

## MODELING INVESTMENTS IN SEEDS, CLONAL OFFSPRING, AND TRANSLOCATION IN A CLONAL PLANT

SHEA N. GARDNER<sup>1,3</sup> AND MARC MANGEL<sup>2,4</sup>

<sup>1</sup>*Center for Population Biology, University of California, Davis, California 95616 USA*

<sup>2</sup>*Department of Environmental Studies, University of California, Santa Cruz, California 95064 USA*

**Abstract.** Clonal plants that can switch facultatively between sexual and asexual reproduction may respond plastically to the environment. We constructed a dynamic state variable model to examine how the measure of fitness, ramet and genet mortality, and the assimilation rates of a parent and its clonal offspring influence behavioral investments in ramet growth, clonal offspring, seeds, and continued resource translocation to clonal offspring after establishment.

The model leads to predictions that ramet and genet mortality rates and/or the fitness payoff from producing seeds must be high for seed production to capture a proportion of reproductive investments. If seed production occurs as a result of high ramet or genet mortality rates, then results indicate that it is better to produce seeds early in the season, regardless of ramet size. In contrast, if seed production is favored as a result of its large contribution to fitness, then it is predicted to depend on ramet size more than on time.

While the total amount of biomass directed to reproduction is predicted to increase with a ramet's own productivity, the proportion of this biomass invested clonally or sexually depends on the resource environment encountered by that ramet's clonal offspring; more productive surroundings favor investment in clonal offspring that forage locally, reduce the risk of genet mortality, and increase the expectation for future seed production by the genet.

The model we present also suggests that a higher rate of translocation to support clonal offspring benefits a genet when the parent and offspring ramets have contrasting productivities. In addition, the model also leads to the predictions that translocation is more advantageous when the currency of fitness selects for increases in ramet size more than ramet number and when the probability of mortality is correlated among ramets.

*Key words:* clonal plants; clonal reproduction; dynamic model; integration; seeds; sexual reproduction; state variable; trade-off; translocation.

### INTRODUCTION

In this paper, we aim to explain how the measure of fitness, ramet productivity, and genet and ramet mortality affect investments by clonal plants in seeds and vegetative propagation. Plants capable of producing potentially independent clonal offspring, called ramets, can spread through the habitat (de Kroon and Hutchings 1995). By enlarging a genet, the production of ramets increases a genet's capacity for making more seeds in the future (Watson 1984, Madga et al. 1993), as well as reduces the risk of genet mortality (Cook 1979, Eriksson and Jerling 1990). Producing seeds or spores provides a genet the chance to disperse a fraction of offspring to colonize new, perhaps richer or safer, habitats, and may be particularly advantageous if rates of ramet or genet mortality are high (Hartnett 1987). Consequently, clonal

plants face reproductive trade-offs (Sohn and Policansky 1977, Law et al. 1983, Westley 1993, Worley and Harder 1996) that are affected by selection on foraging, reproduction, dispersal, and growth.

We focus on the behavioral, rather than the genetic, aspects of reproduction. Therefore, when we refer to seeds or sexual reproduction, it may be interpreted more loosely as investment in any offspring that do not remain connected to a parent ramet and that may disperse and colonize distant areas. Although these offspring are often outcrossed seeds, they may also be a result of agamospermy (Crawley 1997) or, in the case of aquatic plants, widely dispersing clonal fragments (Room 1990, Philbrick and Les 1996). In addition, although sometimes clonal offspring may disperse farther than seeds (Cain and Damman 1997), seeds are often capable of dispersing away from the parent genet (Eriksson 1989, 1992). Since rates of seedling survival in established populations are so low (Harper 1977, Wikberg et al. 1994, Nishitani and Kimura 1995, Jonsson et al. 1996), it may be that the greatest gains from producing seeds are realized from those few seeds that travel farther afield or that establish after major dis-

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<sup>3</sup> Current address: Natural Environment Research Council (NERC) Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK.

<sup>4</sup> Address correspondence to this author:  
E-mail: msmangel@cats.ucsc.edu.

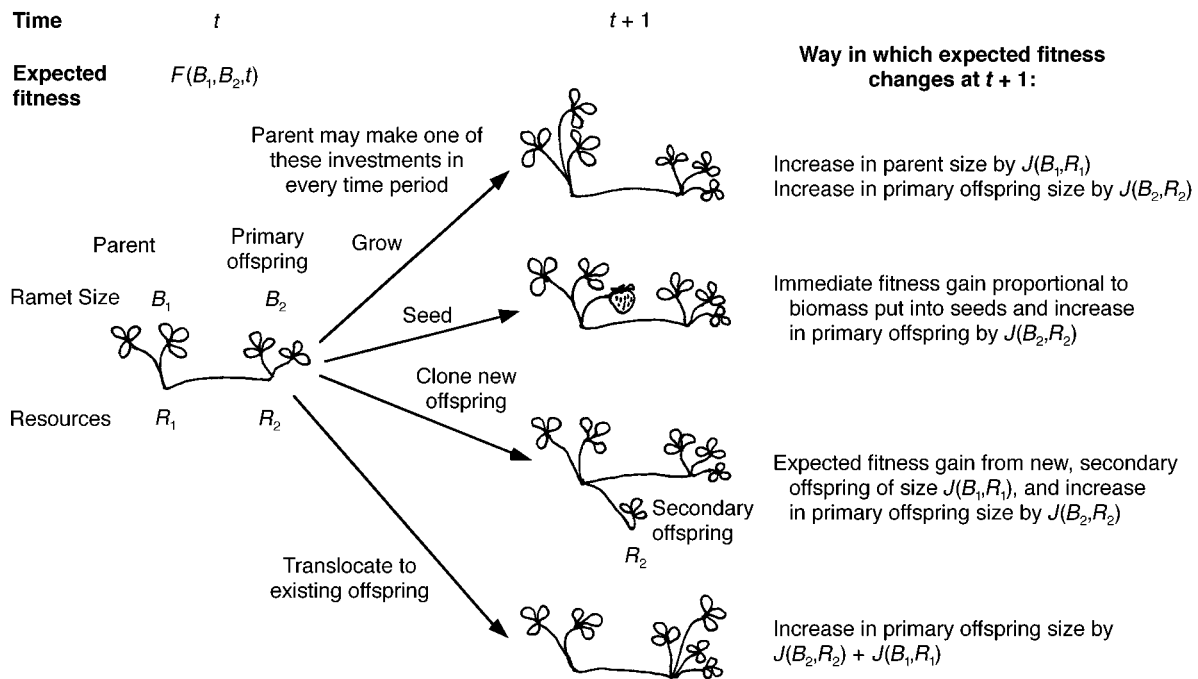


FIG. 1. Diagram of the model illustrating the four allocation options available to a parent ramet for investing the carbon it assimilates in every time period.

turbances. Consequently, the resources they encounter are unpredictable. In contrast, since clonal offspring stay in the same habitat as the parent ramet, the resources they encounter are more predictable than those experienced by widely dispersing seeds. In addition, clonal offspring may remain connected with a parent, leaving open the possibility for continued translocation. We develop a model to investigate reproductive trade-offs between such clonal and sexual offspring, and we maintain that these generalizations about clonal and sexual offspring are reasonable simplifications. Much empirical and theoretical work that has been done in this area explores the effects of density on relative investment in clonal and sexual reproduction (Williams 1975, Abrahamson 1975, 1979, Bishop and Davy 1985, Sackville Hamilton et al. 1987). Instead, we focus on the productivity of parent and clonal offspring ramets, which may be influenced indirectly by density as well as directly by resource abundance.

Across species, populations, and individuals, clonal organisms show a variety of plastic responses in mode of reproduction and growth (Watson 1984, Silander 1985, Hartnett 1990, Kik et al. 1990, Wijesinghe and Whigham 1997). Recent attention has focused on plastic traits that vary with an individual's attributes and its surroundings. We have developed a dynamic state variable model to predict a ramet's allocation to growth, seed production, and clonal offspring that will maximize genet fitness in a clonal plant. Dynamic state variable models (Mangel and Clark 1988, Mangel and Ludwig 1992) enable one to predict plastic patterns of

growth and reproduction, incorporating a number of factors (e.g., an organism's size, the time in the season, and the productivity of and risk of mortality in the environment), while still having a tractable model easily programmed on a personal computer. This type of modeling has been suggested as a good tool to examine the complex life histories of facultatively clonal organisms (Grosberg 1992). Two previous models (Loehle 1987, Sakai 1995) addressed how the resource environment affects clonal and sexual reproductive investments. By using the dynamic state variable approach, we could examine how ramet size and time interact with the resource environment in their effects on reproduction. In addition, we modeled integration between ramets. Caraco and Kelly (1991) developed a dynamic state variable model for integration in clonal plants, but they did not include clonal and sexual reproduction.

The model predicts selection on a ramet's investments that depend on time, the ramet's size, the productivities of a reproductive ramet and its clonal offspring, and the probabilities of ramet and genet death. The genet encompasses a "parent ramet" whose allocation strategies are predicted; the first "primary offspring" ramet, produced clonally by the parent; and additional "secondary offspring" produced after the primary offspring (Fig. 1). In every period of time, a parent ramet may allocate photosynthate to achieve the following purposes: (1) grow and forego immediate offspring production in anticipation of payoffs in the future; (2) produce seeds, which immediately augments

TABLE 1. Summary of variables used in the model.

Variable	Baseline value <sup>†</sup>	Definition <sup>‡</sup>
$B_1$	NA	Biomass of the parent ramet
$B_2$	NA	Biomass of a clonal offspring
$B_{\max}$	10	Maximum ramet size
$R_1$	NA	Resource level in the patch of the parent
$R_2$	NA	Resource level in the patch of clonal offspring
$t_{\max}$	10	Length of the season
$z$	1	Exponent of the contribution of ramet biomass to fitness (Eq. 1)
$k$	0.3	Rate at which carbon fixation slows with increasing ramet size (Eq. 2)
$\mu$	0.02	Probability of genet mortality per unit time
$d$	0.05	Probability of ramet mortality per unit time given that a connected ramet has not been killed in the same time interval
$\nu$	0.05	Probability of ramet mortality per unit time given that a connected ramet has been killed in the same time interval (chance of death correlated between ramets)
$q$	0.1	Gain in fitness per unit biomass invested in seed production
RE	NA	Reproductive effort: mean biomass put into establishing new clonal offspring, translocation to established offspring, and seed production
Vegetative reproductive effort	NA	Proportion of RE invested in cloning new offspring vegetatively in simulated ramets obeying predictions from dynamic programming equations
Sexual reproductive effort	NA	Proportion of RE invested in seed production
Translocational reproductive effort	NA	Proportion of RE invested in translocating fixed carbon to established clonal offspring

<sup>†</sup> NA, not applicable.

<sup>‡</sup> Model units are not explicitly specified, although biomass units for  $B_1$ ,  $B_2$ , and  $B_{\max}$ , and for reproductive efforts may be inferred as grams or decagrams; resource units for  $R_1$  and  $R_2$  may be nutrient concentration or light availability, for example; and time units for  $t_{\max}$  may be inferred as weeks or months.

fitness; (3) establish a new clonal offspring that grows, but that is not mature enough to reproduce; or (4) translocate assimilate to an already-established, primary offspring, so the offspring's biomass increases, not only from its own growth, but also from photosynthate sent from the parent. Clonal reproduction (3) and translocation (4) differ in that clonal reproduction is the establishment of a new clonal offspring, while translocation augments the growth of an offspring that has already been produced. Thus, clonal reproduction increases the number and translocation increases the size of offspring.

The behavior of a ramet is chosen from the four options described, so as to maximize the expected fitness of the genet. Selection in our model operates on both the levels of the ramet (the size, seed production, and clonal offspring production by a given ramet) and the genet (expected fitness gained from all the ramets of the clone), and so incorporates the hierarchical nature of selection in clonal plants (Tuomi and Vuorisalo 1989, Fagerström 1992, Pedersen and Tuomi 1995, Wikberg 1995, Vuorisalo et al. 1997). By enlarging the clone, growth and vegetative reproduction pay off at the end of the season, provided the ramets and the genet survive until then. In contrast, a genet obtains the fitness payoff from seed production immediately, regardless of ramet or genet survival later in the season after those seeds were produced.

To predict how ramet and genet mortality affect investments, we include three mortality probabilities: the

chance that an individual ramet dies, given that no connected ramets die; the chance that an individual ramet dies, given that a connected ramet also dies, allowing for mortality to be correlated among ramets; and the probability that the entire genet is killed.

Clonal offspring may have a different productivity from that of their parent, if those offspring encounter a different resource condition than that of the parent. For simplicity, all clonal offspring of a parent experience the same resource level. Photosynthate may travel acropetally from parent to offspring, but not in reverse (similar to a previous model of translocation; Caraco and Kelly 1991). This relatively simple scenario describes how the availability of one resource affects selection on investment in clonal offspring and seeds. In a subsequent model, we are examining a more complicated scenario in which each clonal offspring may experience different resource levels, assimilation is determined by both nitrogen and light, and translocation of nitrogen and carbon may occur acropetally and basipetally (Gardner and Mangel, *unpublished manuscript*).

#### METHODS: DESCRIPTION OF THE MODEL

Parameters and functions used in the model are summarized in Tables 1 and 2, respectively. In our modeling, we do not specify units explicitly, although time units may be inferred as weeks or months, and biomass units as grams or decagrams.

TABLE 2. Summary of functions used in the model.

Function	Definition
$g(R)$	Photosynthetic rate of ramet in resource level $R$
$J(B, R)$	Assimilation rate (dimensions of biomass per unit time) for ramet of biomass $B$ in resource level $R$
$F(B_1, B_2, t)$	Fitness of genet with parent biomass $B_1$ and offspring biomass $B_2$ at time $t$
$I(B_1, B_2, t)$	Allocation matrix specifying state-dependent strategies of where to allocate photosynthate

*Fitness*

This model describes a single season of genet growth for perennial ramets that can survive to future seasons. We assume that ramets must be perennial, since clonal offspring are immature and cannot reproduce in the season they are produced. Thus, the fitness at the end of one year's season correlates with expected fitness starting the season of the next year. We assume that expected fitness at the season's end depends on ramet size, since larger ramets stand a better chance of surviving to the next season and then begin with a size advantage, and on ramet number, since a genet with more ramets is likely to leave more descendents.

We let  $F(B_1, B_2, t)$  represent the maximum expected fitness of a ramet with biomass  $B_1$ , and primary offspring of biomass  $B_2$ , at time  $t$  (Houston et al. 1988, McNamara and Houston 1996). Maximizing the expected, state-dependent reproductive success identifies the strategies of investment that lead to the highest fitness (McNamara 1991, 1993). Terminal fitness (Mangel and Clark 1988) is the residual fitness in the final time period of the season  $t = t_{\max}$ :

$$F(B_1, B_2, t_{\max}) = B_1^z + B_2^z. \tag{1}$$

Both the parent and the offspring ramet contribute independently to fitness, hence their sum. (Note the importance of the number of ramets.) The exponent  $z$  characterizes the importance of ramet size to fitness. For  $0 < z < 1$ , fitness increases as a concave function of ramet size, so the payoff of increasing ramet size declines with ramet biomass. This might be the case, for example, if over-winter survival (from the end of one season until the start of the next) of larger ramets were lower than that of smaller ramets, perhaps because of exposure or disease (see references in Finch 1990: 206–247), or if ramet number is more important than ramet size (Johansson 1994). For  $z = 1$ , the payoff to fitness of ramet size is linearly dependent on biomass. For  $z > 1$ , expected fitness grows as a convex function of size, so larger ramets contribute relatively more than smaller ramets. This might be the case, for example, in a competitive situation if larger ramets can capture disproportionately more resources than smaller ramets, thus gaining disproportionately by starting the next sea-

son with a size advantage (de Kroon et al. 1992, Johansson 1994).

*The environment and photosynthetic rate*

There are three resource levels,  $R$ : low ( $R = 1$ ), medium ( $R = 2$ ), and high ( $R = 3$ ). The rates of photosynthesis per unit biomass in resource levels 1, 2, and 3 are  $g(1) = 0.10$ ,  $g(2) = 0.25$ , and  $g(3) = 0.40$ . The environment remains homogeneous within a parent ramet's patch, and within the area surrounding a parent where all its clonal offspring establish, but may vary between the parent and its clonal offspring. The resource level of the parent,  $R_1$ , and that of the clonal offspring,  $R_2$ , are specified. For example, a habitat with  $R_1 = R_2 = 1$  is uniformly poor. A situation where  $R_1 = 1$  and  $R_2 = 3$  might occur during colonization where the first ramet establishes in a poor patch, such as right along a stream's edge, and the prospects are good for offspring to spread up the bank into more stable, rich, alluvial soil. If  $R_1 = 3$  and  $R_2 = 1$ , a ramet can establish and persist in an anomalously good patch, but is surrounded by a sea of resource scarcity. For simplicity, we do not include density-dependent competition among the ramets of a single genet or resource depletion, so that  $R_1$  and  $R_2$  are constant throughout the season. Future, more complicated models could incorporate such factors.

The photosynthate  $J(B, R)$  produced by a ramet of size  $B$  with resource level  $R$  in one time period is

$$J(B, R) = Bg(R) \left( 1 - \frac{kB}{B_{\max}} \right). \tag{2}$$

If  $k = 0$ , then carbon production increases linearly with ramet size. If  $0 < k \leq 1$  then sugar production increases at a decreasing rate with ramet size, as typically occurs in plants. Ramets may grow no larger than  $B_{\max} = 10$ . Results were calculated using  $k = 0.3$ , unless specified otherwise (Table 1).

*The dynamic programming equations*

The dynamic program determines the optimal investment, given a plant's current states ( $B_1, B_2, t$ ), by choosing the allocation strategy that maximizes expected terminal fitness. This is accomplished by a backward iteration through time, beginning with terminal fitness  $F(B_1, B_2, t_{\max})$ , specified in Eq. 1. The program starts by solving for the optimal strategy, during time  $t_{\max} - 1$  in terms of fitness in time  $t_{\max}$ , and continues backward, solving for optimal strategies in each time period  $t$  in terms of  $t + 1$ , so

$$F(B_1, B_2, t) = \max(F_{\text{Grow}}, F_{\text{Seed}}, F_{\text{Clone}}, F_{\text{Tran}}) \tag{3}$$

where  $F_{\text{Grow}}$ ,  $F_{\text{Seed}}$ ,  $F_{\text{Clone}}$ , and  $F_{\text{Tran}}$  are the fitness values if the parent ramet grows, produces seeds, establishes a new clonal offspring, or translocates carbon from the parent to the established primary offspring.

We use the notation  $\Delta B_1 = J(B_1, R_1)$  and  $\Delta B_2 = J(B_2, R_2)$ ;  $\mu$  = the probability of genet mortality;  $d$  =

the probability of ramet death, given that a connected ramet does not die in the same time interval; and  $\nu$  = the probability of ramet death, given that a connected ramet has been killed. If a parent ramet grows, then if  $B_2 = 0$ , the expected fitness at time  $t$  in terms of fitness at time  $t + 1$  is

$$F_{\text{Grow}} = (1 - \mu)(1 - d)F(B_1 + \Delta B_1, 0, t + 1) \quad (4a)$$

and, if  $B_2 > 0$ ,

$$F_{\text{Grow}} = (1 - \mu)\{(1 - d)^2F(B_1 + \Delta B_1, B_2 + \Delta B_2, t) + d(1 - \nu)[F(B_1 + \Delta B_1, 0, t) + F(0, B_2 + \Delta B_2, t)]\}. \quad (4b)$$

To garner any fitness in  $t + 1$ , the entire clone must survive during the interval  $t$ , which occurs with probability  $1 - \mu$ . The first term in the sum on the right hand side of Eq. 4b represents the expected fitness if both the parent and the offspring survive to the next time interval, and the second and third terms represents fitness if either the offspring or parent dies, respectively. The parent's biomass increases as a result of its own growth, as does the size of the clonal offspring. The sizes  $B_1$  and  $B_2$  cannot exceed  $B_{\text{max}}$ , so they are set equal to this maximum size if  $B + \Delta B > B_{\text{max}}$ .

If the parent ramet produces seeds, then the parent does not grow, but the offspring does, and the fitness of the clone increases from the seeds produced. Thus, if  $B_2 = 0$ ,

$$F_{\text{Seed}} = (1 - \mu)(1 - d)F(B_1, 0, t + 1) + q\Delta B_1 \quad (5a)$$

and, if  $B_2 > 0$ ,

$$F_{\text{Seed}} = (1 - \mu)\{(1 - d)^2F(B_1, B_2 + \Delta B_2, t) + d(1 - \nu)[F(B_1, 0, t) + F(0, B_2 + \Delta B_2, t)]\} + q\Delta B_1. \quad (5b)$$

The factor  $q$  weights the final term that represents the immediate increase (since it is not expressed in terms of expected fitness at  $t + 1$ ) in fitness from producing seeds; if the parent ramet, or even the entire genet, dies between  $t$  and  $t + 1$ , the genet still gains fitness from those seeds it produced. The factor  $q$  may account for the fact that sexual offspring are less closely related to the parent than vegetative offspring, that creating seeds includes costs of floral structures, and that the probability of seedling establishment may be low (all of which reduce  $q$ ); as well as the benefits from recombination, genetically diverse sexual offspring, and long-distance dispersal and colonization (which raise  $q$ ).

If the ramet produces a new clonal offspring, then, if  $B_2 = 0$ ,

$$F_{\text{Clone}} = (1 - \mu)\{(1 - d)^2F(B_1, \Delta B_1, t + 1) + d(1 - \nu)[F(B_1, 0, t + 1) + F(0, \Delta B_1, t + 1)]\} \quad (6a)$$

and, if  $B_2 > 0$ ,

$$F_{\text{Clone}} = (1 - \mu)\{(1 - d)^3[F(B_1, \Delta B_1, t + 1) + F(B_1, B_2 + \Delta B_2, t + 1) - F(B_1, 0, t + 1)] + d(1 - \nu)^2[F(B_1, \Delta B_1, t + 1) + F(B_1, B_2 + \Delta B_2, t + 1) + F(0, B_2 + \Delta B_2, t + 1) + F(0, \Delta B_1, t + 1)] + d\nu(1 - \nu)[F(B_1, 0, t + 1) + F(0, B_2 + \Delta B_2, t + 1) + F(0, \Delta B_1, t + 1)]\}. \quad (6b)$$

In Eq. 6b, the terms multiplied by  $(1 - d)^3$  represent the contributions of parent and both clonal offspring, corrected by subtracting  $F(B_1, 0, t + 1)$  for counting the parent twice in the fitness function of each offspring. Next, with probability  $d(1 - \nu)^2$  that only one ramet dies, is the contribution to fitness from the parent and newer offspring if the older primary offspring is killed, plus the fitness if the primary offspring continues to grow and the newer offspring dies, plus fitness if the parent dies but both clonal offspring survive. Finally, with probability  $d\nu(1 - \nu)$  that two of the three ramets are killed, is the fitness if both offspring die, plus fitness if the parent and newer offspring die, plus fitness if the parent and primary offspring die. Augmenting fitness from a new clonal offspring by replacing  $B_2$  with  $\Delta B_1$  in the function  $F(B_1, \Delta B_1, t)$  assumes that all offspring of a given size at a given time in the season make an equivalent contribution to fitness, regardless of the order in which they are produced.

The last option, if a parent translocates sugar to a clonal offspring that has already been established (only possible if  $B_2 > 0$ ), then

$$F_{\text{Tran}} = (1 - \mu)\{(1 - d)^2F(B_1, B_2 + \Delta B_2 + \Delta B_1, t) + d(1 - \nu) \times [F(B_1, 0, t) + F(0, B_2 + \Delta B_2 + \Delta B_1, t)]\}. \quad (7)$$

Translocation enlarges the primary offspring, both from its own assimilation and from that of the parent.

The investment that maximizes fitness is denoted by  $I(B_1, B_2, t)$  and can be to grow, to produce seeds, to vegetatively establish a new offspring, or to translocate to the established primary offspring. We used linear



interpolation to calculate fitnesses for noninteger values of state variables (Mangel and Clark 1988).

#### Comparing the fitness of suboptimal strategies

Large differences between the fitnesses resulting from suboptimal behaviors select strongly for behavioral plasticity to make optimal allocations. We compared the fitnesses of ramets without the option of plastically switching between clonal reproduction and seed production with those capable of allocating to variable, fitness-maximizing strategies. To do this, we calculated the fitness of ramets that grew until they reached the maximum allowable size ( $B_{\max}$ ) and then either produced only clonal offspring or only seeds. The fitness of ramets that could only clone or only make seeds was solved by backward iteration according to

$$F_{\text{CO}}(B_1, B_2, t) = \begin{cases} F_{\text{Grow}} & \text{if } B_1 < B_{\max} \\ F_{\text{Clone}} & \text{if } B_1 = B_{\max} \end{cases} \quad (8)$$

and

$$F_{\text{SO}}(B_1, t) = \begin{cases} F_{\text{Grow}} & \text{if } B_1 < B_{\max} \\ F_{\text{Seed}} & \text{if } B_1 = B_{\max}. \end{cases} \quad (9)$$

#### Simulations

All programming was done in True BASIC. We simulated ramets growing and reproducing according to the state-dependent strategies  $I(B_1, B_2, t)$  predicted to result in the highest fitness, which enabled us to examine how the environmental parameters in the model affect the growth of a parent, its production of clonal offspring and seeds, and the size of clonal offspring. These data are easier to interpret than looking at a multidimensional allocation matrix and are analogous to the data one collects in the field. Depending on the assimilation rate and the investments made in the past, a genet may reach some combinations of state variables ( $B_1, B_2, t$ ) only rarely. The simulations, by going forward in time and using the predicted behaviors from the solution of the dynamic equations solved backward in time, summarize the investments of individuals obeying many state-dependent allocation rules.

For each combination of parameters, we began with a population of 500 ramets. To capture the observation that, in a real population, ramets vary in size at the beginning of the season, the starting size of each ramet was randomly chosen from the truncated negative exponential distribution,

$$\Pr\{\text{size} = s\} = \frac{e^{-s/5}}{\sum_{i=1}^{B_{\max}} e^{-i/5}} \quad (12)$$

so that the mean size was approximately five (in the limit as  $B_{\max} \rightarrow \infty$ ). In all cases, ramets began the simulations with no clonal offspring. Ramet productivity was computed according to Eq. 2, and this carbon was put into growth (increasing  $B_1$ ), seeds, clonal offspring,

or translocation according to  $I(B_1, B_2, t)$ . The cumulative amounts over the season that ramets allocated to seeds, clonal offspring, and translocation were averaged over the 500 ramets, and the total reproductive effort (RE) was computed as their sum. The proportion of this RE that is comprised by seeds is called sexual reproductive effort, that by new vegetative offspring is vegetative reproductive effort, and that by translocation to established primary offspring is translocational reproductive effort. The mean sizes of parent and primary offspring ramets were computed at the end of the season. The growth of primary offspring, as well as translocation, increased the size  $B_2$ . The growth of secondary offspring was not simulated, but only the initial investment made by the parent ramet in the establishment of secondary offspring. Although ramet and genet mortalities were used in solving the dynamic programming equations to determine the investment strategies that result in the highest fitness, mortality was not included in the simulations. We did this since ramets that die have zero reproductive biomass after death and a size of zero at the end of the season. Including these ramets in summary calculations would lower the means, raise the standard errors, and make the results bimodal, with a peak at zero and a peak for the mean of the surviving ramets. In addition, reproductive and growth biomasses would appear to decline as the season progressed, since fewer individuals would remain alive, despite the fact that selection on individual ramets may not favor a decline in reproduction.

Although the environment is unrealistic, in that it is predictable with all parent ramets starting in patches of resource level  $R_1$  and their clonal offspring establishing in patches of  $R_2$  (i.e., there is resource heterogeneity between a parent and its clonal offspring, but not among clonal offspring), it does allow one to examine how specific circumstances affect the investments of individual ramets. In another paper, (Gardner and Mangel, *unpublished manuscript*) we present a more realistic, but also more complicated, model in which clonal offspring encounter a spatially heterogeneous environment.

#### RESULTS AND DISCUSSION

We incorporate the discussion with the results, allowing us to assess model predictions in light of empirical findings, and to modify our choice of parameters appropriately in subsequent analyses. First, we assess how well predictions, using baseline parameter values (Table 1), fit empirical observations of investments in clonal plants, and we suggest three reasons that predicted rates of sexual reproduction are below what is observed in the field. Second, we change the parameter values according to these suggestions and examine how ramet size and the time in the season affect predicted allocation strategies. Third, we describe how the resource environment influences allocation strategies. Next, we compare the fitness consequences of subop-

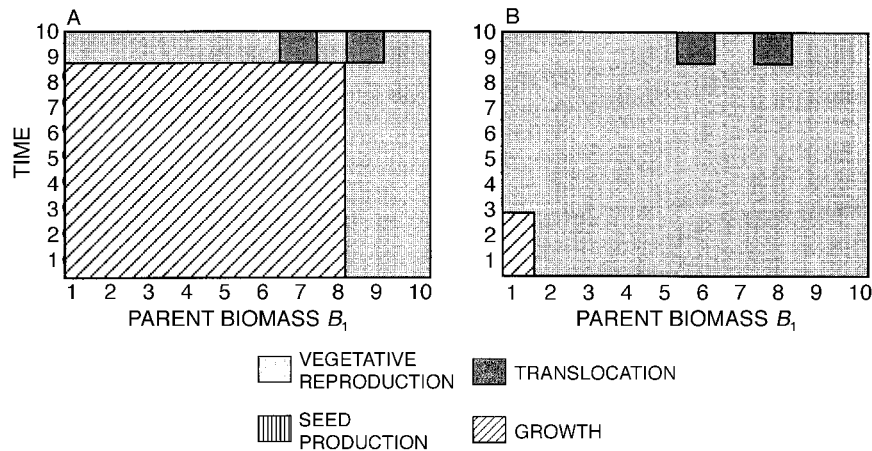


FIG. 2. State space of investment allocations  $I(B_1, B_2, t)$ , when offspring size is  $B_2 = 1$ , for (A) parent resources  $R_1 = 2$  and offspring resources  $R_2 = 1$ , and (B)  $R_1 = R_2 = 2$ . Growth is favorable when offspring resources are less than parent resources ( $R_2 < R_1$ ) and ramets are not very large; vegetative reproduction is favorable otherwise. Parameters are set at the baseline case:  $k = 0.3$ ,  $z = 1$ ,  $d = 0.05$ ,  $v = 0.05$ ,  $\mu = 0.02$ ,  $q = 0.1$ . Unless otherwise noted, the parameter values will be the same in Figs. 3–7.

timal investment behaviors and examine how a size-dependent decline in productivity affects investments. Finally, we discuss how predictions from our model compare with results from other theoretical studies.

#### Investments resulting from baseline parameter values

Using the baseline parameter values specified in Table 1 leads to the prediction that seed production is never the most favorable strategy. The same prediction was made by Nishitani et al. (1995). Instead, parent growth is favorable, if parent resources are greater than offspring resources ( $R_1 > R_2$ ) and the parent ramet is not large (Fig. 2A), so that the parent takes advantage of a good patch that is surrounded by less productive conditions. Otherwise, vegetative reproduction is the best option for most other states (Fig. 2B), as parents start up clonal offspring that can grow independently and take advantage of surrounding conditions that are at least as rich as those in the parent's patch.

However, since clonal plants do invest in flowering, the baseline parameter values of Fig. 2 must assume that either the risks of genet or ramet mortality ( $\mu$ ,  $d$ , and  $v$ ) are too low, the payoff of seeds ( $q$ ) is too low, and/or the importance of ramet size to fitness ( $z$ ) is too high. We will examine the effects of each of these: (1) mortality; (2) fitness payoff of seeds; and (3) ramet size vs. number.

**Mortality rates.**—Model output indicates that sexual reproductive effort increases while vegetative reproductive effort and translocational reproductive effort decline as mortality rates rise. In the field, rates of flowering have been observed to rise in response to events that may indicate an increased risk of ramet mortality (Thompson and Guttridge 1960, Mason 1966, 1967, Gadgil and Solbrig 1972, Abrahamson and Gadgil 1973, Harper 1977, Barkham and Hance 1982, Gut-

tridge 1989, Brewer and Platt 1994), or genet mortality (Hartnett 1987, 1990, Brewer and Platt 1994, Rea and Ganf 1994). A model by Sackville Hamilton et al. (1987) also predicts an increase in sexual reproduction with the chance of genet mortality. A genet mortality of  $\mu = 0.02$  deaths/time interval results in a  $(0.98)^9 = 83\%$  chance of genet survival over the course of the entire season, and  $d = v = 0.05$  results in a  $(0.95)^9 = 63\%$  chance of ramet survival (Fig. 3A–C). Rates of genet mortality or ramet mortality, given that a clone mate is not killed ( $d$ ), would have to be  $>0.20$  deaths/time interval (only 13% survival through the entire season) for seed production to become favorable. Thus, mortality would have to be far higher than what is usually observed in the field (Lovett Doust 1981, Angevine 1983, Hartnett 1987, Nishitani and Kimura 1995, Wijesinghe and Whigham 1997; but see Welker and Briske 1992). The correlated risk of death, given that a clone mate is killed ( $v$ , given that  $d = 0.05$ ), would have to be even higher, at  $v \geq 0.6$  deaths/time interval, which is even further above observations from the wild (Cain and Damman 1997, Gardner 1997).

Looking at the response of the total biomasses invested in reproduction or in ramet growth to rises in the rate of genet or ramet mortality, the model predicts that ramets do better to reproduce (RE in Fig. 3A, B) and forego growth (Fig. 3D, E), if there is a substantial threat that they will not survive the season. Although the effect of the correlated ramet mortality rate on proportional reproductive investments is clear, given that a connected ramet is killed ( $v$ ), the effects of correlated ramet mortality on reproductive effort and ramet size are not obvious, when the uncorrelated ramet mortality rate ( $d$ ) is low, because they are “hidden.” That is, it is fairly unlikely, in any given time interval, that one ramet is attacked, so the chance that two ramets are

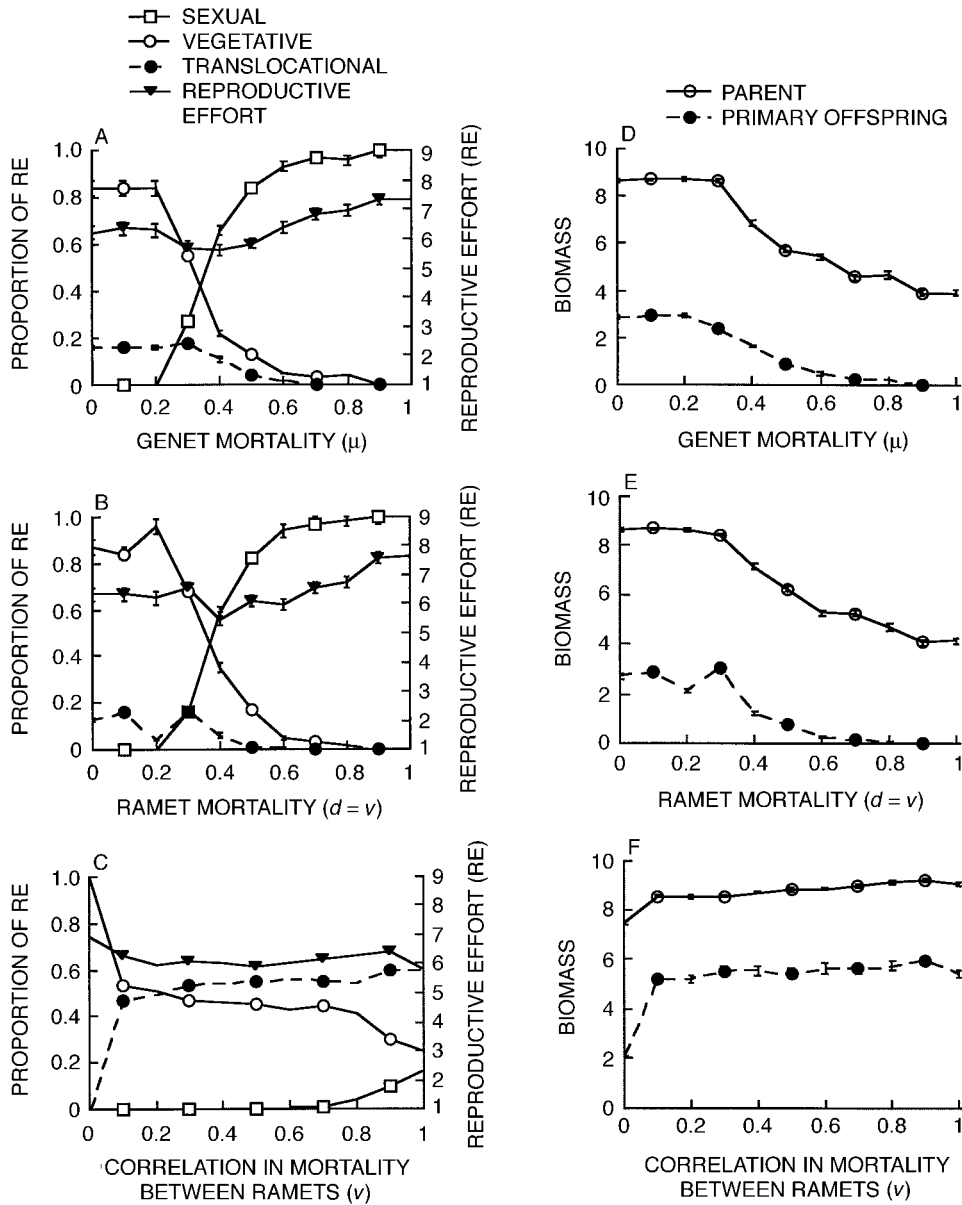


FIG. 3. Proportional sexual, vegetative, and translocational reproductive efforts, total reproductive effort (RE), and parent and primary offspring size of simulated ramets at the end of the season vs. the probabilities of (A) and (D) genet mortality ( $\mu$ ); (B) and (E) ramet mortality, given that a connected ramet survives that time interval ( $d$ ); and (C) and (F) ramet mortality, given that a connected ramet does not survive that time interval ( $v$ ) when  $d = 0.1$ . The vegetative proportion falls at the expense of seed production as mortality rates rise.

attacked (with probability  $d \times v$ ) must be even less. Thus, we plotted the effect of correlated mortality ( $v$ ) on reproductive effort and ramet size using  $d = 0.1$  (Fig. 3C, F). A negative correlation between ramets in the probability of mortality ( $v < d$ ) results in more reproductive effort and smaller ramets than does a positive correlation of mortality between ramets ( $v > d$ ); the influence of correlated mortality ( $v$ ) is, unintuitively, opposite to that of uncorrelated ramet mortality ( $d$ ) or genet mortality ( $\mu$ ). It can be understood, however, when one notes that translocation to established

offspring increases with correlated mortality  $v$  (in contrast to its decrease with  $d$  or  $\mu$ ); when mortality is positively correlated among ramets, the fates of clone mates are not independent, and, therefore, having many ramets does not reduce the risk of genet mortality. This shifts the balance of the size vs. number trade-off toward size, so parent ramets grow more and start up fewer new offspring, but more resources are sent to support those offspring that are established.

*Fitness payoff of seeds.*—In the second case, the value of 0.1 for the fitness gain per unit biomass invested



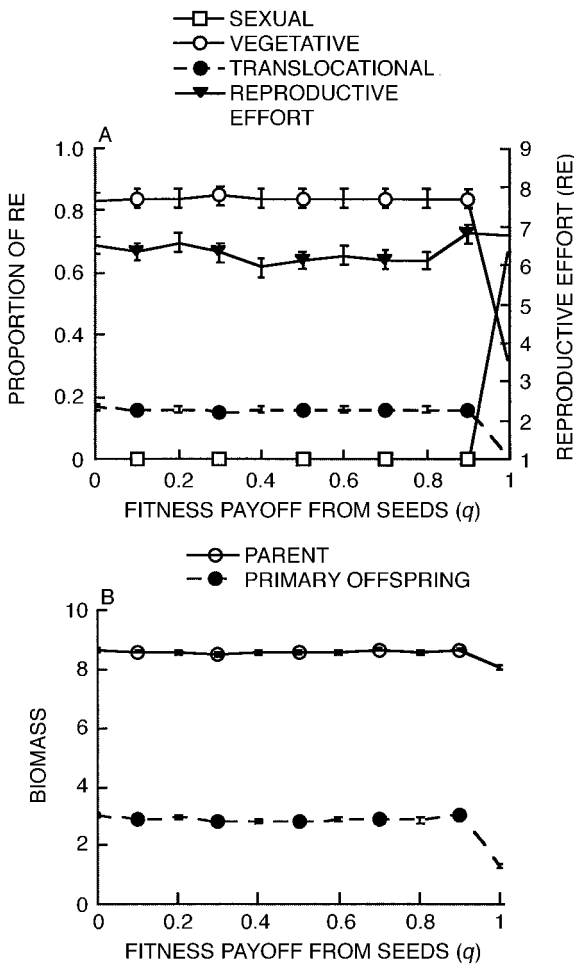


FIG. 4. (A) Vegetative, sexual, and translocational reproductive efforts, and total biomass invested in reproduction (RE) of simulated ramets vs. the fitness payoff per unit biomass invested in seed production ( $q$ ). (B) Parent and primary offspring biomass at the end of the season vs.  $q$ . An increase in sexual reproductive effort and decreases in vegetative and translocational reproductive efforts and ramet size are observed only for high values of  $q$ .

in seeds ( $q$ ) may underestimate the payoff from seed production. For predictions to favor any seed production, given the baseline mortality rates, the payoff per unit biomass from sexual allocation ( $q$ ) would have to be  $>0.9$  (Fig. 4A). Such a high fitness payoff from seeds drives resources from growth, so ramets reach a smaller size (Fig. 4B). The rate of seedling establishment in clonal plants is usually very low in the wild, so low that even  $q = 0.1$  seems too high (Harper 1977, Nishitani and Kimura 1995, Jonsson et al. 1996, Schlöpfer and Fischer 1998). However, high levels of genetic diversity in clonal plant populations indicate that seedlings do establish (Ellstrand and Rouse 1987, Alpert et al. 1993, Eriksson and Bremer 1993, Widen et al. 1994, Schlöpfer and Fischer 1998) and that sexual offspring may be important to genet fitness (Bell 1985,

Stearns 1985, Kondrashov 1988, Ladle 1992, Lynch et al. 1993). In addition, seeds that colonize new habitats may contribute disproportionately to genet fitness; the success of clonal plants as weeds (Lapham 1985, Santos et al. 1997, Smeda et al. 1997, Yenish et al. 1997) and invasive species (Smith 1985, Cudding and Stone 1990, Room 1990, Soukupova 1992, Schmid and Weiner 1993, Philbrick and Les 1996) suggests that when colonization is successful, colossal payoffs ensue. Finally, in some cases ramets may incur few or no costs from producing seeds (Reekie and Bazzaz 1987, 1992, Wikberg et al. 1994).

*Ramet size vs. number.*—With a shift in the size vs. number trade-off favoring size (increase in  $z$ ), sexual reproductive effort falls and vegetative reproductive effort rises, and for increases in  $z > 1$ , vegetative reproductive effort drops, while translocational reproductive effort captures a substantial proportion of reproductive biomass (Fig. 5A). Meanwhile, ramets put less biomass into reproduction and, instead, put more into growth (Fig. 5B). According to the third explanation for the lack of seed production, in which the linear function with  $z = 1$  overestimates the importance of ramet size,  $z = 0$  would be necessary, so that fitness would be independent of ramet size. In other words, vegetative biomass would not contribute to fitness, as might be the case if ramets were annuals. In species that form a dense mat of ramets, ramet number may be more important than ramet size, and  $z$  may be low. For example, in *Hieracium pilosella* a high rate of herbivory by rabbits not only increases the rate of flowering, but also increases clonal growth (Bishop and Davy 1984). This results in dense mats of young, clonally recruited ramets. Two observations, however, do not support the proposition that ramet number is dramatically more important than ramet size (i.e., that  $z \ll 1$ ). First, plant size is often a very good predictor of reproductive investments (Ashmun and Pitelka 1985, Mendez and Obeso 1993, Worley and Harder 1996, Wijesinghe and Whigham 1997). Second, prolonged translocation to clonal offspring is not predicted by the model to occur for values of  $z$  low enough for some seed production to be favorable (at any time in a ramet's life history, not necessarily simultaneously). Yet, we know that many clonal plants both produce seeds and provide continued support to clonal offspring (Ryle and Powell 1972, Ashmun et al. 1982; see references in Pitelka and Ashmun 1985). Consequently, although selection for many small ramets may be important in conjunction with the fitness payoff from seeds and genet and ramet mortalities, overestimating the advantage of ramet number over ramet size in our set of baseline parameter values is unlikely to be the sole factor responsible for the lack of seed production.

#### *Effects of ramet size and time in the season on investments*

Examining predictions more closely by looking at size- and time-dependent strategies illuminates other

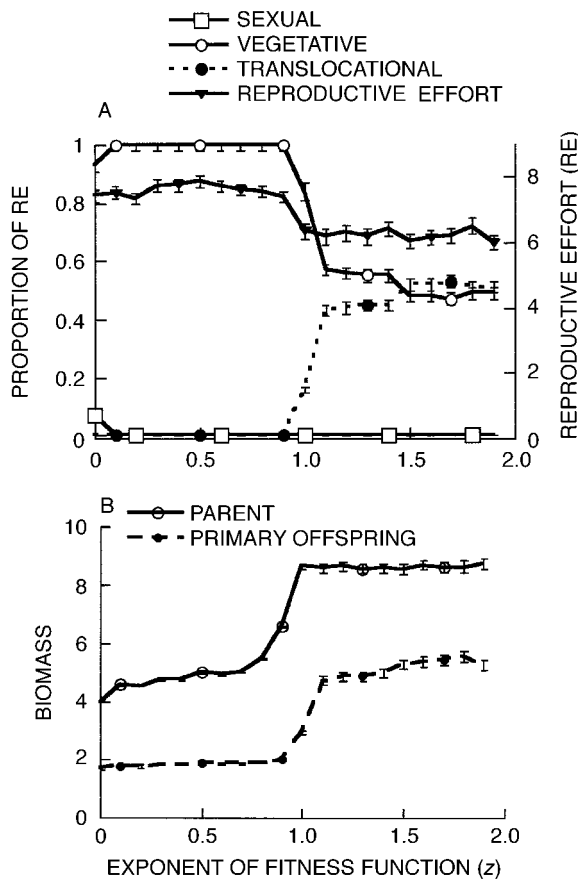


FIG. 5. (A) Proportional and total reproductive biomass and (B) ramet size vs. the exponent of ramet biomass ( $z$ ) in the terminal fitness function (Eq. 1). For  $z > 1$ , large ramets contribute proportionally more than small ramets to fitness, and translocation to established offspring captures as much of reproductive allocations as does producing new offspring.

differences between the cases of seed production as a result of high mortality rates vs. seed production as a result of a high contribution of seeds, and low contribution of ramet size, to fitness. When genet and ramet mortality rates are high, solutions of the dynamic equations indicate that seed production may depend more on time than on ramet size (Fig. 6). Early in time, ramets are predicted to have the highest fitness if they produce seeds (Fig. 6A, B), so as to accumulate some fitness in case death occurs before the season's end. Later in time, they do best to grow if parent resources are greater than offspring resources ( $R_1 > R_2$ ) and the parent is small, to clone new offspring if  $R_1 \leq R_2$  (Fig. 6C), and to translocate resources to established clonal offspring at the end of the season, regardless of  $R_1$  and  $R_2$ . The state variable model by Caraco and Kelly (1991) also predicted that translocation to clonal offspring in the final time interval was a better investment strategy than growth.

If seeds contribute considerably, and ramet size only a little to fitness, then, for poor parent resources ( $R_1 =$

1), time is still the critical factor determining allocation strategies (Fig. 6D). In contrast, for moderate to high parent productivities ( $R_1 \geq 2$ ), ramet size may supersede time as the determinant of states in which seed production is optimal (Fig. 6E, F). Small ramets are predicted to engage in growth (early in the season) and vegetative reproduction (later in the season), and larger ramets to direct resources to seed production throughout the season (Fig. 6E). Like the previous baseline case (Fig. 2) and high mortality case (Fig. 6A–C), as surrounding conditions improve (increasing  $R_2$ ) vegetative reproduction becomes favorable for more states, consequently seed production is delayed at the expense of producing new clonal offspring (Fig. 6F). In the field, ramet size is usually a better predictor of fecundity than ramet age (Nishitani and Kimura 1995), supporting model results based on the assumption that seeds contribute more to fitness than one might guess from scanty rates of seedling establishment. On the other hand, at least in three *Fragaria* species, seed production also depends on time in the season, with fruiting occurring in early spring and most vegetative reproduction happening later (Angevine 1983, Gardner 1997). While a number of factors not included in the model, such as pollinator abundance and temporal opportunities for germination, probably figure more critically into the timing of seed production than mortality rates, high mortality risks cannot be discounted altogether. Thus, the most likely reason for investment in seed production may be a combination of moderately high risks of mortality, as well as big gains from those rare seedlings that do survive. In our analyses, we modified the baseline parameters accordingly ( $\mu = 0.03$ ,  $d = \nu = 0.08$ ,  $q = 0.8$ , and  $z = 1$ ).

#### Effect of resources on sexual and vegetative investments

Average levels of investments in growth and reproduction by simulated ramets show how parent and offspring resources influence the behavior of ramets obeying state-dependent strategies. As the productivity of the parent ramet increases, parents put more biomass into reproduction (Fig. 7A; effect of parent resource level  $R_1$ ). Looking at the effect of parent productivity on the division of reproductive biomass into sexual reproductive effort and vegetative reproductive effort, parents with low or high resources are predicted to devote proportionately more to seed production than do parents with intermediate resources (when  $R_2 = 1$ , so that any seed production occurs at all). Highly productive ramets can afford to do both sexual and clonal reproduction, investing in future payoffs through clonal reproduction as well as hedging bets against mortality of unproductive offspring through seed production. Very unproductive parents gain by expending their resources on seeds that may colonize a better habitat. This leaves parents in intermediate conditions to ap-

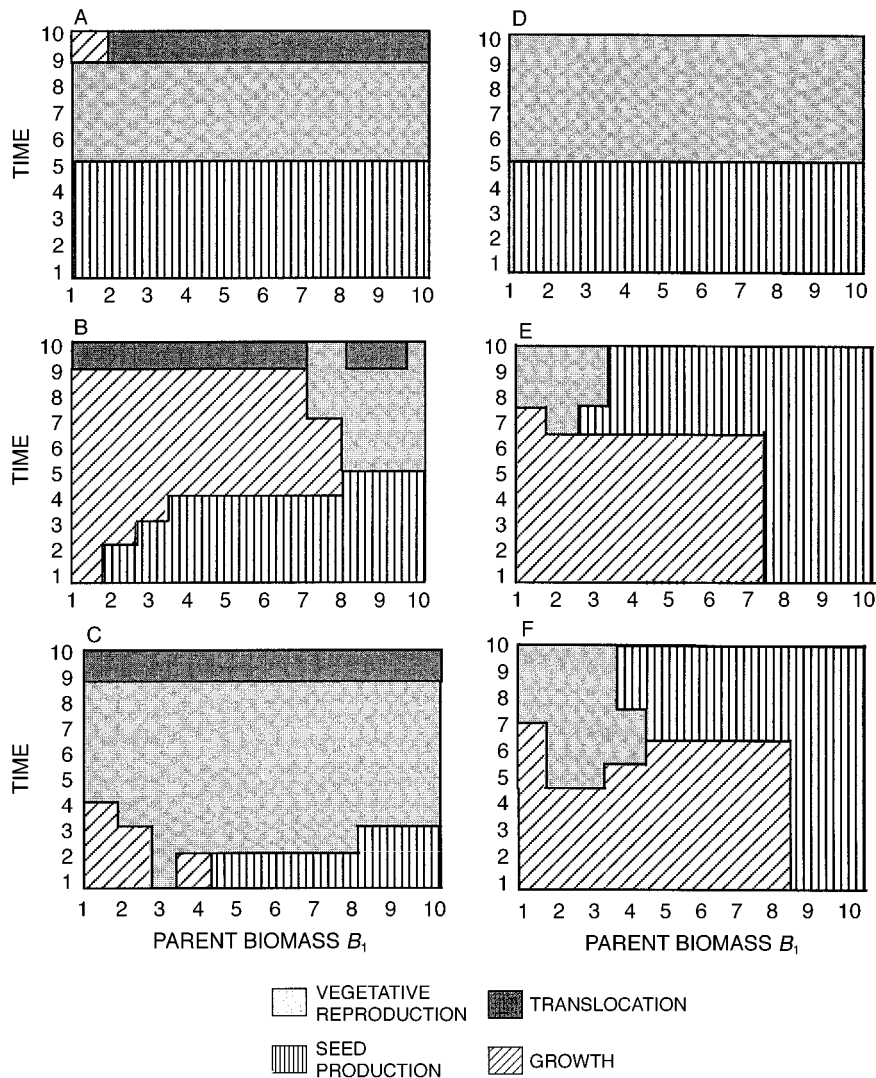


FIG. 6. State space of investment allocations  $I(B_1, B_2, t)$ , when offspring size  $B_2 = 1$ : (A and D) parent and offspring resources are poor ( $R_1 = R_2 = 1$ ); (B and E) parent resources are good, and offspring resources are poor ( $R_1 = 3, R_2 = 1$ ); and (C and F) parent and offspring resources are good ( $R_1 = R_2 = 3$ ). In parts (A)–(C), ramet and genet mortality are higher than in the baseline scenario, at  $\mu = 0.1$  and  $d = \nu = 0.3$ , and seed production is time dependent. In parts (D)–(F), seed biomass has a higher fitness payoff ( $q = 0.8$ ), and ramet number is more important than ramet size ( $z = 0.5$ ) than in the baseline case, but mortality rates are the same as baseline values. Then seed production depends on both ramet size and time, with size having the larger effect, except in (D) where conditions are uniformly unproductive. As parent resources increase, parent growth is the best strategy for a wider range of state space; and as offspring resources increase, vegetative reproduction becomes optimal for more of the state space.

portion relatively more to translocation and less to seeds than parents with more extreme resources.

Although the effect of offspring productivity on RE is slight and inconsistent with different parent resources (Fig. 7A; effect of offspring resources  $R_2$ ), offspring resources do have a strong effect on the way this biomass is divided among sexual, vegetative, and translocational reproductive efforts (Fig. 7B). Poor offspring productivity favors parents that allocate to seeds, while higher offspring productivity favors parents that invest in new vegetative offspring. A static (as opposed

to this dynamic) optimization model by Sakai (1995), based on the assumption that a parent can selectively place vegetative offspring in good patches, results in the same prediction. In contrast, a model by Loehle (1987) concludes that good surrounding conditions favor seed production. This result follows from Loehle's assumption that seed production depends on conditions close to and, therefore, detectable by a parent ramet, and that good conditions (e.g., light or moisture levels) indicate opportunities for germination.

Some empirical support can be found for the pre-

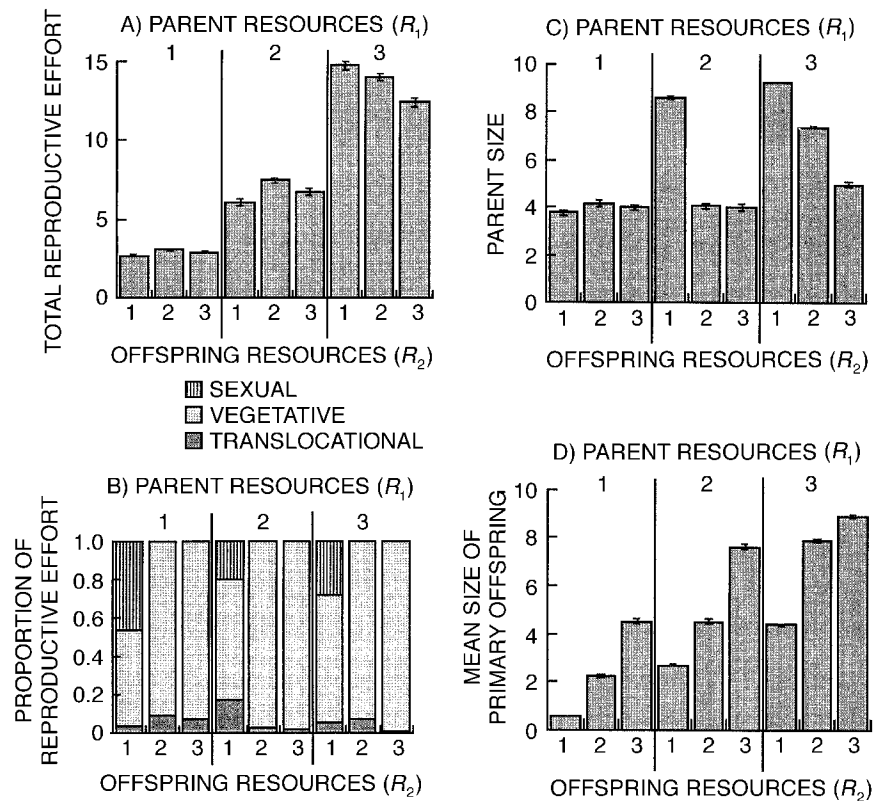


FIG. 7. The effect of parent productivity  $R_1$  and offspring productivity  $R_2$  on mean investments of simulated ramets for (A) total reproductive effort (RE); (B) the proportions of sexual, vegetative, and translocational reproductive efforts; (C) the mean size of parent ramets at the end of the season; and (D) the mean size of primary offspring at the end of the season. Reproductive effort, parent size, and offspring size increase with parent resources. Vegetative reproductive effort increases at the expense of sexual reproductive effort and parent growth with increasing offspring resources. Translocational reproductive effort responds in a complex way to parent and offspring resources. The following parameter values are modified from the baseline case so that some seed production occurs:  $\mu = 0.03$ ,  $d = v = 0.08$ ,  $q = 0.8$ .

diction of this state variable model that high resources for clonal offspring favor vegetative reproduction. In the agricultural literature for strawberries, mineral starvation or drought induces flowering (Guttridge 1969, Galletta and Bringham 1990). Fertilization at a low level stimulates flower formation, compared to that without fertilization, but increasing mineral feeds above low levels inhibits flower formation and causes growth and stolon production (Whitehouse 1928, Arney 1956, Breen and Martin 1981, Guttridge 1989). Over the long term, fertilization encourages the production of more crowns, and ultimately increases the number of flower sites (Guttridge 1989). Research showing that nitrogen, potassium, and phosphorous can delay natural autumn flower initiation led Guttridge (1989:27) to suggest "that the inhibition of flowering is related to stimulation of vegetative growth generally rather than to the supply of any one of these major elements specifically."

Among wild species, adding nutrients to naturally growing plots of *Carex arenaria* resulted in proportionately greater production of new clonal shoots (Noble et al. 1979) and fewer flowering ramets. In *Hydro-*

*cotyle bonariensis*, clonal fragments with offspring ramets rooting in low nitrogen had higher ratios of inflorescence production to ramet production than fragments with offspring ramets rooting in high nitrogen (Evans 1991). The opposite was true, however, when light was variable rather than nitrogen.

Previous theoretical and empirical work has predicted that the relative investment in sexual and vegetative reproduction depends on density (Abrahamson 1975, 1979, 1980, Williams 1975, Loehle 1987). A focus strictly on density confounds the actual level of resources a plant experiences: high density could indicate plentiful resources to support many plants, or low resource levels per plant due to strong competition (Loehle 1987). Density is likely to have different effects in an open habitat than in a closed habitat, and in a nutrient-limited compared with a light-limited habitat. By focusing models specifically on productivity and mortality, it is possible to make specific predictions about the effects of resources on behavior. A resource-based model requires that an empirical test of the model employ soil nutrient analyses, fertilizer treatments, or measurements of photosynthetically active radiation,



rather than counts of plant density. This model addresses the impacts of productivity, but assumes no role for local density- or biomass-dependent competition; future models could include both the effects of resources and competition. Nevertheless, if one uses high density as a proxy for resource scarcity as a result of competition, some studies indicated increasing proportion of reproductive effort as sexual, relative to clonal, with increasing density (Ogden 1974, Abrahamson 1975, Holler and Abrahamson 1977, Eriksson 1986), supporting our model's predictions that selection favors seed production in scarce resource environments. Other studies contradicted this prediction, however, with the maximum balance between sexual and clonal reproduction occurring at intermediate densities (Bishop and Davy 1985) or being unrelated to density (Pitelka et al. 1980).

Predictions in Fig. 7 suggest that it benefits a genet to have some information about the environment where a clonal offspring will land, since the model predicts that the relative gains from investment in seeds and ramets depend strongly on the quality of patches surrounding a parent ramet, as predicted by other models (Loehle 1987, Sakai 1995). This may be an evolutionary process in which genets are selected to respond appropriately to a particular habitat. Alternatively, it may be a developmental process, in which plants respond to gradients in nutrients, water, and light; differences in light quality (red/far red ratio or blue wavelengths) encountered by leaves or stolons; and/or signals received about the surrounding conditions from clonal offspring that have been produced in the past. In an experiment on *Fragaria chiloensis*, ramets placed clonal offspring preferentially in areas richer in the resource that was most limiting to the parent (S. N. Gardner, unpublished data). Other clonal plants also appear to be capable of altering investments based on conditions experienced by inter-connected ramets or earlier ramet generations (Salzman 1985, Kelly 1992, Evans and Cain 1995, Geber et al. 1997). The behavior of *Solidago canadensis* ramets depends on the experiences of connected ramets, so that information is shared about neighboring species through clonal connections (Hartnett and Bazzaz 1985).

#### *Effect of resources on translocation*

Translocation to support established clonal offspring also depends on interacting effects of parent and offspring resources (Fig. 7B): when a parent is in poor conditions ( $R_1 = 1$ ), then some continued support of clonal offspring in any  $R_2$  environment is advantageous, since unproductive parents must continue sharing with the diminutive offspring they produce. Sugar production depends on ramet size (Eq. 2), so, if ramets are too small, their growth rate is negligible. Moreover, when parent productivity is low ( $R_1 = 1$ ), translocational reproductive effort occurs at a higher rate to offspring in relatively better conditions than those of

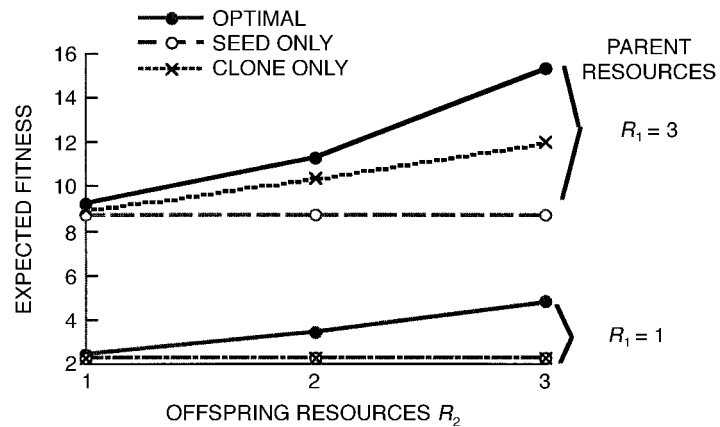
the parent ramet, since with higher productivity they can make better use of the carbon. Some evidence for this has been observed by Alpert (1996) in *Fragaria chiloensis* growing in a nitrogen-poor sand dune: parent ramets whose offspring rooted in a high nutrient patch showed reduced growth compared to parents whose offspring were not in a rich patch, suggesting that these parents shared resources with offspring in fertile conditions. Alpert suggested that water potential gradients generated by increased photosynthesis in rich patches cause more nitrogen to flow in the xylem toward those ramets.

Parents with an intermediate to high productivity ( $R_1 = 2$  or 3) engage in more translocational reproductive effort to offspring in poorer conditions than the parent ( $R_2 < R_1$ ) and less translocation to offspring in better patches than the parent. Productive offspring do adequately on their own, enabling the parent to start up new offspring, rather than helping the old. Empirical data support the model prediction for higher rates of transport to less productive offspring when parents are moderately productive (Hartnett and Bazzaz 1983, Salzman and Parker 1985, Slade and Hutchings 1987, Alpert 1990, Evans 1992, Evans and Whitney 1992, Stuefer et al. 1994, Wijesinghe and Handel 1994).

The dynamic state variable model by Caraco and Kelly (1991), with size-dependent growth, predicted higher rates of translocation than the model we present. This occurred because, in their model, production of more than one clonal offspring and sexual reproduction were not included, leaving resources to be divided between only the two options of growth and translocation. Instead, their model included temporal and spatial uncertainty in the environment, which are factors we omitted for simplicity. In addition, Caraco and Kelly's results indicated that, in richer environments, higher rates of translocation occurred than in poorer environments. In contrast, our results show that translocational reproductive effort declines with offspring resources (Fig. 7B). Again, this disparity between the models is a consequence of the fact that the model we present allows parent ramets to produce numerous clonal offspring that can grow quickly in a rich habitat, unsupported by translocation from the parent. Caraco and Kelly examine a situation in which a parent has only one clonal offspring, so translocation is the only alternative to parent growth. For species in which a parent ramet can produce only one new ramet per year, Caraco and Kelly's predictions about trade-offs between translocation and parent growth may be more appropriate. However, the model by Caraco and Kelly (1991) and the model presented here concur on the effect of spatial variation: when there is greater spatial variation (i.e., when parent and offspring ramets encounter different resource levels), both models predict that higher rates of translocation are favorable.



FIG. 8. Expected fitness  $F(B_1 = 3, B_2 = 0, t = 1)$  for a genet capable of optimizing investments, a genet only capable of growth and seed production, and a genet only capable of growth and cloning new offspring, for different parent and offspring productivities. Selection for optimal behavior is stronger when parent and offspring ramets are more productive. Parameters have been modified as in Fig. 7.



#### Effect of resources on ramet size

Next we examine the effect of parent and offspring resources on parent size (Fig. 7C). High parent resources can result in bigger parent ramets, but they only take advantage of a good patch by growing large if their clonal offspring encounter worse conditions. Otherwise, when their clonal offspring find a rich environment, parents in a good patch may not grow much larger than parents in a poor patch. Instead, they start producing clonal offspring when they are yet small, ultimately augmenting future expectations for genet fitness more than would continued parental growth. The average size of clonal offspring increases with both parent and offspring resources (Fig. 7D).

#### Fitness consequences of suboptimal behavior

The strength of selection depends on the fitness surface (Falconer 1989, Mangel and Ludwig 1992). To compare the expected fitness of genets investing for maximum fitness to genets incapable of behavioral plasticity, we calculated the expected fitness when ramets grow to the maximum size, followed by either clonal reproduction or seed production, but not both, and compared this fitness to optimal levels (Fig. 8). The ability to switch facultatively among behavioral strategies always results in the highest fitness, followed by exclusive vegetative reproduction, and, last, by exclusive seed production. When productivity is low ( $R_1 = R_2 = 1$ ), the fitness differences are relatively small, since ramets invest mostly in growth and have little left over for reproduction of any kind. As the productivity of either parent or clonal offspring ramets increase, the differences grow between optimal and suboptimal behaviors; selection is stronger for plastic, as compared with fixed, investments. This result is similar to the prediction of Grime's (1979: Chapter 1) three-strategy model that plasticity is less important for stress-tolerant plants, with slow growth rates, than for competitive or ruderal plants, with potentially faster growth rates.

Although we do not explicitly include a cost related

to plasticity, the comparisons illustrated in Fig. 8 quantify how the profits of plasticity depend on parent and offspring productivities. In a uniform habitat of high productivity ( $R_1 = R_2 = 3$ ), the fitness of exclusively clonal genets is 78% that of optimally investing genets. Thus, a substantial fitness cost of 22% would be required for plants to forgo plasticity.

The fitness of ramets producing only seeds is independent of the resources that surround a parent ramet, a result of our assumption in Eq. 5 that seeds increment fitness in proportion to the biomass invested, independently of offspring resources. Since rates of establishment of clonal offspring near parent ramets are often orders of magnitude greater than rates of seedling establishment near the parent, it is likely that the real fitness gains from seed production occur when seedlings colonize distant areas. In such a case, our assumption that fitness gains from seed production are independent of offspring resources would be true. However, we recognize that this model is a generalization that may only apply to some species. In other cases, that sexual payoffs are independent of offspring resources may be a dubious assumption (e.g., when major disturbances occasionally result in high seedling success near the parent), so the payoffs from producing seeds, as well as from clonal offspring, would depend on local resources surrounding the parent. We suggest an alternative model (for it is beyond the scope of the present paper) of clonal and sexual trade-offs, in which the distributions of dispersal distances for clonal offspring and seeds are combined with a function characterizing how the predictability of the habitat declines with distance from the parent.

#### Costs of being big

The greater the decline in the rate of assimilation (the parameter  $k$ ) with ramet size, the more ramets are predicted to invest in sexual reproductive effort at the expense of vegetative reproductive effort (Fig. 9A). In addition, big parents become relatively less productive, so total reproductive investment falls and ramets reach smaller sizes with increasing  $k$  (Fig. 9B). A test of this

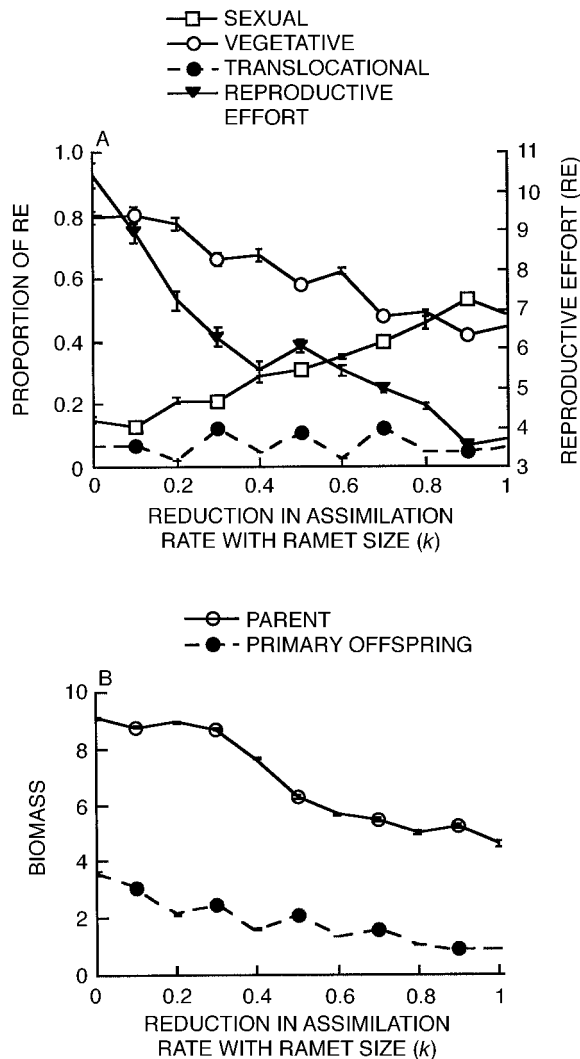


FIG. 9. Effect of a reduction in the assimilation rate with ramet size ( $k$ ) on (A) reproduction and (B) ramet size. The more the photosynthetic rate slows as ramets become larger, the more ramets are capable of producing less biomass for reproduction and growth, and they direct more of this biomass into seeds. Parameters are as in Fig. 7.

prediction could entail comparing sexual and clonal reproductive proportions among species with different size-dependent assimilation rates.

#### Other models

Of the several models concerning allocation to sexual and clonal reproduction in plants (Armstrong 1982, 1984, Caswell 1982a, b, 1985, Loehle 1987, Sackville Hamilton et al. 1987, Harada and Iwasa 1994, Sakai 1995), two of them explicitly address resource-dependent investment in clonal vs. sexual propagules (Loehle 1987, Sakai 1995). To our knowledge, the current study is the first dynamic, state-variable model to examine how the resource environment, genet and ramet mor-

talinity rates, ramet size, and time in the season affect behavioral trade-offs between vegetative proliferation and seed production.

Loehle (1987) reasons that seeds should be produced when conditions for germination are good or nutrients are rich, as this would decrease the cost of producing sexual structures containing high nutrient concentrations. Loehle predicts that as conditions for sexual progeny worsen, vegetative investments should increase, such as increasing shade in a species requiring light for germination. This prediction differs from ours, because we assume that, while clonal offspring can take advantage of good surrounding conditions, the payoff of seed production is independent of resource abundance in the immediate neighborhood. We made this assumption because seed establishment is rare compared to establishment of clonal offspring in habitats with an established population. Therefore, the primary gains from seed production may occur when seeds disperse to new areas with resources that are independent from those experienced by the parent ramet.

Sakai (1995) solved a series of algebraic equations to maximize fitness, where optimal strategies depended on the frequency of good patches and success of sexual and clonal offspring in dispersing to and surviving in those patches. The predictions of Sakai's model match those of the dynamic model we present: good patches surrounding a parent ramet select for clonal investment over seeds. This happens because the placement of clonal offspring will be in good local patches, compared to the random fall of seeds that prevents patch selection by sexual offspring.

The dynamic state variable model we present differs from the two just described by incorporating the ability of a ramet to translocate photosynthate to other parts of the clone, as well as to make time-dependent and size-dependent alterations in strategy.

#### Factors not included in the model

Some plants often use vegetative reproduction both as a means of storage and as a means of growth and reproduction, potentially increasing the relative benefits of clonal propagation over seeds (Gulmon and Mooney 1986, Whitham et al. 1991, Landa et al. 1992). In addition, the model does not examine the effect of the dispersal distance of seeds and the quality of the habitat in which those seeds are likely to land. Reproductive ramets probably respond to signals indicating the likelihood of seedling establishment (Loehle 1987). Alternative models are also needed to predict reproductive strategies in clonal plants that are limited by developmental constraints, such as the number of meristems, rather than by resources (Watson and Casper 1984). Finally, the model assumes there is no temporal variation. Models are needed to investigate how predictions change when resources or rates of mortality vary in time. Temporal variation alters the foraging behavior of clonal plants (Caraco and Kelly 1991,

Oborny 1994, de Kroon and Hutchings 1995, Oborny and Cain 1997), and a model to include this factor would undoubtedly predict different results concerning, for example, investment in translocation and clonal offspring. Temporal variation could be incorporated into a dynamic model like this one by making the level of resources depend on time.

#### CONCLUSION

Our model results indicate that high rates of clonal propagation are advantageous, particularly when a genet proliferates into productive areas. However, while clonal offspring usually outnumber seedlings by orders of magnitude (Cook 1985, Alpert 1995), most clonal plants continue to produce seeds. This behavior implies that seedling establishment matters, despite its rarity. The risk of ramet or genet mortality generates selection for seed production, although the model predicts that mortality rates in the range of empirical observations are not sufficiently high to account for the rates of seed production sometimes observed in the field. In addition, the fitness payoff per unit biomass invested in seeds must be higher than one might suspect, based on low rates of seedling establishment usually found in clonal plant populations. This payoff from seeds may result from selection for genetically diverse and dispersing offspring, factors whose advantages are evident in invasive or weedy species. Model results indicate that a trade-off favoring ramet number over ramet size may play a role as a selective force for seed production. It is unlikely to be a major factor, however, since the trade-off would have to be so severe that translocation to clonal offspring would never be advantageous, contradicting empirical data. We conclude that all three factors, mortality, fitness payoff of seeds, and a trade-off of ramet size vs. number tipped slightly toward number, act in conjunction, with the second factor likely to be the most important.

The model also leads to the prediction that a ramet does better to invest in proportionately more seed production in either a rich or a poor patch, and less seed production in a patch with intermediate productivity. The resource environment encountered by clonal offspring, however, is predicted by this dynamic model to be even more critical than the resources in a ramet's own patch in determining levels of clonal and sexual investments; poor conditions for clonal offspring make seed production by the parent ramet more beneficial. Using a static model, Sakai (1995) made the same prediction. The highest rates of translocation to support clonal offspring are predicted to occur when the parent and offspring ramets have contrasting productivities. This prediction coincides with the result from a previous model (Caraco and Kelly 1991) that focused on translocation, but did not include clonal and sexual reproduction.

Finally, comparing the fitness of genets with reproductive plasticity (the ability to facultatively switch

between clonal and sexual reproduction) with the fitness of genets that cannot make behavioral switches between clonal and sexual reproduction, we conclude that reproductive plasticity is more important in richer habitats than in poorer habitats. Model results suggest that a fitness cost of >20% is required in order for selection to forgo reproductive plasticity.

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