

Multiple Switches between Vegetative and Reproductive Growth in Annual Plants

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A model of growth and reproduction in annual plants was developed by Cohen (1971, *J. Theor. Biol.* 33, 299-307) to determine the allocation strategy which maximizes seed yield. The model divides the plant into vegetative and reproductive parts and predicts that yield is maximized by a strategy consisting of a switch from purely vegetative to strictly reproductive growth. We generalize Cohen's model to include vegetative and reproductive loss terms. Both growth and loss rates are allowed to vary with time. Using optimal control theory we find that seed yield is maximized by a strategy consisting of multiple switches between vegetative and reproductive growth, for certain ranges of the model parameters. In natural systems a predictable vegetative loss burst may be necessary to promote multiple switches.

Theoretical studies of the relationship between seed yield and the timing of reproduction in annual plants suggest that seed output is maximized by an allocation strategy consisting of a single switch from purely vegetative to strictly reproductive growth (Cohen, 1971; Denholm, 1975). The present paper uses optimal control theory to explore the possibility that seed yield may be maximized by multiple switches between vegetative and reproductive growth under certain environmental conditions. Optimal control theory has been used to explore reproductive strategies by Denholm (1975), Mirmirani and Oster (1978), and Oster and Wilson (1978).

The prediction of a single switch in annuals was first made by Cohen (1971) based on the following assumptions:

- (1) Products of photosynthesis are allocated between the vegetative part (leaves, stems and roots), and the reproductive part (the nonphotosynthesizing part of the reproductive structure).
- (2) Net photosynthate production is proportional to the weight of the vegetative body. The constant of proportionality, called the vegetative growth constant, itself does not change through time.
- (3) No vegetative or reproductive losses are incurred.

(4) Cumulative reproductive yield is to be maximized at the end of a season of given length. The switching time which maximizes seed yield is then a function of season length and the vegetative growth constant.

Denholm (1975) extended Cohen's work and presented a proof that seemed to show that seed yield is maximized by a single switch to reproduction even if time dependent vegetative losses occur. The proof consisted of two parts: (1) the use of optimal control theory to show that the strategy which maximizes yield is one consisting of alternating vegetative and reproductive growth phases, (2) a demonstration that in the strategy which maximizes yield no *net* growth occurs in any vegetative phase following the initial switch to reproduction. Because any vegetative phase following the initial vegetative phase cannot result in net growth it was inferred that reproduction is maximized by a *single* switch from vegetative to reproductive growth. In this paper we point out that although both parts of Denholm's proof are correct, the interpretation ruling out multiple switches is incorrect. Specifically, strategies that maximize seed yield can show several vegetative phases even though it remains true that the plant shows no *net* growth in vegetative phases after the first vegetative phase. We present examples where such multiple switches maximize seed yield and we derive necessary and sufficient conditions for their occurrence.

MODEL

We consider the following linear model of plant growth and allocation to reproduction.

$$\dot{x}_1 = r_1(t) u(t) x_1 - \mu(t) x_1, \quad t \text{ in } [0, T], \quad (1)$$

$$\dot{x}_2 = r_2(t)(1 - u(t)) x_1 - v(t) x_2, \quad 0 \leq u(t) \leq 1, \quad (2)$$

$$x_1(0) > 0, x_2(0) = 0.$$

where x_1 is the vegetative weight, x_2 is the reproductive weight, $r_1(t)$ is the vegetative growth constant, $r_2(t)$ is the reproductive growth constant, $\mu(t)$ is the vegetative loss constant and $v(t)$ is the reproductive loss constant. (Both growth and loss constants are time dependent.) The control, $u(t)$, is the fraction of net photosynthate allotted to vegetative growth. Typically $r_1(t) > 0$ and $r_2(t) > 0$, otherwise vegetative growth and seed production are not possible. Also, $\mu(t)$ and $v(t)$ are nonnegative unless reproductive parts contribute to photosynthesis. In the latter case $v(t)$ may be negative.

For any $r_1(t)$, $r_2(t)$, $\mu(t)$ and $v(t)$ it is possible to calculate the optimal control, $u^*(t)$, which maximizes $x_2(T)$, the seed yield at time T by using Pontryagin's maximum principle (Intriligator, 1971). The procedure may be

applied to the model as follows. To maximize $F = x_2(T)$ we define the Hamiltonian

$$H = [r_1(t) x_1 y_1(t) - r_2(t) x_1 y_2(t)] u(t) - \mu(t) x_1 y_1(t) + [r_2(t) x_1 - v(t) x_2] y_2(t), \quad (3)$$

where the costate variables $y_1(t)$ and $y_2(t)$ are given by

$$\dot{y}_1(t) = -\frac{\partial H}{\partial x_1} = [r_2(t) y_2(t) - r_1(t) y_1(t)] u(t) + \mu(t) y_1(t) - r_2(t) y_2(t), \quad (4)$$

$$\dot{y}_2(t) = -\frac{\partial H}{\partial x_2} = v(t) y_2(t), \quad (5)$$

$$y_1(T) = \frac{\partial F}{\partial x_1} = 0, \quad (6)$$

$$y_2(T) = \frac{\partial F}{\partial x_2} = 1,$$

$x_2(T)$ is then maximized by the $u(t)$ which maximizes H . Because the Hamiltonian is linear in the control variable, $u^*(t)$, the allocation strategy which maximizes seed yield alternates between periods of pure vegetative and pure reproductive growth. By inspection of the term in brackets multiplying $u(t)$ in (3) we deduce that when

$$r_1(t) y_1(t) > r_2(t) y_2(t), \quad u^*(t) = 1, \quad (7a)$$

indicating vegetative growth, and when

$$r_1(t) y_1(t) < r_2(t) y_2(t), \quad u^*(t) = 0, \quad (7b)$$

indicating reproductive growth. Switches in allocation should occur at the intersections of $r_1(t) y_1(t)$ and $r_2(t) y_2(t)$ for maximum seed production.

RESULTS

Because the boundary conditions on the costate variables, y_1 and y_2 , are applied at the end of the season, T , the conditions giving switches in $u^*(t)$ can be determined sequentially, working backwards in time from T .

The following results are derived in Appendices I and II. We first note some points concerning the optimum strategy.

1. The optimal strategy, $u^*(t)$, which maximizes $x_2(T)$ always includes a final reproductive interval, $[t, T]$.

2. The optimal allocation strategy, $u^*(t)$, consists of at least one vegetative phase ($u^*(t) = 1$) followed by a final reproductive phase ($u^*(t) = 0$) if and only if at some time, t_3 , in $(0, T)$,

$$r_1(t_3) y_1(t_3) = r_2(t_3) y_2(t_3) \quad (8a)$$

and

$$\mu(t_3) - r_1(t_3) + \frac{\dot{r}_1(t_3)}{r_1(t_3)} < v(t_3) + \frac{\dot{r}_2(t_3)}{r_2(t_3)}. \quad (8b)$$

(See Appendix I.)

Furthermore, if $r_2(t) = \alpha r_1(t)$ where α is a constant of proportionality then $\dot{r}_2(t) = \alpha \dot{r}_1(t)$ and (8b) reduces to

$$r_1(t_3) - \mu(t_3) > -v(t_3). \quad (9)$$

We offer these results.

Result I

The optimal allocation strategy, $u^*(t)$, includes an additional earlier switch from reproductive ($u^*(t) = 0$) to vegetative growth ($u^*(t) = 1$) if and only if at some time t_2 in $(0, t_3)$

$$\ln \left[\frac{r_1(t_3) r_2(t_2)}{r_1(t_2) r_2(t_3)} \right] + \int_{t_2}^{t_3} [\mu(t) - r_1(t)] dt = \int_{t_2}^{t_3} v(t) dt \quad (10a)$$

and

$$\mu(t_2) - r_1(t_2) + \frac{\dot{r}_1(t_2)}{r_1(t_2)} > v(t_2) + \frac{\dot{r}_2(t_2)}{r_2(t_2)}. \quad (10b)$$

As before t_3 denotes the time of the final switch from $u^*(t) = 1$ to $u^*(t) = 0$. (See Appendix II for derivation.)

If $r_2(t) = \alpha r_1(t)$, where α is a constant of proportionality, then (10) reduces to

$$\int_{t_2}^{t_3} [\mu(t) - r_1(t)] dt = \int_{t_2}^{t_3} v(t) dt \quad (11a)$$

and

$$\mu(t_2) - r_1(t_2) > v(t_2). \quad (11b)$$

Result II

If an interval of vegetative growth ($u^*(t) = 1$ in $[t_2, t_3]$) occurs between two periods of reproductive growth, then the vegetative weight after this interval is

$$x_1(t_3) = x_1(t_2) \frac{r_1(t_3) r_2(t_2)}{r_1(t_2) r_2(t_3)} \exp \left(- \int_{t_2}^{t_3} v(t) dt \right). \quad (12)$$

According to (1), $\dot{x}_1 = [r_1(t) - \mu(t)] x_1$ when $u^*(t) = 1$ and growth is vegetative. Solving for $x_1(t_3)$ in terms of $x_1(t_2)$ gives

$$x_1(t_3) = x_1(t_2) \exp \left(- \int_{t_2}^{t_3} [\mu(t) - r_1(t)] dt \right). \quad (13)$$

Substituting (10a) into (12) then yields (13).

We note that when $r_2(t) = \alpha r_1(t)$ and $v(t) = 0$, no net growth occurs in $[t_2, t_3]$.

In a similar vein to (8a) and (8b) we have

Result III

Necessary and sufficient conditions for a switch in $u^*(t)$ from 1 to 0 at t_1 , preceding switches at t_2 and t_3 are that

$$r_1(t_1) y_1(t_1) = r_2(t_1) y_2(t_1) \quad (14a)$$

and that

$$\mu(t_1) - r_1(t_1) + \frac{\dot{r}_1(t_1)}{r_1(t_1)} < v(t_1) + \frac{\dot{r}_2(t_1)}{r_2(t_1)}. \quad (14b)$$

EXAMPLES

We offer an example where two vegetative and reproductive phases are predicted by the model. For simplicity we assume that the reproductive growth constant, $r_2(t)$, equals the vegetative growth constant, $r_1(t)$, in this example.

To determine optimal allocation strategies, trajectories of the costate variables, $y_1(t)$ and $y_2(t)$, were determined by integrating (4) and (5) backward from time T . Switches between vegetative and reproductive growth occur where $y_1(t) = y_2(t)$ in the strategy which maximizes seed yield, if $r_2(t) = r_1(t)$.

As a baseline for comparison we begin trajectories of the costate variables corresponding to constant r and μ where also v is taken as zero. See Fig. 1a.

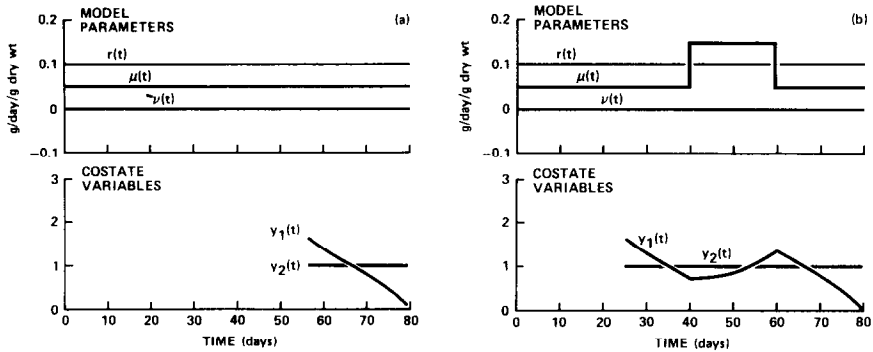


FIG. 1. Trajectories of costate variables. (a) Constant model parameters. (b) A midseason vegetative loss burst. The growth rate constant, $r(t)$, the vegetative loss rate, $\mu(t)$, and the reproductive loss rate, $\nu(t)$, are plotted at the top of each figure. y_1 and y_2 are plotted on the lower half of each figure.

In the illustration $r - \mu > 0$ and therefore $\dot{y}_1(t) < 0$ over the entire season. Hence one intersection of y_1 and y_2 occurs. Thus, seed yield is maximized by a single switch from vegetative to reproductive growth.

An example where reproduction is maximized by multiple switches is presented in Fig. 1b. This example is a specific case of the model analyzed by Denholm (1975). The model parameters have identical values to those of Fig. 1a, except for an intermediate period where $\mu(t) = 1.5r_1$. This high loss period forces two earlier intersections of the costate variables to occur, implying that $x_2(T)$ is maximized by two phases of vegetative and reproductive growth. The burst of vegetative loss does not affect the final switch to reproduction which is predicted at identical times in Figs. 1a and b.

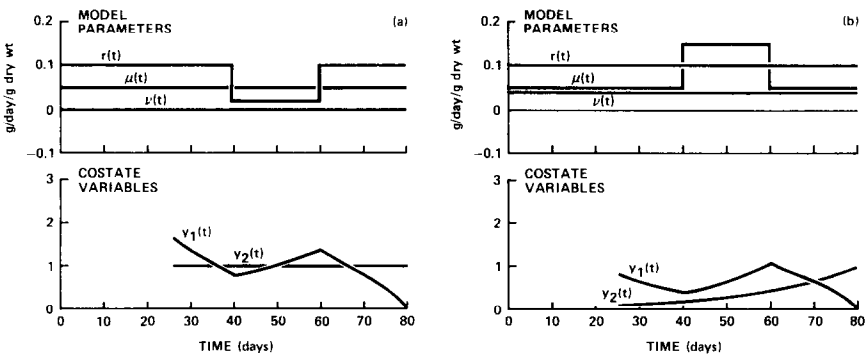


FIG. 2. Trajectories of costate variables. (a) A midseason slow growth period. (b) A midseason vegetative loss burst plus a constant reproductive loss.

If $r_1(t)$ is allowed to vary with time, multiple switches may be promoted by a temporary decline in $r_1(t)$, as well as by an increase in $\mu(t)$, as illustrated in Fig. 2a. No net change in vegetative weight occurs during the second vegetative growth period, in both Figs. 1b and 2a, which is consistent with Result II. Vegetative weight simply decreases when $\mu(t) > r_1(t)$ and increases when $r_1(t) > \mu(t)$, such that net growth is zero over this interval.

If reproductive losses occur, even greater bursts of vegetative loss are necessary for multiple switches to maximize seed yield. Model parameters of Fig. 2b are identical to those of Fig. 1b, except for the inclusion of reproductive losses in the former. Because reproductive material is depreciated, only one switch is predicted in Fig. 2b.

However, if reproductive parts contribute substantially to photosynthesis, as was observed by Bazzaz and Carlson (1979), $v(t)$ may be negative. In this case $\dot{y}_2(t) < 0$, so is no longer necessary that $\dot{y}_1(t) > 0$ on some interval to give multiple intersections of the costate variables, i.e., a period of $\mu(t) > r(t)$

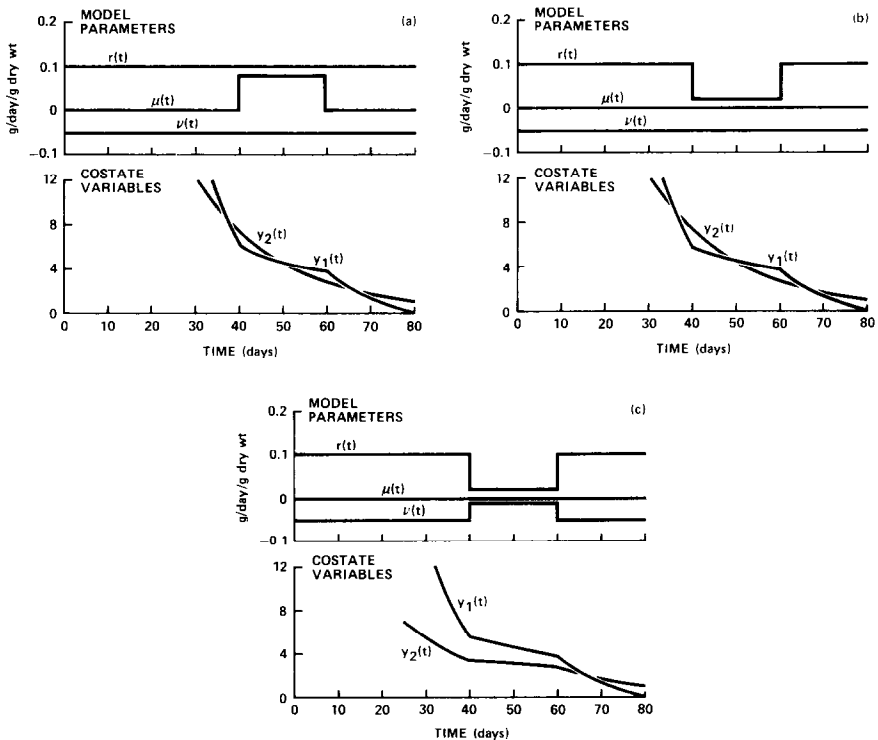


FIG. 3. Trajectories of costate variables. (a) A Midseason vegetative loss plus a constant reproductive gain. (b) A midseason slow growth period plus a constant reproductive gain. (c) A midseason slow growth period plus a variable reproductive gain, such that $|v(t)| < r(t)$.

is no longer necessary for the prediction of multiple vegetative and reproductive phases. Figures 3a and b illustrate cases where multiple switches are promoted when $r_1(t) > \mu(t)$ for all t in $[0, T]$. On the other hand, if reproductive photosynthesis declines with vegetative photosynthesis, multiple switches become less probable, as illustrated by Fig. 3c.

DISCUSSION AND CONCLUSIONS

Analysis of a general linear allocation model for annual plants shows that seed yield at time T may be maximized by a strategy consisting of two vegetative and two reproductive growth intervals under certain growth conditions. Interpretation of model results is simplified by the assumption that the reproductive growth constant $r_2(t)$ is proportional to $r_1(t)$, the vegetative growth constant. This proportionality results if $r_1(t) = e_1 r_0(t)$ and $r_2(t) = e_2 r_0(t)$ where $r_0(t)$ is the photosynthetic rate per unit vegetative mass and e_1 and e_2 are respectively the conversion efficiencies of photosynthate to vegetative and reproductive biomass.

In all cases the allocation strategy, $u^*(t)$, which maximizes seed yield includes a final reproductive interval. We expect conditions to be favorable for growth following germination, such that $r_1(t) > \mu(t) - v(t)$ at this time. Hence $u^*(t)$ will include an initial vegetative phase in all annual plants. We thus expect plants to exhibit an odd number of switches between vegetative and reproductive growth. If conditions are favorable for vegetative growth throughout the season, such that $r_1(t) > \mu(t) - v(t)$, seed yield is maximized by a strategy consisting of a single switch from vegetative to reproductive growth. This strategy also maximizes seed yield if conditions for vegetative growth decline toward the end of the season. However, large midseason vegetative losses may promote an additional earlier period of reproduction. When $r_2(t)$ is proportional to $r_1(t)$ a necessary condition for two reproductive phases is the existence of at least one time interval where $r_1(t) < \mu(t) - v(t)$ before the final reproductive phase.

If $v(t) = 0$ and $r_1(t)$ and $r_2(t)$ are constant over the entire season, the model reduces to the formulation considered by Denholm (1975). Like Denholm, we conclude that no net vegetative growth occurs during the vegetative phases following the initial reproductive period of the strategy which maximizes seed yield in this case. However, this no-net-growth condition does not preclude the existence of subsequent vegetative phases in $u^*(t)$. If a later vegetative phase is promoted by a single loss burst, it is timed such that vegetative weight first decreases and then increases with no net change over the entire vegetative phase.

In natural systems vegetative losses may be due to herbivory or to leaf senescence caused by unfavorable conditions, such as drought. For model

predictions to apply, the timing of losses must be predictable (to the plant) and vegetative and reproductive losses must be proportional to the vegetative and reproductive weights, respectively.

Most annuals exhibit a single reproductive phase, often with a sudden onset (Paltridge and Denholm, 1974). However, two reproductive periods have been noted in *Plantago aristata* and *Teesdalia nudicaulis*. According to Primack (1979) *Plantago aristata* usually does after an initial reproductive phase, but may produce a second seed crop in years of heavy summer rains. The winter annual *Teesdalia nudicaulis* exhibits a period of flowering in late April followed by a second burst of flowering in June (Newman, 1964). These examples are consistent with model predictions, but we cannot conclude that such multiple switches were promoted by vegetative loss bursts, since no measurements of model parameters are known for these species.

APPENDIX I: DERIVATION OF POINTS CONCERNING THE FINAL SWITCH IN $u^*(t)$

According to boundary condition (6), $y_1(T) = 0$ and $y_2(T) = 1$. Substituting these values into (7) shows that (7b) is necessarily satisfied at $t = T$ provided $r_2(T) > 0$ as assumed. (See Fig. 4.) Thus the optimal control always includes a final reproductive interval.

Equation (8a) must hold for a switch in $u^*(t)$ to occur at t_3 according to (7). (See Fig. 4.) If the switch is from vegetative to reproductive growth,

$$\frac{d[r_1(t) y_1(t)]}{dt} < \frac{d[r_2(t) y_2(t)]}{dt} \quad (\text{I.1})$$

at t_3 , i.e.,

$$r_1(t_3) \dot{y}_1(t_3) + \dot{r}_1(t_3) y_1(t_3) < r_2(t_3) \dot{y}_2(t_3) + \dot{r}_2(t_3) y_2(t_3). \quad (\text{I.2})$$

Substituting (4), (5) and (8a) into (I.2) then results in (8b).

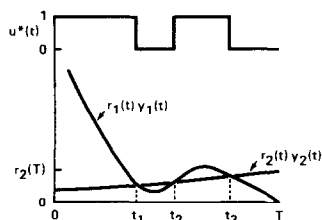


FIG. 4. Sketch of $r_1(t)y_1(t)$ and $r_2(t)y_2(t)$ illustrating the model conditions required for multiple switches between vegetative and reproductive growth (see text). The optimal control function, $u^*(t)$, corresponding to these costate variables is shown at the top of the figure.

APPENDIX II: DERIVATION OF RESULT I

Result I is derived by determining the conditions for an additional intersection of $r_1(t) y_1(t)$ and $r_2(t) y_2(t)$. According to (7)

$$r_1(t_2) y_1(t_2) = r_2(t_2) y_2(t_2) \quad (\text{I.3})$$

if a switch in $u^*(t)$ occurs at t_2 . As illustrated in Fig. 4, $u^*(t) = 1$, i.e., growth is vegetative for t in $[t_2, t_3]$. Equation (4) then becomes

$$\dot{y}_1(t) = \mu(t) y_1(t) - r_1(t) y_1(t) \quad (\text{I.4})$$

over the above interval.

Integrating (I.4) and (5) over $[t_2, t_3]$ gives

$$y_1(t_3) = y_1(t_2) \exp \left(\int_{t_2}^{t_3} [\mu(t) - r_1(t)] dt \right) \quad (\text{I.5})$$

and

$$y_2(t_3) = y_2(t_2) \exp \left(\int_{t_2}^{t_3} v(t) dt \right). \quad (\text{I.6})$$

Noting that $r_1(t_3) y_1(t_3) = r_2(t_3) y_2(t_3)$ from (8a) and substituting (I.5), (I.6) and (I.3) into this expression yields

$$\frac{r_1(t_3)}{r_1(t_2)} \exp \left(\int_{t_2}^{t_3} [\mu(t) - r_1(t)] dt \right) = \frac{r_2(t_3)}{r_2(t_2)} \exp \left(\int_{t_2}^{t_3} v(t) dt \right). \quad (\text{I.7})$$

Equation (10a) is obtained by taking the log of both sides of (I.7) and rearranging.

Equation (10b) results from the fact that

$$\left. \frac{d[r_1(t) y_1(t)]}{dt} \right|_{t_2} > \left. \frac{d[r_2(t) y_2(t)]}{dt} \right|_{t_2} \quad (\text{I.8})$$

if $u^*(t)$ switches from 0 to 1 at t_2 . (The derivation is identical to that of (8b).)

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REFERENCES

- BAZZAZ, F. B. AND CARLSON, R. W. 1979. Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer, *New Phytol.* **82**, 223–232.
- COHEN, D. 1971. Maximizing final yield when growth is limited by time or by limiting resources, *J. Theor. Biol.* **33**, 299–307.
- DENHOLM, J. V. 1975. Necessary condition for maximum yield in a senescing two-phase plant, *J. Theor. Biol.* **52**, 251–254.
- INTRILIGATOR, M. D. 1971. "Mathematical Optimization and Economic Theory," Prentice-Hall, Englewood Cliffs, N. J.
- MIRMIRANI, M. AND OSTER, G. F. 1978. Competition, kin selection and evolutionarily stable strategies, *Theor. Pop. Biol.* **13**, 304–339.
- NEWMAN, E. I. 1964. Factors affecting the seed production of *Teesdalia nudicaulis*, *J. Ecol.* **52**, 391–404.
- OSTER, G. F. AND WILSON, E. O. 1978. "Caste and Ecology in the Social Insects," Princeton Univ. Press, Princeton, N. J.
- PALTRIDGE, G. W. AND DENHOLM, J. V. 1974. Plant yield and the switch from vegetative to reproductive growth, *J. Theor. Biol.* **44**, 23–34.
- PRIMACK, R. B. 1979. Reproductive effort in annual and prennial species of *Plantago* (Plantaginaceae), *Amer. Natur.* **114**, 51–62.