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Ecological and Evolutionary Conditions for Fruit Abortion to Regulate Pollinating Seed-Eaters and Increase Plant Reproduction

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Coevolved mutualisms, such as those between senita cacti, yuccas, and their respective obligate pollinators, benefit both species involved in the interaction. However, in these pollination mutualisms the pollinator's larvae impose a cost on plants through consumption of developing seeds and fruit. The effects of pollinators on benefits and costs are expected to vary with the abundance of pollinators, because large population sizes result in more eggs and larval seed-eaters. Here, we develop the hypothesis that fruit abortion, which is common in yucca, senita, and plants in general, could in some cases have the function of limiting pollinator abundance and, thereby, increasing fruit production. Using a general steady-state model of fruit production and pollinator dynamics, we demonstrate that plants involved in pollinating seed-eater mutualisms can increase their fecundity by randomly aborting fruit. We show that the ecological conditions under which fruit abortion can improve plants fecundity are not unusual. They are best met when the plant is long-lived, the population dynamics of the pollinator are much faster than those of the plant, the loss of one fruit via abortion kills a larva that would have the expectation of destroying more than one fruit through its future egg laying as an adult moth, and the effects of fruit abortion on pollinator abundance are spatially localized. We then use the approach of adaptive dynamics to find conditions under which a fruit abortion strategy based on regulating the pollinator population could feasibly evolve in this type of plant–pollinator interaction.

Key Words: **pollinating seed-eaters; fruit abortion; adaptive dynamics; mutualism; evolutionarily stable strategy; benefits; costs; population size**

1. INTRODUCTION

Interspecific mutualisms are defined as relationships between species in which some aspect of the life history of each species benefits directly from the presence of the other species. However, the benefits of mutualism nearly always come at some cost. To a large extent, it is the balance between these costs and benefits that determines whether an interaction is mutualistic and maintained as such through time. In many cases, mutualisms have the potential to shift from purely mutualistic to antagonistic interactions when the costs to one species exceed its

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benefits through overexploitation by its partner. This is clearly exemplified in pollinating seed-eater mutualisms. In these mutualisms, the pollinator not only pollinates flowers, but may also oviposit on the flowers it pollinated, where its larvae then consume seeds and fruit tissue. Among these types of mutualisms are interactions between fig trees and fig wasps (Janzen, 1979; Wiebes, 1979; Addicott *et al.*, 1990; Bronstein, 1992; Herre, 1996), *Silene vulgaris* and *Hadena* moths (Pettersson, 1991, 1992), *Lithophragma* spp. and *Greya* moths (Thompson and Pellmyr, 1992; Davis *et al.*, 1992), *Trollius* spp. and globeflower flies (Pellmyr, 1989, 1992), yucca plants and yucca moths (Riley, 1892; Aker and Udovic, 1981; Addicott, 1986; Pellmyr *et al.*, 1996), and senita cacti and senita moths (Fleming and Holland, 1998; Holland and Fleming, 1999a, b). For senita, yuccas, figs, and *Trollius europaeus*, the insects are obligate pollinators and are the only, or virtually the only, means of pollination for the plant.

It can be expected in such mutualisms, in which the pollinator is not only the sole means of pollination but also a consumer of the fruit and seeds, that the plant maximizes the benefits of pollination and minimizes the costs of seed and fruit consumption by larvae. One way by which a plant could possibly alter the benefits and costs of the mutualism is by limiting the population size of the insect pollinator. A small to moderate population of pollinators may be sufficient for pollination of most of the flowers without so many eggs being laid that a heavy toll is paid through seed eating, a large population, however, may overwhelm fruit with larval seed-eaters.

It has been observed empirically that yucca and senita plants mature only a portion of their pollinated flowers. Some pollinated flowers are aborted as immature fruit. Because fruit abortion is a source of mortality for the pollinator's larvae, it may have some effect on pollinator abundance. Other factors, such as limitations of water and nutrients, can result in fruit abortions (Stephenson, 1981), but the relative constancy of the fractions of pollinated flowers initiating fruit development in space and time for both yucca and senita suggests that resources may not be the only explanation for fruit abortion (Schaffer and Schaffer, 1979; Udovic, 1981; Udovic and Aker, 1981; Aker, 1982a, b; James *et al.*, 1993, 1994; Pellmyr and Huth, 1994; Huth and Pellmyr, 1997; Addicott, 1998; Fleming and Holland, 1998; Holland and Fleming, 1999a, b).

In this paper we explore the idea that fruit abortion by plants, such as those of yucca or senita, can limit the population size of pollinators, thereby reducing the loss of seeds to larval consumers and leading to an increase in net fruit production. We consider a generic system of a patch of plants and an insect that is the obligate pollinator of the plant species (Fig. 1). The patch of plants produces flowers, some of which are not pollinated and are abscised from the plant. Of the pollinated flowers, some are aborted as undeveloped fruit, while others set fruit and initiate fruit development.

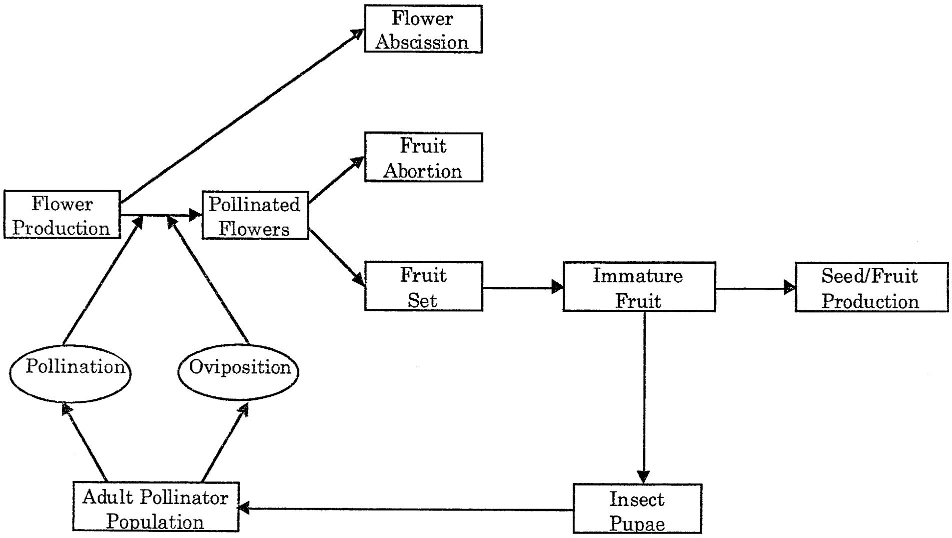

FIG. 1. Schematic diagram of the relationship between a plant and an insect pollinator whose larvae consume the seeds and fruit pollinated by its mother. The diagram depicts the relationships among pollinator population, pollination, flower production, fruit abortion, seed eating, and fruit production (see text for description).

Eggs and larvae of fruit that abort do not survive to produce adult pollinators. Only eggs and larvae of those flowers setting fruit can contribute to recruitment to the pollinator population. Of those flowers setting fruit, some have been oviposited on and contain larval progeny of the pollinator. Other immature fruit do not contain larvae and their seeds are thus not consumed. The fruit lacking larvae are assumed to survive (losses to other consumers are ignored here) and add to fruit production. Seeds of fruit with larvae are destroyed and larvae pupate and emerge to join the adult pollinators.

For this generalized pollinating seed-eater system, we will establish answers to the following sequence of questions: (1) Is plant reproduction, as measured by fruit production, a maximum for some particular population size of pollinators? (2) Can the population size of an obligate pollinator be limited through fruit abortion by plants? (3) Can the production of fruit by plants be maximized through its use of fruit abortion to limit pollinator abundance? If so, under what ecological conditions is this likely to occur? (4) Can fruit abortion evolve in a population of plants and be an evolutionary stable strategy? Intuitively, it would appear that the abortion of fruit would not be the best means of increasing fruit production. However, we show that the ecological conditions under which fruit abortion can limit pollinators and increase fruit production may not be so unusual and that fruit abortion might even evolve for this function.

2. MODEL ANALYSES

2.1. *Is Fruit Production a Maximum for a Particular Population Size of the Pollinating Seed-Eater?*

To answer this question, we first make some assumptions. We focus on a plant or patch of plants and the local pollinator population. In particular, we assume a functional response for both the number of flowers pollinated and the number of flowers whose fruit contain seed-eaters as a function of the number of flowers, F, and the size of the adult pollinator population, M. A reasonable assumption is a ratio-dependent model based on Poisson probability considerations, that is, a random search, which Thompson (1939) initially used to describe parasitoids searching for hosts. In our model, both the number of flowers not pollinated and the number of flowers without larval seed-eaters decrease exponentially as a function of an increasing ratio M/F. The amount of time that pollinators spend searching for flowers is proportional to the population size of the pollinator. But as the number of flowers not pollinated and not containing larval seed-eaters decreases, greater search time by the pollinators is required for each succeeding flower to be pollinated and its seeds eaten. Moreover, for seed consumption, we assume that as the M/F ratio increases, more eggs are laid per flower such that the likelihood of seeds being eaten increases.

Functional forms for pollination and seed consumption can be written as

$$P = 1 - e^{-\gamma_1 M/F} \tag{1}$$

and

$$D = 1 - e^{-\gamma_2 M/F}, \tag{2}$$

where P is the fraction of flowers pollinated, D is the fraction of flowers that are subsequently consumed as fruit by seed-eaters, and γ_1 and γ_2 are constants. We also make the assumption that $\gamma_1 > \gamma_2$ because seeds cannot be consumed by larvae unless the ovules of flowers are first pollinated. The difference between Eqs. (1) and (2), that is, $P - D$, for a particular abundance of pollinators is the fraction of flowers that produce mature fruit (Fig. 2). The M/F ratio that maximizes fruit production is

$$M/F = 1/(\gamma_1 - \gamma_2)\ln(\gamma_1/\gamma_2). \tag{3}$$

Thus, there is a single, particular abundance of pollinators that maximizes fruit production. It is not indispensable for our argument that pollination and seed and fruit consumption have the exact functional forms of Eqs. (1) and (2). Typical functions increasing

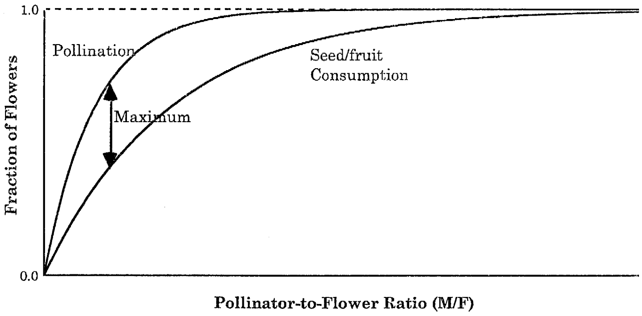

FIG. 2. General curves showing the fraction of flowers pollinated and immature fruit eaten during a given time period as a function of the ratio of the number of pollinators to the number of flowers (Eqs. (1) and (2)). Note that there is necessarily a maximum difference between these curves, signifying the maximum production of fruit by the patch of plants for one particular ratio of pollinators to flowers.

monotonically from zero toward an asymptote at 1 should have this property.

2.2. Can Fruit Abortion Limit the Abundance of Pollinators?

Here, we investigate whether a patch of plants can limit its local abundance of pollinating seed-eaters through the abortion of fruit. We assume the following: (1) Recruitment into the adult pollinator population comes from pupae of the local patch of plants and from adult immigrants from outside the local plant patch, the latter coming at a rate, M_{imm}, per day. (2) Each fruit with a larval seed-eater produces one pupa, and only a fraction of pupae, S_p, survive to become adults. Some fraction, C, of fruit abort, which reduces the pre-adult survivorship of the pollinator by a fraction, $1 - C$. (3) There is a daily adult survival rate of S_a. (4) Other than resource dependence (number of fruit) there is no density-dependent regulation of the pollinator population (i.e., no density-dependent self-regulation or limitation by predators or parasitoids). (5) The plants produce F flowers each day and each flower can be pollinated and oviposited only during 1 day.

Given these assumptions, a difference equation for pollinator dynamics is

$$M_{t+1} = S_a M_t + F(1 - C)(1 - \mathrm{e}^{-\gamma_2 M_{t-T}/F})S_p + M_{imm}, \qquad (4)$$

where, for definiteness, we used Eq. (2) to represent the fraction of flowers per day with larval seed-eaters. The value of M in the exponent is written as M_{t-T}, representing the fact that new adults are recruited from oviposition events that occurred a number of days, T, earlier.

The daily fraction of abortions, C, can affect the pollinator population. However, the extent of this effect depends critically on the input of adults from outside the local population, M_{imm}. If we make a further assumption, that all rates continue as constants over time, then we can solve for a steady-state population, M^*:

$$M^* = [1/(1 - S_a)]\Big(F(1 - C)(1 - \mathrm{e}^{-\gamma_2 M^*/F})S_p + M_{imm}\Big). \qquad (5)$$

This implicit equation for M^* is transcendental and cannot be solved analytically, but a casual inspection of the equation indicates that, when immigration is low, abortion can have a strong influence on the steady-state population of pollinators.

To quantitatively illustrate the effect of fruit abortion on the population of pollinators, we solved Eq. (5) numerically, using parameter values that are in general agreement with what is known of pollinating seed-eater mutualisms, particularly that of senita cacti and senita moths (Holland, 2001; J. N. Holland, unpublished data). This allowed us to examine the effect of fruit abortion on pollinator abundance, under a variety of immigration rates of adult pollinators from outside the local patch of plants. Fruit abortion can limit pollinator abundance, either in the absence or presence of pollinator immigration (Fig. 3). The more localized a pollinator population is to a plant or patch of plants (i.e., the lower the immigration rate), the more effective fruit abortion can be in limiting pollinator abundance. The larger the immigration rate, the more abundant pollinators are at steady state for any given fraction of flowers aborting as immature fruit. If there is no immigration or the immigration rate is small, then a high fruit abortion fraction can lead to the extinction of the pollinator (Fig. 3). However, if immigration is high enough, then fruit abortion is not effective in limiting the pollinator population.

2.3. Can Fruit Abortion Lead to Greater Net Production of Fruit?

The preceding sections showed that fruit production can vary with the population size of pollinators, that there is a single population size under which fruit production is maximum, and that fruit abortion can influence the pollinator's population size. We next show that fruit abortion can limit pollinator numbers such that it maximizes the production of fruit.

To address this issue, first we determine the theoretical feasibility for fruit abortion to maximize fruit production, under special conditions that make analysis simple. Then, we numerically examine a case in which parameters lie in the expected range for one pollinating seed-eater mutualism. We build on the model components developed so far and assume that fruit abortion is random. To simplify the analysis, we consider the case in which the pollinator is so effective at pollination that we can assume virtually all flowers are pollinated for the range of population numbers that are relevant. We also assume that the fraction of immature fruit with larvae is relatively high. Finally, we assume that the system reaches a steady state. Daily steady-state production of mature fruit by the patch of plants, W^*, is represented by the difference between Eqs. (1) and (2), multiplied by both F and $(1 - C)$:

$$W^* = F(1 - C)(\mathrm{e}^{-\gamma_2 M^*/F} - \mathrm{e}^{-\gamma_1 M^*/F}). \qquad (6)$$

Equations (5) and (6) are used to determine the increment in W^* for an incremental increase in the

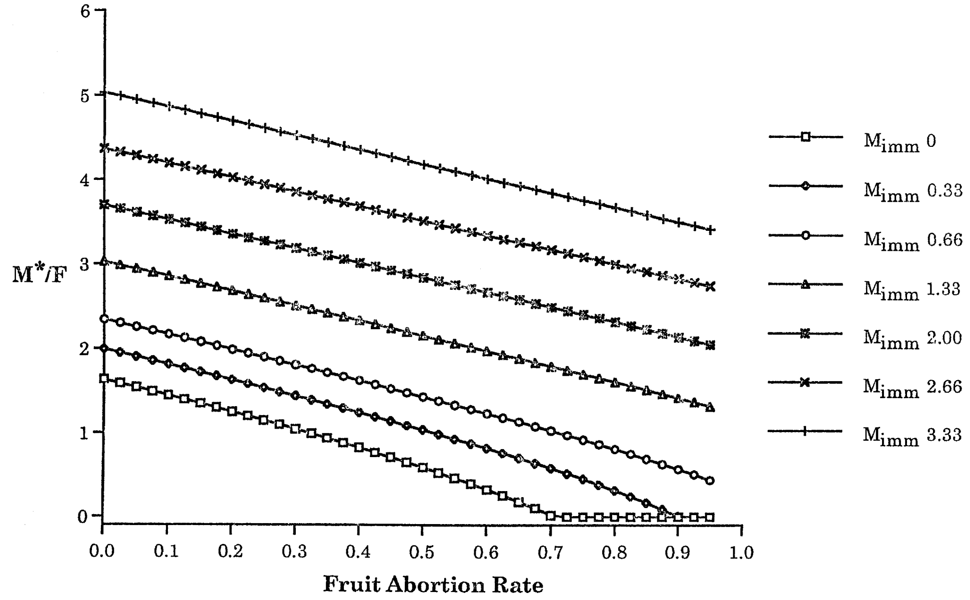

FIG. 3. The steady-state population size of the pollinator, represented as a ratio to the number of flowers, M^*/F, as a function of the fruit abortion rate, C, for different immigration rates of pollinators from outside the patch of plants (M_{imm}). M_{imm} is represented as a ratio to the number of flowers, M_{imm}/F. Parameter values for the numerical solutions to Eq. (4) are $\gamma_1 = 4.0$, $\gamma_2 = 2.0$, $F = 150$, $S_a = 0.5$, and $S_p = 0.85$. The number of flowers per day, F, is typical of that for a single plant, though the model is meant to apply to a patch of plants of any size.

fraction of flowers aborting, ΔC. An analysis is carried out in the Appendix, using the above assumptions, with the result that the increment in W^*, ΔW^*, is approximately

$$\Delta W^* = F\Delta C\left[-1 + \frac{(1 - C)\gamma_2 s_p}{(1 - s_a)}\right] e^{-\gamma_2 M^*/F}. \qquad (7)$$

Fruit production increases if abortion is increased for parameters satisfying the inequality when the right-hand side of (7) is greater than zero. This occurs if

$$\frac{(1 - C)\gamma_2 s_p}{1 - s_a} > 1 \qquad (8)$$

is satisfied. This inequality will typically be satisfied for parameters of the senita/senita moth system (e.g., $s_a = 0.5$, $s_p = 0.85$, $\gamma_2 > 1$; see Holland, 2001; J. N. Holland unpublished data) as long as $(1 - C)$ is of order 1. Inequality (8) allows one to understand intuitively the circumstances under which it might be advantageous for a plant to abort fruit, sacrificing both larval-infested and uninfested fruit, in order to limit pollinator abundance. The factor $1/(1 - s_a)$ is the expected lifetime of an adult pollinator, and $(1 - C)s_p$ is the fraction of larvae that survive to adulthood. Therefore, the ratio $(1 - C)s_p/(1 - s_a)$ is a measure of the expected number of days that a pollinator, currently in the larval stage, will spend ovipositing during its lifetime. Because γ_2 is a measure of the probability, per unit of time, of the pollinator laying eggs that become larvae, the left-hand side of Eq. (8) is an expression of how destructive each pollinator can be, in terms of what fraction of flowers will be destroyed by the larval seed-eaters. The inequality states that if this number is greater than unity, fruit abortion can be effective, because a single fruit lost is compensated for by killing a larva that would likely leave many successful larval seed-eaters as an adult. This result should be relatively general, and not depend on the particular model equations used above.

The assumptions made in the Appendix enabled us to obtain a simple analytic expression (Eq. (8)), which helps in the explanation of the effect of fruit abortion on fruit production. We briefly discuss those assumptions here. We assumed first that the rates of both pollination and oviposition are high enough that the majority of flowers are pollinated and have eggs; that is, $e^{-\gamma_2 M^*/F}$, $e^{-\gamma_1 M^*/F} \ll 1$. Our second assumption was that the efficiency with which pollinators pollinate flowers is much greater than the efficiency with which they destroy seeds and fruit. It is biologically self-evident that larvae of pollinators can only consume seeds if the ovules were first fertilized, so the pollination rate is necessarily higher than the rate of seed eating, or $\gamma_1 > \gamma_2$. It is reasonable to assume this, and even a modest difference in these rates can allow us to ignore the term $e^{-\gamma_1 M^*/F}$ relative to $e^{-\gamma_2 M^*/F}$.

It is not necessary to make these assumptions to demonstrate the possible advantage of fruit abortion. We also solved Eqs. (5) and (6) numerically, relaxing the assumption of extremely effective pollination made in the theoretical analysis above, to verify under typically expected parameter values of the senita/senita moth mutualism that fruit production can be maximized by limiting pollinators through fruit abortion. Figure 4 illustrates how C affects W^* for a variety of rates of pollinator immigration from outside the local patch of plants. As fruit abortion increases from zero to one, fruit production follows a unimodal curve, increasing toward a maximum production rate, and then falling off more rapidly. When immigration of moths from other patches is small, abortion can be so effective that fruit production increases dramatically in comparison to no fruit abortion. However, when the immigration rate is large, fruit abortion is not sufficiently effective in limiting pollinator populations, and fruit production is low due to high levels of seed consumption.

2.4. Can a Fruit Abortion Strategy Evolve?

Results of the model analyzed above indicate that, given reasonable assumptions, fruit abortion is a strategy by which the pollinator population can be limited and fruit production can be maximized. Here, we use the theory of adaptive dynamics to investigate whether a fruit abortion strategy could evolve or be maintained for the function of limiting pollinators. The theory of adaptive dynamics is ideal for investigating evolution and coevolution based on ecological conditions such as density dependence and interspecific interactions (Dieckmann, 1997; Doebeli and Dieckmann, 2000).

Evolutionary theorists have taken the concepts of "evolutionarily stable strategy" (Maynard Smith and Price, 1973) and "convergence stability" (Christiansen, 1991) and expanded them to derive the theory of adaptive dynamics (Dieckmann, 1997; Geritz *et al.*, 1997, 1998; de Mazancourt and Loreau, 2000a; Doebeli and Dieckmann, 2000). Adaptive dynamics theory is usually applied by assuming that there is a single resident strategy and determining whether a mutant strategy can invade and replace the resident strategy and become the new resident strategy. A few definitions are first necessary. A "singular strategy" is a strategy along a trade-off axis at which the fitness gradient becomes zero. Such a singular strategy can have two primary independent properties: convergence and stability. The singular strategy is convergent if it can be reached through the course of evolution; that is, given that the resident has a neighboring strategy, successful mutant

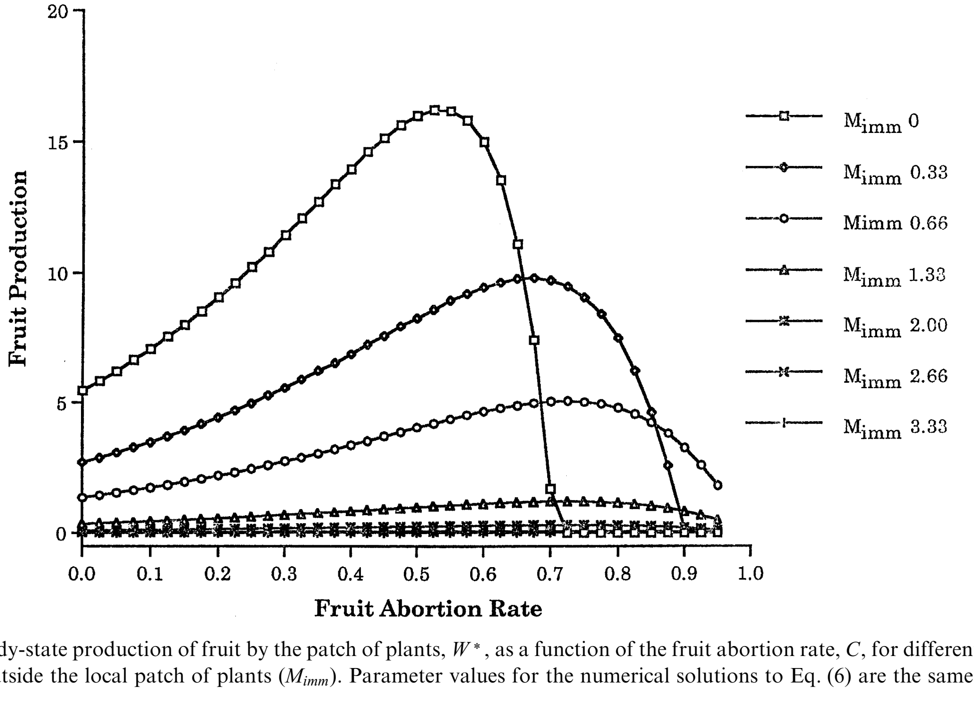

FIG. 4. The steady-state production of fruit by the patch of plants, W^*, as a function of the fruit abortion rate, C, for different rates of pollinator immigration from outside the local patch of plants (M_{imm}). Parameter values for the numerical solutions to Eq. (6) are the same as those in Fig. 3.

invaders lie closer to the singular strategy. A singular strategy is stable, or is an evolutionary stable strategy (ESS), if it cannot be invaded by a neighboring strategy once established.

There are several evolutionary scenarios that could result from adaptive dynamics. The specific scenario that occurs is determined by examining, in state-plane space, the pairwise invasibility of a resident strategy with a mutant or invading strategy (Geritz *et al.*, 1997, 1998). Depending on the configuration of the state-plane space, the primary scenarios that can occur include the following: (1) an evolutionarily singular strategy that is both a convergent stable strategy and an evolutionarily stable strategy, such that it is a stable endpoint of evolution, called a continuously stable strategy, or CSS; (2) an evolutionarily singular strategy that is not convergence stable, which acts as an evolutionary repeller; and (3) an evolutionarily singular strategy that is convergence stable but not an evolutionarily stable strategy, such that once this strategy is approached through convergence, two different, but close, strategies invade the singular strategy and evolutionary branching occurs (Geritz *et al.*, 1997, 1998). Which of these scenarios occurs can be analyzed using a "pairwise invasibility plot." We do this below, after specifying our model more carefully for the case in which the competing host plants may have different fruit abortion strategies.

We analyze the evolution of fruit abortion in plants interacting with pollinating seed-eaters using the approach of adaptive dynamics. The implicit assumption so far is that the model represents one plant or a patch of plants that employs the same fruit abortion strategy (i.e., are homogeneous in that trait), to which pollinators are isolated. However, in nature pollinators are rarely isolated to only one plant or local patch of plants. Instead, pollinators migrate among plants within a landscape. In fact, in plants such as the senita cactus, which is self-incompatible, migration of pollinators among plants is essential, and we have implicitly been assuming that the modeled plant or patch of plants is part of a larger population that is genetically homogeneous in the trait for fruit abortion. We must consider now that this larger population of plants is not homogeneous, but may contain a mixture of genotypes with different fruit abortion strategies.

Intuitively, it would appear that in a mixture of aborting and non-aborting plants, the non-aborting plants could reap the benefits of reduced pollinator abundance without paying the reproductive trade-off of aborting fruit. If so, then the plants with a non-abortion strategy could have greater reproductive output. Non-aborting plants may be able to coexist among those employing a fruit abortion strategy, leading to either evolutionary branching or the eventual exclusion of a fruit abortion strategy. Such an approach to plants with different strategies of fruit abortion assumes that the effect of fruit abortion on pollinator population size and fruit production is equally accrued among all plants and that there is no spatial localization of these effects. Spatial homogeneity of the effects of fruit abortion may occur if the rate of pollinator migration among patches is high enough that pollinator abundance is essentially the same for every plant.

Our approach is to extend our model of one plant or patch with a single strategy to a heterogeneous plant population, in which there are different fruit abortion strategies ranging from $C = 0.0$ to 1.0. In addition to different strategies of fruit abortion, the main extension of the model is to allow the migration of pollinators among the plants comprising the population. This movement of pollinators could reduce or eliminate the effectiveness of a fruit abortion strategy to limit its local pollinator population and allow plants with a non-aborting strategy to share the advantage of a limited pollinator population and thus experience increased fruit production without aborting fruit.

The dynamic forms of the equations for the pollinator population and fruit production, evaluated at steady state, are

$$M_i^* = (S_a - E)M_i^* + F(1 - C_i)(1 - \mathrm{e}^{-\gamma_2 M_i^*/F})S_p + (E/(n-1))\sum_j M_i^* \tag{9}$$

and

$$W_i^* = F(1 - C_i)(\mathrm{e}^{-\gamma_2 M_i^*/F} - \mathrm{e}^{-\gamma_1 M_i^*/F}) \tag{10}$$

for $i = 1, 2, \ldots, n$. We now assume that there are n plants within a metapopulation, all identical except that each can have a different fruit abortion strategy, C_i. The constant, E, is the daily fraction of pollinators that migrate from one plant to another. Pollinators are assumed to be evenly distributed among plants and it is assumed that there is no biased movement of pollinators to plants with differing strategies. We developed a specific model with five plants, representing a situation in which a particular plant receives immigrants from its four nearest neighboring plants (Fig. 5). Four plants are considered the residents, sharing a single abortion strategy, C_{res}, while the fifth plant is the invader, with a different abortion strategy, C_{inv}.

As stated above, the rate of migration of pollinators between plants is important in terms of how homogeneous their distribution is among plants and,

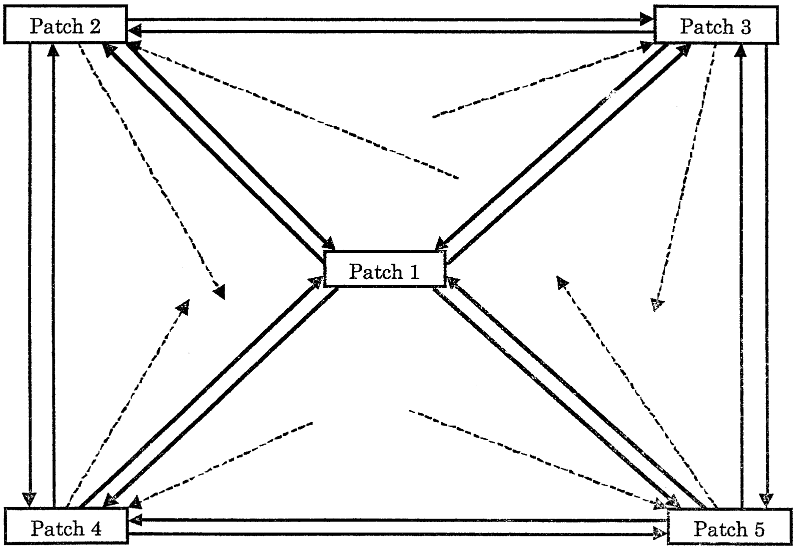

FIG. 5. Schematic diagram of indirect intraspecific interactions between plants through the use of a common pollinator population. The solid and dotted lines represent the direct and indirect movement of pollinators among plants.

therefore, whether or not there is evolution toward a fruit abortion strategy. To investigate the effects of different levels of migration, we performed simulations of Eqs. (9) and (10) for the situation where $C_{inv} = 0.4$ for one plant, and $C_{res} = 0.0$ for the four resident plants. Values of migration, E, were allowed to vary.

Migration among plants has a clear effect of spatially homogenizing the pollinator population among plants (Fig. 6a), which has a marked effect on the relative production of fruit by the two types of plants (Fig. 6b). For low rates of pollinator migration, fruit production is greater for the plants that abort fruit than for the non-aborting plant (Fig. 6b). But when the rate of pollinator movement among plants is large, the aborting plants have lower fruit production.

It is clear from this specific example that relatively low migration rates of pollinators among plants, in fact rates below roughly 0.05, are necessary for fruit abortion to be an optimal strategy. We first assume that this can be the case, letting the migration rate be 0.05, and proceed with a more general adaptive dynamics analysis to investigate the convergence and stability properties of the fruit-aborting strategy.

We first create a pairwise invasibility plot (Geritz *et al.*, 1997, 1998) for the model. To construct the pairwise invasibility plot, it is necessary to allow both the resident genotype and the invader genotype to take on all possible values of the fruit abortion trait, C. The pairwise invasibility plot, based on low pollinator migration rates among genotypes, is shown in Fig. 7. The resident strategy, C_{res}, is plotted on the x-axis and the invader's strategy, C_{inv}, is plotted on the y-axis. The strategy that produces the most mature fruit per unit time is considered the superior strategy, as it will leave more seeds on average and ultimately displace the other strategy (de Mazancourt, 1998). The shaded regions of Fig. 7 represent the combinations of C_{res} and C_{inv} for which the invader is superior to the resident.

According to the method of the pairwise invasibility plot of adaptive dynamics theory (Geritz *et al.*, 1997, 1998; de Mazancourt, 1998), determination of whether there is a stable strategy and for what value of fruit abortion, C, that occurs proceeds in two steps. The first step is to determine the location of the evolutionarily singular strategy. Consider the diagonal from the lower left to upper right in Fig. 7. An evolutionarily singular strategy will be located at the intersection of this diagonal and the line crossing it. If shading is above the diagonal before the singular strategy and below the diagonal after the singular strategy, then it is a convergent stable strategy. Second, if a vertical line drawn through the point representing the evolutionarily singular strategy lies in the white (unshaded) region, then the strategy is immune to invasion and is also an ESS; that is, no invader strategy with C greater or less than this one can invade, once the singular strategy point is reached through progressive evolutionary steps.

It appears then that under conditions of relatively low migration of pollinators, evolution toward a plant strategy of fruit abortion is possible, and an abortion fraction of about $C = 0.4$ is both a convergent stable strategy and ESS, and thus is a continuous stable

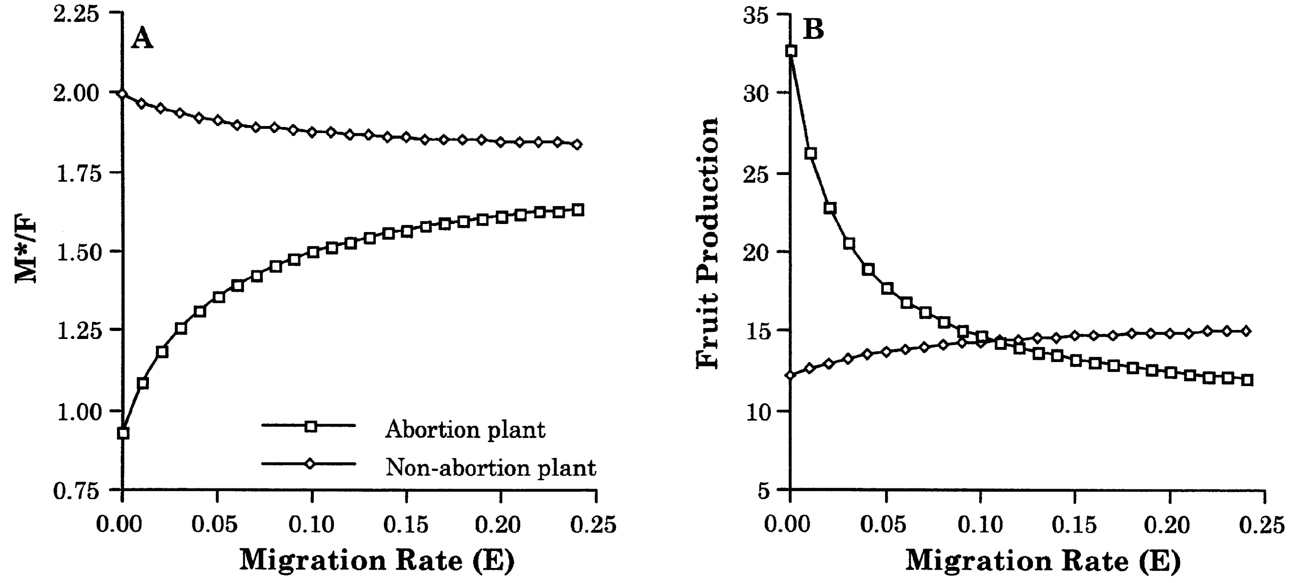

FIG. 6. The steady-state pollinator population (A) and fruit production (B) for a plant employing a fruit aborting strategy (open squares) and non-aborting plants (open diamonds) as a function of the fraction, E, of pollinators migrating among plants per day, for the scenario of one fruit aborting plant ($C_i = 0.4$) surrounded by non-aborting plants ($C_i = 0.0$). Parameter values for numerical solutions to Eqs. (9) and (10) are $\gamma_1 = 4.0$, $\gamma_2 = 1.4$, $F = 200$, $S_a = 0.6$, $S_p = 0.85$, and $e = 0.05$.

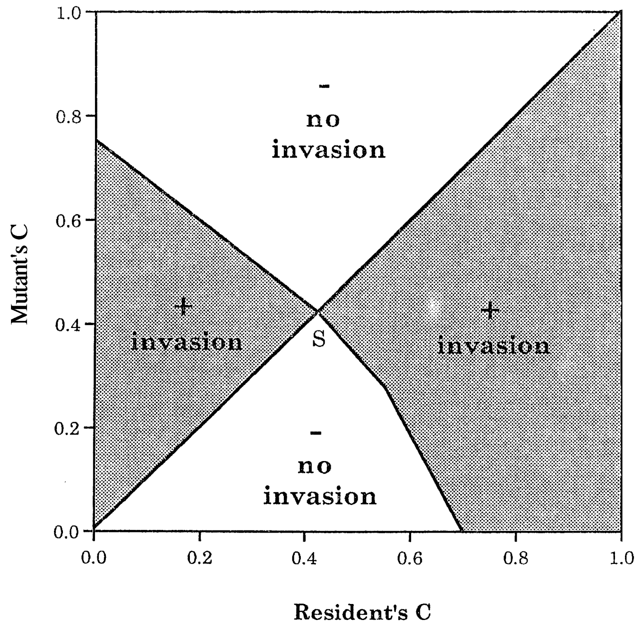

FIG. 7. Pairwise invasibility plot for reproduction by a resident versus mutant plants employing strategies of fruit abortion, C, ranging from 0.0 to 1.0, based on simulations of Eqs. (9) and (10) at intervals of 0.05 for these rates. The shaded regions represent those for which the invader's strategy produces more mature fruit than the resident's strategy; therefore the invader's strategy is considered superior in those regions, so that invasion should occur. The evolutionarily singular strategy is denoted by S, at approximately $C = 0.4$. Because the perpendicular line from the x-axis through this point falls only in white regions, S is both a convergent and an evolutionarily stable strategy.

strategy, or CSS. If resource-limited fruit abortion was an ancestral trait for a plant, as is likely the case for yucca (Pellmyr *et al.*, 1996), fruit abortion could be maintained and selected for in the absence of resource limitation due to the advantage of limiting the pollinator population.

Are known rates of migration of pollinators between plants, the senita cactus in particular, low enough that the above analysis is relevant? The senita cactus is a self-incompatible species, so rates of interplant migration are likely to be high. For this reason, we cannot say from our model analysis that fruit abortion is likely to have evolved in the senita cactus as a mechanism for regulating its pollinator population, although it seems feasible in self-compatible species.

However, this above finding does not rule out evolution of the abortion strategy, if competition between small local population patches were possible. The rates of migration among local patches of the senita cactus are known to be low. A low value for pollinator movement among local patches of plants is consistent with genetic evidence of pollinator movements in yucca and senita mutualisms. Genetic evidence, in the form of G_{st} values (a multilocus measure of among population genetic variation) for senita and one species of yucca ($G_{st} = 0.24$ and 0.18, respectively), indicates that pollen-mediated gene flow is highly restricted spatially (Massey and Hamrick, 1998; Hamrick *et al.*, in press). In fact, of four species of columnar cacti occurring in the Sonoran

Desert, and five species in Venezuela, senita cactus had the highest G_{st} value. This in turn suggests that the small, short-lived insect pollinators are spatially localized to the neighborhood of plant patches and subpopulations from which they pupated. Thus, it is plausible that a fruit abortion strategy could evolve if it is possible for competition to occur among patches made up of genotypes employing the same strategy. However, rigorous demonstration of this would require a much more complicated argument, including assumptions about the relative rates of extinction of different patches and the appearance of "cheater" strategies within a given patch. Such an analysis is beyond the scope of this paper.

3. DISCUSSION

The interactions, and possible coevolution, between plants and animals is a topic of fundamental importance in ecology (Thompson, 1994; Pellmyr *et al.*, 1996). Although relatively few pollinating seed-eater interactions are known at this time, their features, including those examined in this study, are not at all unusual in nature. The evolutionary problem we examined for pollinating seed-eater interactions may represent a large class of problems between plants and animals and plants and heterotrophs. Our conceptual view of the pollinating seed-eater system, and the strategy of the plant that we analyzed, is analogous to other contemporary ideas concerning plant-heterotroph interactions, including, for example, cotton and the boll weevil (Gutierrez and Regev, 1983) and the interaction of a nutrient-limited plant and a grazing animal. This latter interaction, and in particular the idea that limited grazing can optimize plant production, has been examined by de Mazancourt and others in a series of recent studies (de Mazancourt, 1998; de Mazancourt *et al.*, 1998, 1999; de Mazancourt and Loreau, 2000a, b).

This paper was a response to the observation that senita cacti and species of *Yucca* regularly mature only a small portion of their flowers into fruit. Other pollinated flowers are aborted as immature fruit. The traditional explanation for fruit abortion is that resource limitation prevents a plant from maturing all of its flowers into mature fruit. Such an explanation (along with others) has been sufficient to account for large flower-to-fruit ratios in many plants (Stephenson, 1981; Sutherland, 1986). However, we have argued that other factors may be involved in the explanation for fruit abortion in plants with pollinating seed-eaters, because fruit abortion is a source of mortality for developing larvae. Such mortality has direct feedbacks on both benefits and costs and should be under strong selection pressure. We have shown that this source of mortality can be an effective mechanism to limit and regulate the population size of the pollinator, if external factors, such as predation and weather, do not play a large role in determining the size of the pollinator population. We demonstrated that such regulation of the pollinator population is optimal for plants because it can maximize the plants' reproductive fitness. Fruit abortion, for the function of maximizing fruit production, could feasibly evolve and be maintained in some plant populations, although that is less certain from our analysis.

Based on these results, we argue that plants interacting with pollinating seed-eaters could potentially use fruit abortion as a means of regulating their pollinators and increasing their reproductive fitness. We do not suggest that such a strategy is a fact, but have shown conditions under which it can occur. In order to clarify why a strategy of fruit abortion is worth considering, we recapitulate several objections to such a concept, and apologize for their rhetorical nature.

Why should plants produce flowers and immature fruit that do not contribute to fecundity, based on the chance that it will have an effect on the pollinator population? Random fruit abortion appears to be a waste of resources and energy, as not only parasitized but also unparasitized fruit are aborted. Plants across all taxa allocate energy and resources to diverse mechanical, chemical, and biological defenses. If plants involved in these pollination systems employed chemical defenses against the seed-eaters, it could prove disadvantageous because they would deter the pollinator's larvae in general, which would potentially eliminate the benefits of pollination. Limited fruit abortion, on the other hand, will not lead to the demise of the pollinator population (Holland and DeAngelis, 2001).

Furthermore, in its most basic nature, fruit abortion is no different from any other plant defense. It simply redirects energy and resources from direct use in reproduction for indirect uses that increase long-term reproduction. We acknowledge that selective abortion of fruit may be a more advantageous strategy, and our models do indicate that selective abortion can have higher net benefits for plants than random abortion (Holland and DeAngelis, 2001). However, we wish to point out that even a random fruit abortion strategy can be, under conditions that are not unusual, better than no fruit abortions.

While our results show that the fruit abortion strategy is ecologically plausible as a way of regulating pollinator seed-eaters, it does not at first appear evolutionarily feasible. However, our analyses have shown that under certain conditions, selection can favor a fruit abortion strategy. If the effects of fruit abortion can be localized to some extent via limited movement of pollinators, then selection can increase the relative frequency of plants employing an abortion strategy (de Mazancourt and Loreau, 2000a). Some plants involved in mutualisms with seed-eaters, such as the senita cactus, are self-incompatible, so a high degree of migration of pollinators between plants certainly occurs. Our present results do not support evolution of fruit abortion as a strategy to regulate the pollinator population. However, more complex modeling might demonstrate whether evolution toward an abortion strategy could still occur through competition between local patches of plants, if movement of pollinators between plants within a patch is high, but movement between patches is low. In any case, our main purpose has not been to show the likelihood of any particular evolutionary mechanism. As we stated above, the general view that it is probable that the fruit abortion strategy evolved as the plant's way of dealing with resource limitation is a reasonable one, as far as it goes. Our purpose here has been to show that the strategy may possess another effect, the limitation of seed-eating pollinators, which could be an advantage to the plant.

A number of other objections to the present model can also be raised. In particular, the model assumes steady-state production of flowers, by which we ignored seasonality of flower production common to senita cacti and yucca. We have considered elsewhere (Holland and DeAngelis, 2001) the effects of seasonality by conducting detailed simulation models that take into account seasonality of flower production and diapause of pollinators. Results indicate that such seasonality should make no difference to the effectiveness of fruit abortion as a strategy. In this present work, our goal has been to establish some generalities based on simple models. In this respect, our work is very similar to the models of de Mazancourt and others (de Mazancourt, 1998; de Mazancourt *et al.*, 1998, 1999; de Mazancourt and Loreau, 2000a, b), who theoretically considered the possible advantages of grazing to a plant when the benefits also affect neighboring plants. We suggest that the similarity of the ecological and evolutionary problems analyzed in this paper with those of plant-grazer interactions analyzed by de Mazancourt and others is no coincidence, but reflects a broad class of problems in which the sacrifice of some production by a plant is compensated by an overall greater rate of production. This is a theoretical genre that is much in need of empirical testing.

The senita cactus and senita moth interaction, which has already been studied extensively (Fleming and Holland, 1998; Holland and Fleming, 1999a, b; Holland, 2001), is a system where a number of experimental manipulations could be performed to test the ideas discussed here. If it can be shown that fruit abortion can reduce the pollinator population size and can increase fruit production, it would be a novel and significant finding.

APPENDIX

From Eq. (6) we can obtain the incremental change in the steady-state production of fruit resulting from a change, ΔC, in the fraction of flowers aborted as immature fruit,

$$\Delta W = -F\left[e^{-\gamma_2 M^*/F} - e^{-\gamma_1 M^*/F}\right]\Delta C - (1-C)\left[\gamma_2 e^{-\gamma_2 M^*/F} - \gamma_1 e^{-\gamma_1 M^*/F}\right]\Delta M,$$

where ΔM is a function of ΔC. To determine ΔM as a function of ΔC we use Eq. (5) for the steady-state value of the pollinator population size. For simplicity, we assume that the exponential term in Eq. (5) is small compared to unity; i.e., most fruit contain seed-eaters. Then, we obtain

$$\Delta M^* \approx -\frac{F s_p \Delta C}{1-s_a}.$$

Now, ΔW can be written as

$$\Delta W = -F\left[e^{-\gamma_2 M^*/F} - e^{-\gamma_1 M^*/F}\right]\Delta C + \frac{F(1-C)s_p}{1-s_a}\left[\gamma_2 e^{-\gamma_2 M^*/F} - \gamma_1 e^{-\gamma_1 M^*/F}\right]\Delta C.$$

Under conditions where pollination is not limiting and is far greater than larval seed-predation, such that the inequality

$$e^{-\gamma_1 M^*/F} \ll e^{-\gamma_2 M^*/F}$$

holds, we can obtain expression (7) for ΔW.

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