid curve in Fig. 1 (an exponential $h(A)$ and a linear $f(x)$), and $A = 0.990$ for the case corresponding to the broken curve in Fig. 1 (an hyperbolic $h(A)$ and a linear $f(x)$). In both cases, the defense level is lower than the $A(0)$ for the corresponding case in which free reallocation is allowed.

The Malthusian parameter r , or the exponential rate of leaf growth for this constrained case, is certainly smaller than that for unconstrained case of changing A , the latter being more efficient. For example in the case

indicated by the solid curve in Fig. 1 (an exponential $h(A)$ and a linear $f(x)$), $r^* = 0.0671$ with reallocation. In the corresponding case with the optimal fixed defense level has a lower growth rate: $r^* = 0.0678$. In the case shown by the broken curve in Fig. 1, $r^* = 0.0659$ with allocation, and $r^* = 0.0658$ for the optimal fixed defense level. This difference of r^* between the cases with and without reallocation can be called as the selective value of the cost-free reallocation of defense chemical, which allows efficient use of defense chemicals.

DISCUSSION

In this paper we study the optimal level of chemical defense as a function of leaf age for a constantly growing plant. We show that if a plant can reallocate the defense chemical from old leaves to young leaves without loss or cost for transportation, and if the photosynthetic ability of a leaf decreases with its age, the defense level should decrease with leaf age, as observed in *C. officinale* by van Dam *et al.* (1994, 1996). The optimal defense level decreases monotonically with age for all the cases we examined by numerical computation and the defense ends before the age at which the production rate vanishes. However, the details of the age-specific defense level may differ: An exponential mortality-defense function $h(A)$ would produce a rather constantly high defense level more than half of the leaf's lifetime followed by a quick decrease in defense. Especially the final drop of defense level should be sharp (Fig. 2B). In contrast, even if the same $f(x)$ function is used, a hyperbolic $h(A)$ predicts a linear decrease in chemical defense level throughout leaf's lifetime, and there is no sudden drop of protection level. The optimal pattern of age-specific defense $A(x)$ should also depend on the net photosynthesis-age relation $f(x)$, as shown by the contrast between Figs. 1, 2, and 3.

However, in most cases we studied numerically, the overall pattern of optimal $A(x)$ was rather similar, probably because we restricted our numerical analyses only for those cases with functions and parameters that can approximate the experimental data in van Dam *et al.* (1996).

According to sensitivity analyses, illustrated in Fig. 3, defense level, expressed by $A(0)$, the amount of defense chemicals contained in a newly produced leaf, increases with cost of leaf production (a), and herbivory intensity (h_0), but decreases with the cost of defense chemicals (b), the effectiveness of the chemical (c), and productivity (f_0). These results are consistent with a simpler model without considering leaf age structure (Yamamura and Tsuji, 1995).

The theory of optimal chemical defense discussed in this paper is mathematically equivalent to the theory for the evolution of life history strategy.

This is clear if we consider the production of the chemical is the plant's effort to protection, hence to reduce mortality of leaves (but not of the whole individual). A close analogy, or mathematical equivalence, exists between a population of leaves in the present paper and a population of individuals in the life history evolution model. The acquisition of material by photosynthesis and thereby producing new leaves is analogous to the reproduction. In both cases, the optimization criterion is exponential rate of population growth. Analogy is, however, not exact, as in the present model reallocation of material from a leaf to another is included.

It is worth noting that the costate variable $\lambda(x)$, computed as Eq. (C1) in Appendix C, is of the same form as Fisher's reproductive value for an individual of age x . The equivalent to fertility is production minus reallocation of defense chemical ($f(x) - bA(r + h(A))$).

In this paper we assumed that reallocation is costless. However, it is plausible that some fraction of material may be lost during transportation from old leaves to new ones and that transportation would be accompanied by significant energetic cost. We have examined an extreme case in which the cost is very high so that the plant would not try to reallocate the defense chemical once it is produced. Then the plant is forced to use a constant defense level independent of leaf age. The optimal defense level under such a constraint is lower than the youngest leaves for reallocating plants but is higher than old leaves. The fitness for such a constrained plant should be lower than the fitness for a reallocating plant, and the fitness difference between these two cases can be regarded as the selective value of reallocation ability. This selective value becomes larger when plant grows slowly.

The present model includes a number of simplifying assumptions that make the model tractable, and some of these may be removed:

We have assumed that the loss of leaves is caused only by the herbivory expressed by mortality $h(A)$. However, there may be an additional mortality of leaves caused by physical disturbances. Alternatively the mortality of leaves is caused by specialist herbivores that can overcome the chemical defense (van Dam *et al.*, 1995). These damaging factors independent of $A(x)$ can be expressed as an additional mortality of leaves, say m , that are independent of leaf age. Then we should just replace $h(A)$ by $h(A) + m$ throughout the text and the same mathematics hold if we replace r by $r - m$. The optimal age-specific defense $A^*(x)$ is independent of this additional mortality m but the optimal growth rate r simply decreases by m .

We here neglected the seasonal change in the environment in this paper. Yamamura and Tsuji (1995) in contrast analyzed the optimal seasonal schedule of chemical defense, but they did not consider the difference in defense level between old and young leaves. In temperate regions or seasonally dry tropics, plants are living under clear seasonality and we

must consider both the time within the season and the age of leaves to discuss the chemical defense level.

One of the basic assumptions of the model is exponential growth of the whole plant. However, exponential growth is not required for a very long period for the present analysis to apply. Iwasa and Roughgarden (1984) have proven that the vegetative growth pattern realizing the fastest growth rate is the one that achieves the maximum lifetime reproductive success of the whole plant. Even if exponential growth holds only for a finite period of time, we can compute the optimal balance of the different organs of a plant based on the fastest growth rate criterion, which is the same as the one that is the optimal when exponential growth lasts forever.

In the present paper, we only consider carbon as the limiting resource. In spite of that, cost of nitrogen in constructing alkaloid is often regarded more important, as is discussed in detail in a companion paper (van Dam *et al.*, 1996). However, Vrieling and van Wijk (1994) found that PA production in *Senecio jacobaea* was costly only under light limiting conditions, and not under nitrogen limitation, suggesting that the carbon cost of PA is more important than the nitrogen cost.

One of the simplifying assumptions of our model is that the herbivore attack $h(A)$ is a function only of defense chemical, $A(x)$, but is not dependent directly upon leaf age x . However, young leaves contain more nitrogen and less fiber than old leaves, and hence young leaves tend to attract more herbivore attack than old ones if they contain the same amount of defense chemicals. Hence it is more likely that mortality is expressed as $h(A, x)$, which is a decreasing function of both age x and defense chemical concentration $A(x)$. It tends to decrease with age x both direct dependence and indirect dependence through chemical defense.

Distribution of alkaloids over vegetative and reproductive parts is beyond the scope of this article. In *C. officinale* the whole plant dies back after seed production. Reallocation from the senescing leaves may explain the high PA concentrations in flowers and fruits (van Dam *et al.*, 1995).

A potentially important aspect we did not consider in this paper is the evolutionary or adaptive response of herbivores. We treated the herbivore's response simply as a leaf mortality $h(A)$, as a decreasing function of defense chemical concentration. The system of herbivores and their host plants has been considered as an important example of coevolution (Futuyma 1983; Cates 1975; Feeny, 1970, 1976). Coley *et al.* (1985), however, give a simpler picture in which most behavior of plant-herbivore systems can be understood mostly as the optimal resource allocation of plants under different resource availability, without consideration of the evolutionary response of herbivores a more recent review is given by Feeny, 1992).

Modelling using dynamic optimization is needed to understand and to predict quantitatively the age-specific chemical defense of leaves. One way

to test the model is to estimate all the parameters in the model corresponding to a particular plant population in the field and to compare the model's predictions with the observed defense chemical concentration in leaves. We will develop this enterprise in a separate paper (van Dam *et al.*, 1996).

APPENDIX A

Derivation of Characteristic Equation. Eq. (5)

We first note that Eq. (1) can be solved as

$$n(x, t) = n(+0, t - x) \exp \left[- \int_0^x h(A(y)) dy \right]. \quad (\text{A1})$$

During the exponentially growing phase, the number of newly produced leaves is

$$n(+0, t) = \hat{B} e^{rt}.$$

Using this equation and Eq. (A1), Eq. (3) becomes

$$\begin{aligned} & \hat{B} \exp[rt](a + bA(0)) \\ &= \int_0^{x_{\max}} \left(f(y) - b \frac{dA}{dy} \right) \hat{B} \exp \left[r(t - y) - \int_0^y h(A(z)) dz \right] dy, \end{aligned}$$

and hence we have Eq. (5).

APPENDIX B

Derivation of Basic Theorem of Optimal Life History

Let $A^*(\cdot)$ be the optimal schedule and r^* be the maximum Malthusian parameter. Let $A(\cdot)$ be the suboptimal schedule and r be the Malthusian parameter produced by $A(\cdot)$. Then we have

$$a = G(A^*(\cdot), r^*) \quad \text{and} \quad a = G(A(\cdot), r). \quad (\text{B1})$$

Note that $G(A(\cdot), r)$ given by Eq. (7a) is a decreasing function of r , and that $r^* > r$ by definition. Then we have

$$G(A(\cdot), r^*) \leq G(A(\cdot), r). \quad (\text{B2})$$

Using Eq. (B1), Eq. (B2) becomes Eq. (7b). Equation (7b) states that optimal schedule $A(\cdot)$ can be obtained by the maximization of $G(A(\cdot), r^*)$.

APPENDIX C

Costate variables $\lambda(x)$ can be calculated from differential equation (11) with terminal condition (11) as follows:

$$\lambda(x) = \int_x^{x_{\max}} \{f(y) - bA(r^* + h(A(y)))\} \exp \left[-\int_x^y (r^* + h(A(z))) dz \right] dy. \quad (C1)$$

For each x the optimal level of chemical defense $A(x)$ is the value that maximizes Eq. (14) with $\lambda(x)$, which is computed by Eq. (C1). However, to calculate $\lambda(x)$ at age x , we need to know the trajectory for the future $\{A(y), x \leq y \leq x_{\max}\}$. Hence the optimal schedule is determined from the final age $x = x_{\max}$ to the initial age $x = 0$ moving backward, as is common to dynamic programming (Bellman, 1957).

Subarc of Positive Chemical Defense

Optimal A that maximizes Eq. (14) is either zero or positive. At a positive equilibrium, we have the first and the second derivatives of H with respect to A :

$$\frac{\partial H}{\partial A} = -b(r^* + Ah'(A) + h(A)) S - h'(A) S \lambda = 0, \quad (C2a)$$

$$\frac{\partial^2 H}{\partial A^2} = -b(Ah''(A) + 2h(A)) S - h''(A) S \lambda < 0. \quad (C2b)$$

Equation (C2a) becomes

$$b \left\{ \frac{r^* + h(A(x))}{-h'(A(x))} - A \right\} = \lambda(x). \quad (C3)$$

If we consider an interval in which the optimal strategy is to take a positive A , we have a differential equation (17) in text derived by taking derivative of Eq. (C3) with respect to x and by rewriting it using Eq. (11). We can prove that the sum of the terms within braces in the left-hand side of Eq. (17) is always positive, using second order condition for local optimality given by Eq. (C2b) together with Eq. (C3).

Final Period of No Defense

Because instantaneous mortality $h(A)$ is finite, $r > 0$ and terminal condition is given by Eq. (12), we see that $A(x_{\max}) = 0$ is the optimal solution that maximizes H in Eq. (14) on x_{\max} . Because of continuity, the optimal A is zero over some interval near the maximum age x_{\max} . Leaves of age in

such an interval (say from x_e to x_{\max}) are no longer protected by the chemical. During this period, H for $A=0$ is larger than that for any positive A . The final period of no defense is rather very short in most of numerical examples we examined, as shown later.

However, as age x moves backward, λ increases following Eq. (C1). At a certain age $x = x_e$, λ is sufficiently large so that H for a positive A may become as large as H for $A=0$. Before critical age x_e , the optimal path is subarc of internal optimum of positive chemical defense. On this critical age, where switching occurs, we have the following equation:

$$H(A) - H(0) = -bA(r^* + h(A)) - (r^* + h(A))\lambda + (r^* + h(0))\lambda = 0. \quad (C4)$$

Equations (C3) and (C4) give two independent equations for critical size $\hat{A} = A(x_e)$ and the critical level of costate variable $\lambda(x_e)$, which can be determined by Eq. (15).

From the critical costate variable, we can compute x_e , the actual age of ending of chemical protection, from Eq. (16), which is Eq. (C1) with $A(x) = 0$ for x larger than x_e . The optimal level of defense chemical $A(x)$ can be calculated by integrating differential equation (17) from $x = x_e$ backward using the terminal condition of $A(x_e) = \hat{A}$. Once we know $A(x)$, we can compute costate variable $\lambda(x)$ from Eq. (C1) and stable leaf age distribution $S(x) = \exp[-r^*x - \int_0^x h(A(z)) dz]$.

We can confirm that all the necessary condition are satisfied by this solution composed of singular subarc (from 0 to x_e) followed by the interval of no Protection (after x_e).

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