YIELD FOR ANNUAL PLANTS AS AN ADAPTIVE RESPONSE

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ABSTRACT. Because of the adaptive nature of biological systems, it follows that a given system may undergo a significant adaptive response when controlled by an imposed management program. In such cases, models used for management purposes should include the adaptive effect. An investigation of this effect is made here. Analysis is confined to a model for the growth of asexual annual plants under a limited nutrient resource and the adaptive response of this model to constant harvesting and mixed cropping.

Adaptive parameters are identified in the model. The value of these parameters is determined from one situation to the next by employing the hypothesis that an individual plant adapts by maximizing individual fitness. It is found that under constant harvesting the adaptation process will tend to make a species a less efficient user of resources. This means that for a given limited nutrient level the species has less potential yield under harvesting stress than without it.

Mixed cropping is of interest as a means to alleviate pest damage. A change in yield due to an adaptive response due to competition between plants for nutrients under mixed cropping is examined for some simple situations and it was found that again adaptation tends to reduce yield of all species in the mixed crop over what would be obtainable if adaptation were not to take place. In a competitive situation the resultant reduced yields represent a direct consequence of maximizing a specie's individual fitness. This effect, if found to be predictable, could be significant for the proper management of untended ecosystems such as rangelands.

1. **An Annual Plant Model.** The following model is obtained from the more detailed development presented by Trenbath and Vincent (1979). It will be assumed here that each species of plant is asexual. Specifically, it is assumed that the characteristics of an individual plant of species i is the same as for all plants of species i during a given growing season on a given identified plot of land. It is further assumed that these characteristics may change from season to season in response to environmental changes by the process of genetic concentration as described by Pimentel (1968).

Let there be growing in a given plot of land i species of plant. A given identified characteristic, common within a species, but varying from species to species will be identified for a given species by the sub-

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script i. A mass property attributed to the mth plant of the ith species will be designated by the subscript im. Let p represent plant biomass and n mass of nutrient in a plant. The sunlight conversion efficiency for a plant is found to be a function of nutrient concentration n_{im}/p_{im}, moreover, sunlight conversion efficiency is usually found to be maximum over a range of concentrations. Thus, while a plant may operate at a maximum sunlight conversion efficiency, the range of nutrient concentrations which make this possible allows for the identification of an adaptive parameter.

Assume that all plants within a given species maintain a specific value for the nutrient concentration defined by

$$(1) \qquad\qquad c_i = n_{im}/p_{im}.$$

Then the demand for nutrient is given by

$$(2) \qquad\qquad \dot{n}_{im} = c_i \dot{p}_{im}$$

where the dot refers to the derivative with respect to time t. Let B represent the amount of nutrient taken in by a plant per unit root mass r per unit time. Then the rate at which the root system can supply nutrient is given by $B_i r_{im}$. If the demand is exactly met by the supply, it follows from (2) that

$$(3) \qquad\qquad \dot{p}_{im} = (B_i/c_i)r_{im}.$$

Equation (3) should be valid during the early stages of growth, before a canopy has developed and plant growth slowed due to sunlight limitations or other factors. When this happens the root system could supply nutrient in excess of the demand.

The factor B_i will depend on the nutrient density of the soil N. It is assumed here that

$$(4) \qquad\qquad B_i/BMAX_i = e_i N/(1 + e_i N)$$

where $BMAX$ is the maximum value for B and e is a root foraging factor. Note that according to (4) other plants do not interfere with the foraging capabilities of a given plant. If a plant allocates a given constant fraction u_i of total growth to the root so that

$$(5) \qquad\qquad r_{im} = u_i p_{im}$$

then upon introducing (4) into (3) the following model for plant growth is obtained

$$(6) \qquad\qquad \dot{p}_{im} = G_i e_i N p_{im}/(1 + e_i N)$$

where

(7) $$G_i = BMAX_i u_i / c_i.$$

It is assumed that G_i is constant with time, however, Trenbath, et al. (1979) suggest that a tradeoff exists between G_i and e_i to the effect that if G_i is large then e_i must be small and vice versa. This effect is not unexpected as each of the parameters are related to an efficiency of operation. The tradeoff simply expresses the difficulty in being efficient with all aspects of development simultaneously. This effect is introduced here by assuming that

(8) $$G_i^2 = 1/e_i.$$

Thus from (7) and (8) it follows that

(9) $$G_i e_i = \gamma_i c_i$$

where

(10) $$\gamma_i = 1/(BMAX_i \, u_i).$$

Assume now that at the beginning of the growing season, the soil has a nutrient concentration $N(0)$ and that no nutrients are added to the soil during the growing season. Assume further that the initial concentration is sufficiently low so that $e_i N \ll 1$ for all i. This assumption is compatible with the condition that the plants are growing in a nutrient limited environment and hence is consistent with the supply equals demand assumption which remains valid as long as other factors such as sunlight are not limiting. Using (9) equation (6) now becomes

(11) $$\dot{p}_{im} = \gamma_i c_i N \, p_{im}.$$

Consider now all the plants of a given species i in the plot. Assume that there are q such plants. Equation (7) governs the growth of each of these plants. By adding the growth equation for each plant and letting

(12) $$p_i = (p_{i1} + p_{i2} + \cdots + p_{iq})$$

equation (11) becomes

(13) $$\dot{p}_i = \gamma_i c_i N \, p_i.$$

Under the supply equals demand assumption nutrient is depleted from the soil according to

(14) $$\dot{N} = - \sum_{i=1}^{r} c_i \dot{p}_i$$

where the summation is taken over the number of species r in the plot. The nutrient concentration in the soil at any time t is given by

$$(15) \qquad N(t) = N(0) - \sum_{i=1}^{r} c_i[p_i(t) - p_i(0)]$$

where $p_i(o)$ is the biomass of all the plant seedlings of species i at the beginning of the growing season. Let

$$(16) \qquad \ell = N(0) + \sum_{i=1}^{r} c_i p_i(0)$$

then equation (15) may be written

$$(17) \qquad N = \ell - \sum_{i=1}^{r} c_i p_i.$$

Substituting (17) into (13) yields

$$(18) \qquad \dot{p}_i = \gamma_i c_i p_i \left(\ell - \sum_{i=1}^{r} c_i p_i \right).$$

In what follows, fitness of a given plant is taken to be proportional to the biomass of the plant at the end of the growing season. If all plants of a given species start with the same initial biomass $p_i(0)$, then the biomass of any plant within that species will be directly proportional to the yield $p_i(T)$ where T is the time corresponding to the end of the growing season. Growth under (18) implies the existence of "optimum" values for the adaptive parameters c_i. Suppose the initial values for $p_i(0)$ were fixed. Clearly by varying c_i the yields $p_i(T)$ will also vary. The particular value of c_i utilized by a plant should reflect the result of the process of maximizing fitness.

2. **Adaptation in Monoculture.** With only one species present in a monoculture $(r = 1)$ the subscripts may be dropped and equation (18) becomes

$$(19) \qquad \dot{p} = \gamma c p(\ell - cp).$$

Because of the asexual assumption, every plant will have the same value for the adaptive parameter c at the beginning of each season. There are no mutant plants present within a season, but the value of c may change from season to season by the process of genetic concentration. This would be possible if, for example, c represented the mean value of nutrient concentration. At the end of the season each plant would pro-

duce a crop of seeds in which the genetic trait for nutrient concentration has the same distribution and mean as the plant itself. The mean for the entire species could then shift from season to season due to the higher survival rate of the seeds with the more favorable value of c.

Since no mutant plants are present within a season, the usual optimization concepts may be used to obtain c. Namely, c will be determined by maximizing $p(T)$.

Let $r = \gamma c \ell$ and $K = \ell/c$ then equation (19) may be written as

$$(20) \qquad\qquad \dot{p} = \frac{r}{K}(K - p)p$$

which is the familiar logistics equation, except that here the carrying capacity K and the intrinsic growth rate r are identified in terms of the adaptive parameter c. Note the tradeoff between r and K. If r is small then K will be large resulting in slow growth with large carrying capacity.

Let $x = p/\ell$ and $\tau = t\gamma\ell$ then equation (20) becomes

$$(21) \qquad\qquad dx/d\tau = cx(1 - cx)$$

which is easily integrated and evaluated at the final time T to yield

$$(22) \qquad cx(T) = \exp(cT)/((cx(0))^{-1} - 1 + \exp(cT)).$$

Assuming $x(o)$ to be fixed, the necessary condition for maximizing $x(T)$ is obtained by setting the partial derivative of $x(T)$ with respect to c equal to zero to obtain

$$(23) \qquad\qquad cx(0) = cT/(cT - 1 + \exp(cT)).$$

For a given value of cT, values for $cx(o)$ and $cx(T)$ are obtained from (23) and (22). It follows then that one can calculate $x(T)/x(o)$ and $T/x(o)$ from

$$(24) \qquad\qquad x(T)/x(0) = cx(T)/cx(0)$$

$$(25) \qquad\qquad T/x(0) = cT/cx(0).$$

Equation (23) represents a necessary condition for determining the value of the adaptive parameter c which will maximize final yield $x(T)$. The value of c as determined by (23) is seen to depend upon the length of the growing season T and the initial number of sites $x(o)$. These latter two quantities may be thought of as the environmental inputs to the system. The effect of varying the ratio of these inputs on the optimum value of c as well as yield $x(T)$ are obtained from equations (22)–(25) and are plotted in Figures 1–3 designated as the "monoculture" case.
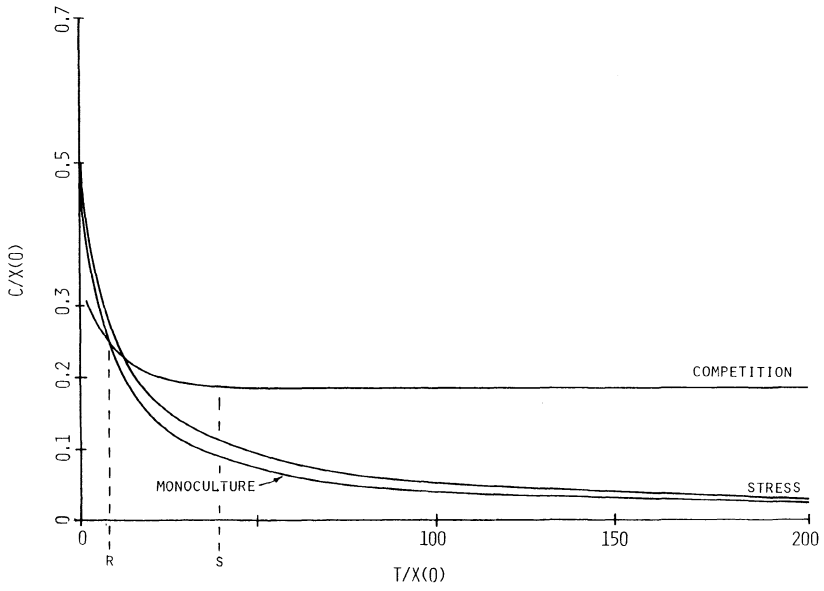
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Figure 1.
Variation in the adaptive parameter with length of growing season.
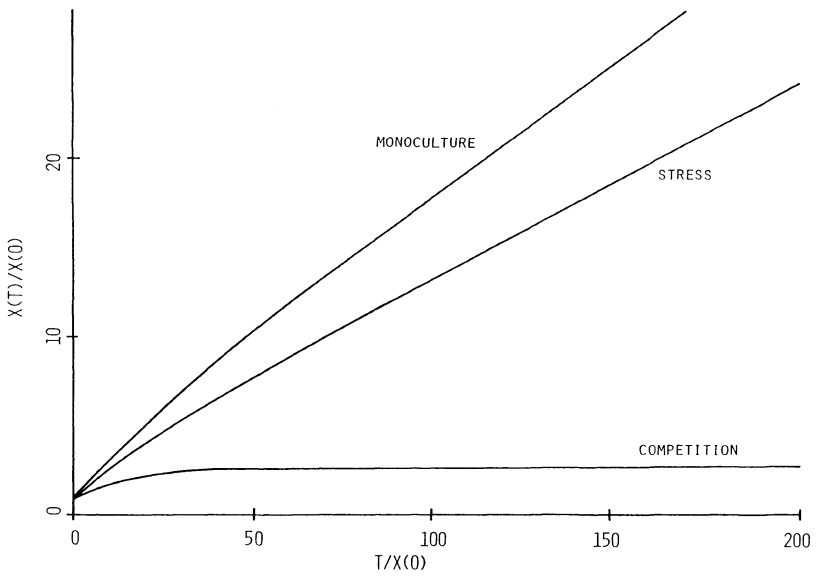

Figure 2.
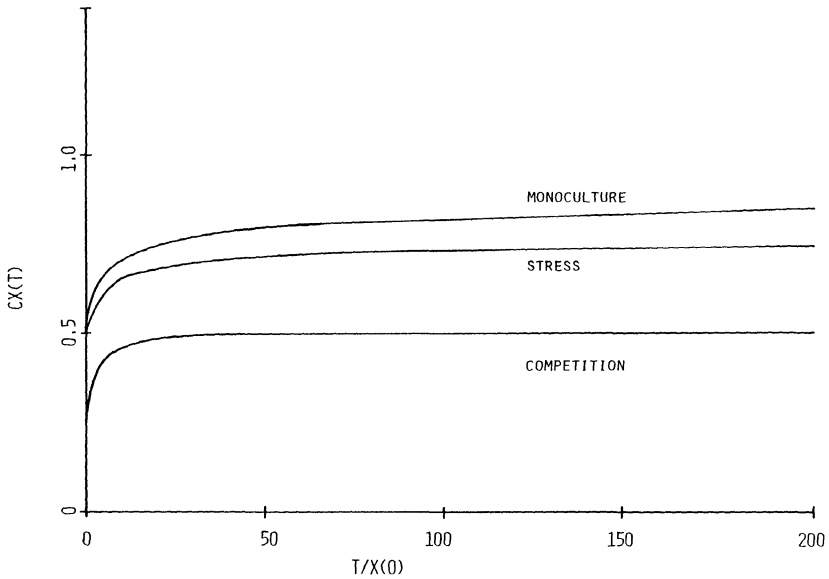Variation in yield with length of growing season.

Figure 3.
Variation in soil nutrient utilization with length of growing season.

The effect of environmental conditions on the adaptive parameter and yield is easily determined from these curves. Note, for example, if the initial number of sites $x(o)$ is held constant then from Figure 1 it follows that increasing the growing season will decrease c. That is, a given species should tend toward K selection when the growing season is long and should tend toward r selection when the growing season is short. From Figure 2, it follows that lengthening the growing season most favorably increases yield. The effect of the length of the growing season on the product $cx(T)$ is illustrated in Figure 3. By examining the limit $T/x(o) \to \infty$ it follows from (22) that $cx(T) \to 1$. The product $cx(T)$ is equal to the fraction of soil nutrient which has been utilized during the growing season. Note that for very short growing seasons at least half of the total soil nutrient is utilized. This fraction very rapidly rises to about 80% and then very slowly increases with further increases in T.

3. **Adaptation Under Stress.** The effect of stressing a species of plant growing in monoculture may be simulated by adding a harvesting term to equation (21)

$$(26) \qquad dx/d\tau = cx(1 - cx) - sx.$$

For example, the term sx could represent the effect of cattle grazing on a pasture where s would represent the size of the herd. Equation (26) is easily integrated and evaluated at the final time T to yield

(27)
$$cx(T) = \exp(aT)/((cx(0))^{-1}$$
$$- c/a + (c/a)\exp(aT))$$

where $a = c - s$. Note that c must be greater than s for growth to occur. In what follows it is assumed that $c > s$. Assuming again $x(o)$ is fixed, the necessary condition for maximizing $x(T)$ is obtained by setting the partial derivative of $x(T)$ with respect to c equal to zero to obtain

(28)
$$cx(o) = aT/(cT - (2 - c/a)$$
$$+ (2 - c/a)\exp(aT)).$$

For given values of cT and c/a, equations (27) and (28) may be used to evaluate $cx(T)$ and $cx(0)$ so that equations (24) and (25) may be used again for computing tthe ratios $x(T)/x(0)$ and $T/x(0)$. The results of these calculations for $c/a = 1 + s/a = 1.2$ are illustrated in Figures 1–3 as the curves labeled "stress". Note from Figure 1 that for $x(o)$ fixed, stress will increase c for all values of T. This will make the plant a less efficient user of soil nutrient or equivalently, the plant tends toward r selection under stress. There is a corresponding drop off in yield as shown in Figure 2. Note that in this calculation of yield no account is taken of the biomass consumed by the herd. Figure 3 shows that the product $cx(T)$ increases with $T/x(o)$ ultimately approaching 1. Thus for very long growing periods all of the soil nutrient will be utilized.

   4. **Adaptation Under Competition.** Assume now that two different species are growing under the limited nutrient hypothesis used to obtain equation (18). Specifically, equations (18) become

(29) $$\dot{p}_1 = \gamma_1 c_1(\ell - c_1 p_1 - c_2 p_2)p_1$$

(30) $$\dot{p}_2 = \gamma_2 c_2(\ell - c_1 p_1 - c_2 p_2)p_2$$

Let $x_1 = p_1/\ell$, $x_2 = p_2/\ell$, $\tau = \ell\gamma_1 t$, and $K = \gamma_2/\gamma_1$, then the above equations may be written in the following non-dimensional form

(31) $$dx_1/d\tau = c_1 x_1(1 - c_1 x_1 - c_2 x_2) = f_1(x_1, x_2, c_1, c_2)$$

(32) $$dx_2/d\tau = Kc_2 x_2(1 - c_1 x_1 - c_2 x_2) = f_2(x_1, x_2, c_1, c_2)$$

where K is a fixed constant associated with the given species and c_1 and c_2 are parameters subject to adaptation by the species. If values for c_1 and c_2 are specified and the initial values $x_1(o)$ and $x_2(o)$ given, then

the integral solutions to (31) and (32) may be designated by functions of the form

$$(33) \qquad x_1 = X_1(t, c_1, c_2)$$

$$(34) \qquad x_2 = X_2(t, c_1, c_2)$$

with fitness for each species measured by the amount of plant biomass at the time T, then the question remains as to what values of c_1 and c_2 will "maximize" fitness. Clearly the fitness of either species depends on *both* c_1 and c_2.

An evolutionarily stable strategy for a single population genotype is defined by J. M. Smith (1976) as one which, when common, will be fitter than any mutant. This definition is satisfied when the fitness of an individual adopting strategy J when the majority of the group is adopting strategy I is less than the fitness under strategy I. This concept can be extended to the case of two asexual plant species under consideration here. Instead of considering a mutant within a given population genotype, a comparison of fitness must be made between species. The fitness of one species employing a given evolutionarily stable strategy must be greater than its fitness under any other strategy when the other species is employing its evolutionarily stable strategy and vice versa.

Consider the two plant species in competition for limited resources with initial conditions fixed so that fitness at time t is given by (33) and (34). If $c_1{}^*$ is the strategy employed by all plants of species 1 and $c_2{}^*$ the strategy employed by all plants of species 2 then $c_1{}^*$ and $c_2{}^*$ will be evolutionarily stable if at time T

$$(35) \qquad X_1(T, c_1{}^*, c_2{}^*) > X_1(T, c_1{}^*, c_2) \qquad c_2 \neq c_2{}^*$$

and

$$(36) \qquad X_2(T, c_1{}^*, c_2{}^*) > X_2(T, c_1{}^*, c_2) \qquad c_2 \neq c_2{}^*$$

Values of $c_1{}^*$ and $c_2{}^*$ which satisfy (35) and (36) also satisfy the Nash (1951) equilibrium solution concept.

A necessary condition for (35) and (36) to be satisfied is that

$$(37) \qquad \frac{\partial X_1}{\partial c_1} = \frac{\partial X_2}{\partial c_2} = 0.$$

However, since

$$(38) \qquad dX_i/d\tau = f_i(X_i, c_i) \quad i = 1, 2$$

it follows that

(39)
$$\frac{\partial}{\partial c_j}\left(\frac{\partial X_i}{\partial \tau}\right) = \frac{d}{d\tau}\left(\frac{\partial X_i}{\partial c_j}\right)$$

$$= \sum_{K=1}^{2}\left(\frac{\partial f_i}{\partial x_K}\frac{\partial X_K}{\partial c_j}\right) + \frac{\partial f_i}{\partial c_j} \quad i, j = 1, 2$$

Let $x_3 = \partial X_1/\partial c_1$, $x_4 = \partial X_2/\partial c_1$, $x_5 = \partial X_1/\partial c_2$, $x_6 = \partial X_2/\partial c_2$ then equations (39) become

(40)
$$dx_3/d\tau = (\partial f_1/\partial x_1)x_3$$
$$+ (\partial f_1/\partial x_2)x_4 + \partial f_1/\partial c_1$$

(41)
$$dx_4/d\tau = (\partial f_2/\partial x_1)x_3$$
$$+ (\partial f_2/\partial x_2)x_4 + \partial f_2/\partial c_1$$

(42)
$$dx_5/d\tau = (\partial f_1/\partial x_1)x_5$$
$$+ (\partial f_1/\partial x_2)x_6 + \partial f_1/\partial c_2$$

(43)
$$dx_6/d\tau = (\partial f_2/\partial x_1)x_5$$
$$+ (\partial f_2/\partial x_2)x_6 + \partial f_2/\partial c_2.$$

Boundary conditions for these equations are obtained from (37) above

(44) $$x_3(T) = x_6(T) = 0$$

and from the fact that the initial state is not a function of c_1 or c_2, that is

(45) $$x_3(0) = x_4(0) = x_5(0) = x_6 = 0.$$

The necessary condition (37) may be satisfied by choosing c_1 and c_2 and then simultaneously integrating (31), (32) starting from the initial values $x_1(o)$ and $x_2(o)$ along with equations (40)–(43) under the initial conditions (45) until time T. If the boundary conditions (44) are met, then the values chosen for c_1 and c_2 satisfy the criteria (37).

Results for this case are also illustrated in Figures 1–3 by the curves labeled "competition". In order to obtain a direct comparison with previous results the competition curves were evaluated using $x_1(0) = x_2(0)$ and $K = 1$. Under these conditions both species respond identically. Thus c, $x(0)$ and $x(T)$ are the same for both species and no subscript is needed.

The effect of competition on the adaptive parameter c is illustrated in Figure 1. Assume that $x(0)$ is held constant. Then the overall effect of increasing the growing season is to decrease c just as in the mono-

culture case. However, this is only true up to a point as for values of $T/x(0)$ greater than s (about 40) the value for $cx(0)$ remains constant. Note that there is only one growing season length r in which the value of c for mixture and monoculture are the same. For short growing seasons with $T/x(0) < r$ the effect of competition is to decrease c (tendency toward K selection) and for longer growing seasons with $T/x(0) > r$ the effect of competition is to increase c (tendency toward r selection).

Figure 2 illustrates that the result of competition is to noticeably decrease yield. For $T/x(0) > s$ there is no increase in yield for an increase in growing season. This effect is explained by Figure 3. Note that for $T/x(0) > s$, $cx(t) \cong .5$. Since this value is obtained by each plant, clearly the nutrient level in the soil has been depleted $(2cx(T) \cong 1)$ and no further increase in the growing season can produce further plant growth. This movement toward r selection for $T/x(0) > r$ was sufficiently large so that the plants quickly depleted the available nutrient. Competition resulted in gluttony, leaving no prospect for increasing yields by increasing the growing season beyond s. Compare this result with the monoculture case where prudence can afford to prevail. In this case movement toward K selection with increases in growing season results in a corresponding increase in yield.

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