The Demographic Cost of Reproduction and Its Consequences in Balsam Fir (*Abies balsamea*)

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ABSTRACT: It is an axiom of life-history theory that reproduction involves age-specific costs in terms of survival or future reproduction. The measurement of costs of reproduction in plants is difficult, and few field studies have measured these costs in terms of fitness or demographic components, thus creating a hiatus between theory and data. In this article, we describe methods for overcoming the problem, illustrated by a field study of balsam fir. We used serial correlation and a permutation test to detect growth costs of reproduction and show how these translate into demographic costs when relative tree size (and therefore growth) is critical to survival. Using chronosequences, we reconstructed the age- and size-specific dynamics of a subalpine population of *Abies balsamea*. A matrix model describing these dynamics was then used to estimate age- and size-specific probabilities of future survival to maturity (Z_{ix}). By using a regression model of the relationship between tree size, age, and Z_{ix}, we were able to estimate the maximum age-specific demographic cost of reproduction for trees of all ages. The shape of the age-specific cost curve for *A. balsamea* may explain why, contrary to a previously published hypothesis, age at first reproduction in *A. balsamea* does not vary between wave-regenerating and normal populations.

Keywords: cost of reproduction, fir wave, *Abies balsamea*, plant demography, self-thinning, life-history evolution.

Other things being equal, natural selection should favor over all others the individual that begins to reproduce at birth and that continues to multiply indefinitely by producing infinite numbers of well-endowed offspring. No real organism is able to achieve this formula for the unbeatable life history because reproduction carries a cost that forces trade-offs between (inter alia) fecundity, survival, and growth. Costs of reproduction are age specific,

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and thus the timing of reproduction influences fitness and the optimality of any particular life history. The diversity of life histories observed among living species is witness to the variety of possible compromises that may be struck by trade-offs between life-history traits.

The existence of a cost of reproduction is fundamental and axiomatic to life-history theory, but the measurement of such costs is not straightforward. Four approaches to the measurement of costs of reproduction may be identified (Reznick 1985): first, phenotypic correlation between life-history parameters; second, experimental manipulations of one life-history component, such as fecundity, in order to observe a response in other components; third, genetic correlations between life-history components determined through quantitative genetic analysis of breeding experiments; and fourth, selection experiments to test whether the response of life-history components is negatively correlated. Although there are those who argue that only genetic approaches (third and fourth) are informative, these approaches require very large sample sizes or many generations of selection that make them impractical for whole groups of organisms, including long-lived trees (Roff 1992), and most workers recognize the value of employing a variety of approaches. In this study, we employ the approach of phenotypic correlation and show that with a carefully chosen system some of the well-known limitations of the phenotypic approach may be circumvented. Of course, it is recognized that phenotypic correlations must reflect underlying genetic correlations if a cost of reproduction that is visible in the phenotype is to shape the evolution of life history. Equally, a genetic correlation determined under laboratory conditions that is not manifested phenotypically in the field cannot be subject to natural selection.

Phenotypic evidence of a cost of reproduction in field populations can be difficult to obtain for a number of reasons (Reznick 1985; Roff 1992; Stearns 1992), even in plants, which are much easier than animals to census, measure, and manipulate. The first problem in detecting the negative consequences of reproduction for other activities such as growth is that there is often a size threshold

for reproduction (Samson and Werk 1986; Schmid et al. 1995) and a positive relationship between individual size and fecundity (Shipley and Dion 1992; Greene and Johnson 1994) that can obscure costs of reproduction in phenotypic correlations. Size thresholds for reproduction also create another problem in that testing optimality models requires an estimate of the potential cost of reproduction above and below the optimum, but if the threshold size for reproduction is actually at the optimum, precocious reproduction must be artificially induced or its effects estimated indirectly. This has rarely been done (Antonovics 1980; Reekie and Reekie 1991; Saulnier and Reekie 1995), and, indeed, most investigations of the cost of reproduction in plants have not estimated how these vary with size or age at all.

A further problem is that perennial plants draw on stored resources during reproduction (Muir 1995; Geber et al. 1997) and that unless these reserves can be measured before and after reproduction the costs may be underestimated, particularly in older plants. Saulnier and Reekie (1995) detected negative effects of reproduction on the growth of young plants of *Oenothera biennis*, but no effect in larger plants with greater nutrient reserves. Storage is probably one reason why costs of reproduction are sometimes not detectable (Reekie and Bazzaz 1987; Horvitz and Schemske 1988; Cunningham 1997) until several years after a reproductive event, requiring long-term studies to detect them (e.g., Primack and Hall 1990; Ashman 1992). Costs of reproduction may be more evident in resource-poor than in resource-rich environments (Bell and Koufopanou 1986), which possibly explains why studies sometimes detect costs at certain sites and not others (Obeso 1993; Syrjanen and Lehtila 1993).

There have been numerous studies of the effect of reproduction on the growth of trees, many of them reporting a negative effect of fruit or cones on the subsequent growth of adjacent shoots (e.g., Morris 1951; Gross 1972; Hoffman and Alliende 1984; Dick et al. 1990; Fox and Stevens 1991; Newell 1991; Karlsson et al. 1996; Obeso 1997) and on the diameter growth of the main trunk (Holmsgaard 1956; Eis et al. 1965; Tappeiner 1969; El-Kassaby and Barclay 1992). Trees have the potential advantage in the study of the costs of reproduction, in that growth before and after a reproductive event can be measured retrospectively so that effects with long time lags can be studied, but little advantage has been taken of this fact until now.

Substantial though the evidence is that reproduction incurs a cost in terms of subsequent growth, it is difficult to deduce the potential evolutionary consequences of such costs unless they are incorporated into a demographic model based on parameters for age- or stage-specific growth, survival, and fecundity (Sohn and Policansky 1977; Law 1979; Piñero et al. 1982; Calvo and Horvitz

1990; Calvo 1993). In this article, we report a study of the costs of reproduction in natural populations of balsam fir (*A. balsamea*) in subalpine forest. Our study system allows us to overcome many of the obstacles that have hampered previous field studies of the cost of reproduction in plants and enables us to obtain an estimate of the age-specific cost of reproduction in terms of a component of fitness (survival to reproduction). In the "Discussion," we use this result to test hypotheses advanced by Silvertown (1996) and Silvertown and Dodd (1999) concerning the evolution of age at first reproduction in *A. balsamea*.

The first important feature of the *A. balsamea* system is that age-specific fecundity (m_x) can be estimated retrospectively. Female cones shed their scales when they disperse their seeds, but the central rachis of the cone remains attached to the branch. Rachises up to 40 yr old have been observed in *A. balsamea* (Morris 1951). New female cones are produced only on the penultimate whorl of branches and only near the top of the tree. As in many conifers, *A. balsamea* produces one new whorl on the main stem and on each branch axis each year. It is therefore possible to determine how long ago a particular rachis was produced by counting whorls back to the location of the rachis.

A second feature of our study system is that age-specific size and growth can also be measured retrospectively. Internode distances between whorls on the main stem give the height growth made by a tree in each year of its life. A core taken near the base of the trunk shows clear annual growth rings whose number indicates the age of the tree and whose width gives the diameter growth increment made each year. Since growth and reproduction can be both retrospectively measured and dated, it is possible to correlate fecundity at any age x with prior growth, for which a positive relationship is expected, and with subsequent growth, for which a negative relationship is expected. By including growth made before and after each reproductive event in a serial correlation analysis, we can disentangle the positive effects of prior size on reproduction from the negative effects (costs) of reproduction on subsequent growth, thus solving the first problem alluded to above. The second problem (stored resources) is also solved by virtue of the fact that we can measure growth and costs for a series of years either side of year x, thus allowing for time lags.

The third and perhaps most important feature of our study system enables us to translate growth costs of reproduction into demographic costs. The technique relies on the fact that our study populations have a stable age and size structure and form a chronosequence created by wave regeneration. Wave regeneration occurs almost exclusively in pure stands of *Abies* in the subalpine zone of mountains in northeastern North America and in Japan. The tallest, most exposed trees in these forests die standing

up, most probably killed by defoliation caused by the accumulation of rime ice in winter (Marchand et al. 1986; Marchand 1995). This mortality propagates downwind along a front in a wavelike manner. Cellular automaton models of the phenomenon suggest that it is emergent from the very simple fact that tall trees with intact canopies protect their shorter, downwind neighbors (Sato and Iwasa 1993). Mortality waves at our study site tend to travel at a constant speed of between 0.8 and 2.7 m/yr, depending on local topography (Sprugel 1976).

The dead zone created by a mortality wave is colonized by an even-aged cohort of seedlings, and hence a wave leaves in its wake a succession of even-aged cohorts of trees whose age increases with distance from the receding wave front. Competition for light among the members of a cohort is intense, and density-dependent mortality (self-thinning) is severe (Mohler et al. 1978). Density-dependent competition for light is highly asymmetric (Weiner 1990) and rapidly produces a strongly skewed size distribution within a cohort from which only the largest, fastest-growing individuals survive. This link between size, growth, and survival within a cohort is the key to calculating age-specific fitness costs of reproduction (measured as the decreased probability of future survival) from the growth costs of reproduction. Further details of how the calculation was made are given under "Methods."

Methods

Sites

Fieldwork was conducted in July and August 1997 at Whiteface Mountain in New York (44°22′N, 73°54′W). Sprugel (1976) describes the site in detail. For this study, four fir waves were sampled on the slopes of Mount Esther and Mount Lookout (subsidiary peaks of Whiteface Mountain), between an altitude of 1,128 and 1,227 m. *Abies balsamea* was virtually the only tree present at all sites, with only a very few individuals of *Betula papyrifera* and *Picea rubens* encountered during sampling. A vegetation history of Whiteface Mountain (J. Battle, unpublished data) shows that our study area escaped the logging and burning that occurred at lower elevations all over the Adirondacks region in the early 1900s.

Growth Costs of Reproduction

In the fir waves on Whiteface Mountain, reproduction occurred only in trees >48 mm dbh (diameter at breast height, or 1.4 m from the ground). Using binoculars from vantage points, it was possible to check for rachises in the crowns of trees of this size and therefore to record whether or not they had commenced reproduction, but it was not possible to count the number of rachises accurately. To obtain quantitative estimates of age-specific fecundity and growth, we therefore sampled 115 small, mainly reproducing trees growing at the same altitude as the fir waves but occurring on the forest edge along a road that goes to the summit of Whiteface Mountain. These trees reproduced at smaller size than those in the interior of the forest and could be accurately recorded throughout their canopies.

Each of the 115 trees in the sample was cored 250 mm from its base to estimate age and to measure diameter growth increments in the core. These increments were measured under a binocular microscope in the laboratory. Each of the six internodes on the main trunk representing the past 6 yr height growth was individually measured. Fecundity was recorded by counting the number of rachises and cones on every internode of each branch in the six topmost whorls of the main stem. Each rachis or cone was dated by using its location.

Two types of analysis were used to detect negative effects of cone production on growth. Separate analyses were conducted for height growth and for diameter increment growth, but we shall refer to the variables collectively as "growth." First, we used linear regression of total growth per tree on rachis production per tree during the past 6 yr. Though this crude regression approach is useful in detecting potential costs of reproduction, it does not separate out the potentially antagonistic relationships of prior growth on subsequent reproduction and of prior reproduction on subsequent growth. Second, we therefore used serial correlation to determine the relationship between the number of cones produced in any year t and growth from years $t - 5$ to $t + 5$. To illustrate the procedure, let $t = 1, ..., 6$, with $t = 1$ referring to the most recent year, and let m_t, g_t be, respectively, age-specific measurements of fecundity and growth. Because we had only 6 yr of data per tree, we resampled, and sample sizes (n) varied with the length of the time lag; n_d for lag, d being the number of trees multiplied by $(6 - |d|)$. So, for time lags of +5 and −5, we had one sample of each lag per tree: correlations of lag +5 were made using m_6, g_1; correlations of lag −5 were made using m_1, g_6. For lags of +4 and −4, we had two samples per tree, (m_6, g_2), (m_5, g_1) and (m_1, g_5), (m_2, g_6), respectively, and so on for lags 3–0.

Because serial correlation involved using each measurement of growth and reproduction more than once, and because there was autocorrelation between repeated measurements made on individual trees, we used a permutation test to calculate the statistical significance of correlations. For this test, we permuted annual growth measurements within each tree, used the same permutation for all trees (giving 6! = 720 permutations in all), and calculated a serial correlation between fecundity and growth

Table 1: A worked example of the calculation of a **P** matrix from column vectors s_t, s_{t+1} from early in a chronosequence where mortality over the interval t to $t+1$ is severe

Element	s_t	s_{t+1}
s_1	325	25
s_2	0	12
s_3	0	1
s_4	0	0
...	...	...
s_9	0	0

Table 2: Matrix $\mathbf{P}_t$ for table 1

	j					
i	1	2	3	4	...	9
1	$[s_1(t+1)]/[s_1(t)] = .077$	0	0	0	...	0
2	$[s_2(t+1)]/[s_1(t)] = .037$	0	0	0	...	0
3	$[s_3(t+1)]/[s_1(t)] = .003$	0	0	0	...	0
4	0	0	0	0	...	0
...	...	...	...	...	...	0
9	0	0	0	0	0	0

for each permutation. The distribution of correlation coefficients obtained by this procedure was used as a null distribution against which to compare our observations. Permutating growth measurements within trees rather than across trees preserved tree-specific differences in fecundity and growth, and synchronizing permutations across trees preserved year-specific differences. This prevented year-specific and tree-specific differences from artificially inflating the number of correlations around 0 in our null distribution, which would have biased the test in favor of rejecting the null hypothesis.

Population Size and Age Structure

Sampling was conducted along one transect in each population laid perpendicular to wave fronts using compass bearings. All sampling locations were referenced using a global positioning system to a base map and to aerial photographs taken in 1995.

In each meter or alternate meter section of the transect, we recorded the number of stems falling in each of four size classes: class 1 was seedlings ≤0.5 m tall, class 2 was saplings >0.5 m tall and <10 mm dbh, class 3 was stems >10 mm dbh and <48 mm dbh, and class 4 was stems ≥48 mm dbh. Stem density and stem diameter were negatively correlated across classes, so sampling areas of different size were used for each class to achieve more comparable sampling intensities. Class 4 stems were recorded

2.5 m either side of a tape running the length of transect, class 3 stems were recorded 1 m either side, class 2 stems were recorded 0.5 m either side, and class 1 stems were counted in a 0.2×0.2 m quadrat. Stem densities in each class were later standardized to numbers m^{-2}. Diameter at breast height was measured for all living stems in classes 3 and 4. Dead stems were not recorded.

The main trunk and branches of *A. balsamea* all grow one new whorl each year, and whorls that are shed leave behind characteristic scars that in *Abies* encircle the main trunk. The number of whorls and whorl scars was counted on all stems in classes 1–3 to provide an estimate of age. In addition, a sample of class 2 stems was sectioned near

Table 3: A worked example of the calculation of a **P** matrix from column vectors s_t, s_{t+1} from late in a chronosequence where mortality over the interval t to $t+1$ is 0

Element	s_t	s_{t+1}
s_1	0	0
...	...	...
s_4	.5	0
s_5	1.5	1
s_6	0	1
s_7	.4	.4
s_8	0	0
s_9	0	0

Table 4: Matrix $\mathbf{P}_t$ for table 3

			j					
i	1	...	4	5	6	7	8	9
1	0	...	0	0	0	0	0	0
...	...	...	0	0	0	0	0	0
4	0	0	$[s_4(t+1)]/[s_4(t)] = 0$	0	0	0	0	0
5	0	0	$1 - p_{64} = 1$	$1 - p_{65} = .33$	0	0	0	0
6	0	0	0	$[s_6(t+1)]/[s_5(t)] = .66$	0	0	0	0
7	0	0	0	0	0	$[s_7(t+1)]/[s_7(t)] = 1$	0	0
8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0

ground level to obtain ring counts, and up to three class 3 stems per recorded meter of transect were cored 250 mm from the base with an increment borer for the same purpose. Class 4 stems encountered were cored 250 mm from the base for age estimation. Annual rings were clearly visible in virtually all cores and were counted under a hand lens in the field or in the lab soon after coring. A sample of age estimates were cross-checked by different workers to identify and eliminate systematic counting errors.

Size Structure and Population Dynamics

The size structure of a cohort changes through time as some trees die and the survivors grow (Mohler et al. 1978). The changing size structure along each of our transects represents a continuous chronosequence that reproduces in space the changes in size structure that occur through time. The first step in translating a chronosequence into a dynamic model that relates growth to survival was to divide the transect into q segments, each segment representing the population at a successive interval between when a new cohort germinates and when it is killed by the mortality wave. The size structure of the trees in each segment was then described by dividing the trees into r size classes. Values of r and q were chosen to achieve a balance between maximizing the sample size for each size class and minimizing the time interval between segments of the chronosequence under the constraint that time intervals should not exceed the time taken for a tree to grow one size class (Caswell and Twombly 1989; in practice, a small number of cases transgressed this). On this basis, we divided the trees into nine size classes and divided the transects into eight (two waves) or nine (two waves) segments, depending on transect length. The size classes were: (1) seedlings (as defined above), (2) saplings (as defined above), (3) trees 10–19 mm dbh, (4) trees 20–29 mm dbh, (5) trees 30–39 mm dbh, (6) trees 40–48 mm dbh, (7) trees 49–59 mm dbh, (8) trees 60–69 mm dbh, and (9) trees ≥70 mm dbh.

If the size structure of trees at time t is represented by a column vector s_t of dimension 9 × 1, and the size structure at time $t + 1$ is represented by a vector s_{t+1}, then the relationship between the two vectors is

$$s_{t+1} = P_t s_t, \qquad (1)$$

where P_t is a square transition matrix of dimension 9 × 9 whose elements (p_{ij}) represent rates of tree survival and growth between size classes (1, …, i, …, 9) over the interval t to $t + 1$. The elements (s_1, …, s_i, …, s_9) of a vector s_t are the number of trees recorded in the nine size classes at time t. The values of s_t and s_{t+1} are known for $t = 1$

to $t = q$, so there are $q - 1$ transition matrices, and the complete chronosequence can be described as follows:

$$s_2 = P_1 s_1; \qquad (2)$$

$$s_3 = P_2 s_2; \qquad (3)$$

$$\ldots$$

$$s_q = P_{q-1} s_{q-1}. \qquad (4)$$

Solving for P_t when s_t and s_{t+1} are known is a recognized problem in demography with several solutions when transition matrices are time invariant (Lefkovitch 1965; Caswell and Twombly 1989), but in the present case we know that transition matrices are not time invariant and that they vary systematically through the life cycle. Consider the case of seedlings, for example: the probability of these surviving one time interval are relatively high early in life, but within a year or two of germination, any surviving individuals still in this size class have virtually zero chance of surviving in competition with larger members of the same cohort. Fortunately, it proved possible to estimate transition probabilities by following some simple rules: first, recruitment occurred in a single pulse in s_1, represented by plants in s_1 (and sometimes s_2) of the first sample; second, trees could not regress a size class, so all p_{ij} above the leading diagonal of a P matrix were 0; third, a size class s_i that was empty at time t but that contained individuals at time $t + 1$ was filled by growth of individuals from the next smallest size class (s_{i-1}), thus when $s_i(t) = 0$, but $s_i(t + 1) > 0$, then $p_{ij}(t) = [s_i(t + 1)]/[s_{i-1}(t)]$, and when the calculated value $s_{i-1}(t)p_{ij}(t)$ was less than the observed value of $s_i(t + 1)$, the deficit was assumed to be filled by growth from size class $s_{i-2}(t)$; fourth, elements in the leading diagonal of matrices (p_{ii}) were calculated as: $p_{ii} = [s_i(t + 1)]/[s_i(t)]$, subject to rule 5; and fifth, columns ($i = 1, \ldots, 9$) of the transition matrix could not sum to more than one: $\sum_{i=1}^{i=9} p_{ij} \leq 1$. Two worked examples showing the application of these rules to actual data are given tables 1–4.

Once all transition matrices had been estimated, we checked the accuracy of the estimates by using them in the sequence of equations (2)–(4) to predict s_q' from s_1. The correlation between the predicted size structure s_q' and the actual size structure s_n was used to measure accuracy.

Demographic Costs of Reproduction

With accuracy of the transition matrices established, the sequence of equations (2)–(4) was then used to estimate the probability of future survival to maturity (Z_{ix}) of trees in each size class i at every age x in which at least one stem had been sampled. We estimated x as the mean age
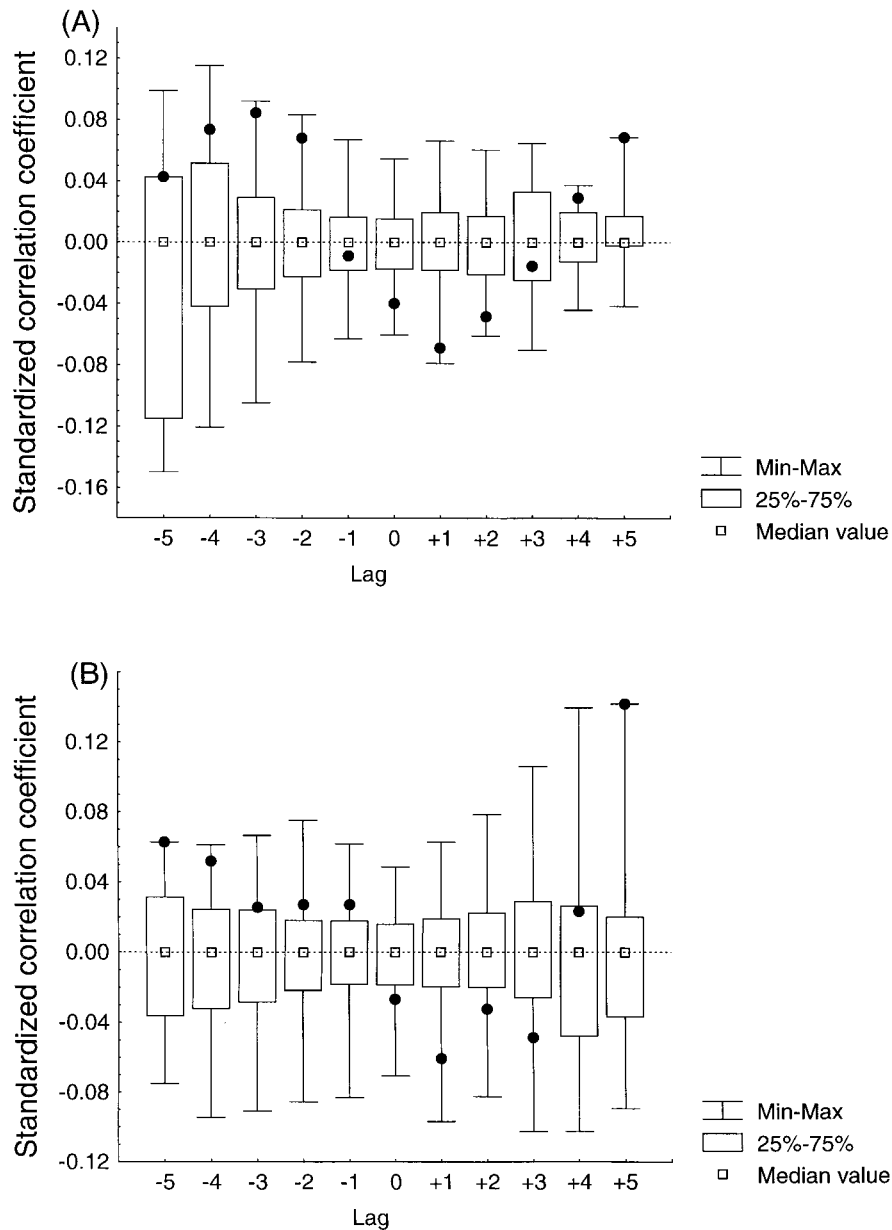
Figure 1: Serial correlation of (*A*) height growth and (*B*) diameter increment growth in years $t - 5$ to $t + 5$ with fecundity (rachis number) in year *t*. Solid dots show observed correlations, box and whisker plots show the median, 25%–75% range, and maximum and minimum values for 720 correlations calculated in a permutation test. All correlations have been rescaled by setting the median from the permutation test to 0.

of trees in the sample. For an individual in size class *i* at age *x*, we set element s_i of matrix $\mathbf{s}_x$ to a value of 1,000 and all other elements in $\mathbf{s}_x$ to 0. The vector $\mathbf{s}_x$ was then substituted into its chronologically correct place in the sequence of equations (2)–(4), and the vector $\mathbf{s}_q'$ was calculated; Z_{ix} was then estimated as the total number of survivors from $\mathbf{s}_x$ present in the reproductive size classes ($i = 7, 8, 9$) of the vector $\mathbf{s}_q'$.

The value of Z_{ix} gives us a means of estimating the change in partial fitness that occurs as individuals grow (change size class) from one time interval to the next. The relationship between Z_{ix}, size class, and age was determined by multiple regression of the combined data for the four fir waves. An estimate of the maximum age-specific survival cost of reproduction can be calculated from the three-dimensional surface of the Z_{ix}, size, and time graph if it

is assumed that reproduction at age x would halt growth and a comparison is made between such a tree and one that delays reproduction and continues to grow. Calvo and Horvitz (1990) used a similar assumption to incorporate costs of reproduction into a matrix model of orchid demography.

To make the comparison between reproducing and nonreproducing trees, we first had to specify a growth trajectory across the graph surface for a nonreproducing tree (100% growth : 0% reproduction). Many different trajectories are theoretically possible, but all must begin in the smallest size class at time 0, and successful survivors must reach the largest size class as early as possible. We therefore chose a line over the surface connecting these two points as our reference trajectory for a nonreproducing tree and calculated the slope of the line at small intervals along the reference trajectory, using standard calculus methods. This slope gives the age-specific change (increase) in Z_{ix} for a tree that grows but does not reproduce. On the assumption that reproduction halts growth (0% growth : 100% reproduction), the change in Z_{ix} for a tree reproducing at age x in size class i is given by the slope of a line starting from the corresponding point i, x on the reference trajectory, and drawn over the surface, parallel to the time axis. Since size class is fixed along such a line (i.e., there is no growth), its slope on the surface gives the change in Z_{ix} for a tree whose growth is halted by reproduction. Subtracting the slope of this line from the slope of the relevant part of the reference trajectory gives an estimate of the survival

cost of reproduction at age x. To determine the sensitivity of cost estimates to our assumption that reproduction entirely halts growth, we calculated the slope of a second trajectory representing a 50 : 50 ratio of growth and reproduction and lying halfway between the reference trajectory and the trajectory representing 0% growth : 100% reproduction.

Results

Growth Costs of Reproduction

Linear regression showed a significant effect of total fecundity on total height growth over 6 yr (growth [mm] = 807.73 − 3.69 × rachis number, $F = 9.504$, df = 1, 113, $P < .0026$), though rachis number explained only 7% of the variance in growth (adjusted $R^2 = 0.069$). Fecundity had no significant effect on total diameter increment over 6 yr (increment [mm] = 7.80 − 0.009 × rachis number, $F = 1.156$, df = 1, 110, $P < .285$). Sample size for the second regression was three trees smaller than for the first regression because three cores were damaged and could not be accurately measured.

Serial correlations between growth and fecundity (rachis number) are shown in figure 1. Rachis number and height growth were positively correlated before cone initiation and negatively correlated afterward (fig. 1*A*). The negative correlation began to reduce 2 yr after cone initiation and this trend resulted in a positive correlation 5 yr after cone initiation (fig. 1*A*). Rachis number showed the same overall pattern of correlation with diameter increment as with height growth, although all correlations were weaker (fig. 1*B*). The negative correlation of rachis number with diameter increment was strongest 1 yr after cone initiation, though the overall trend with time was more erratic. The strongest positive correlation occurred 3 yr before cone initiation (fig. 1*B*).

Demographic Costs of Reproduction

We found that our estimated transition matrices ($\mathbf{P}_t$) for the four waves yielded highly accurate predictions of size structure in year q from the stage structure vectors (s_1) at time $t = 1$. The correlation of s_n with s_q' measured over nine size classes was unity for two waves ($r = 1$) and was $r = 0.924$ and $r = 0.977$ for the two others.

A quadratic multiple regression of log ($Z_{ix} + 0.001$) on size class i and age x explained 74% of the variance (table 5) and gave the best fit to the data. The regression was weighted by the number of trees sampled for each data point and included 0 values of Z_{ix} (resolved on the log scale by adding 0.001 to all values of Z_{ix}), but the coefficients in the model were little changed by omitting
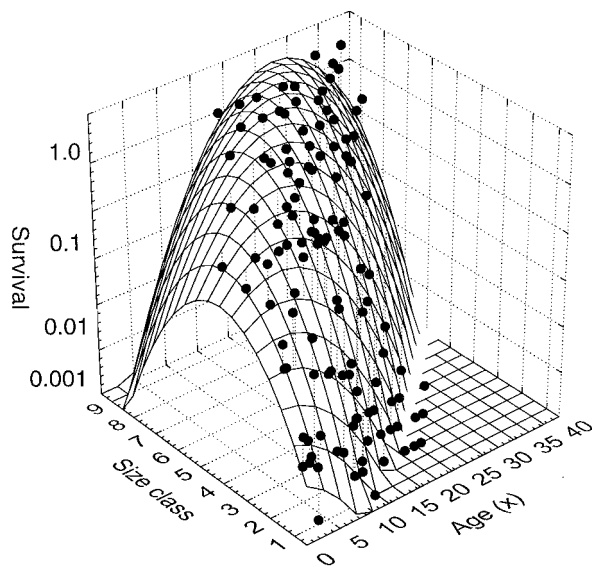

Figure 2: Three-dimensional surface plot for the quadratic regression of future survival to maturity (log $Z_{ix} + 0.001$) on size class i and age x. Regression statistics are given in table 5.
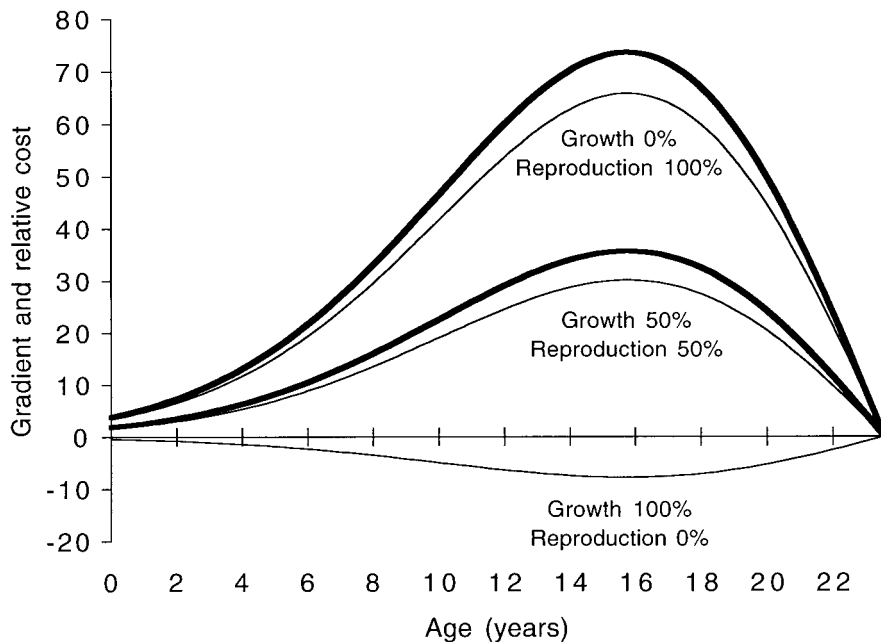
Figure 3: Age-specific cost of reproduction in *Abies balsamea* (*thick lines*) calculated as the difference between the gradient of the reference trajectory (see "Demographic Costs of Reproduction") for trees not reproducing (*thin line* labeled *Growth 100% : Reproduction 0%*) and gradients of trajectories representing growth completely halted by reproduction (*thin line* labeled *Growth 0% : Reproduction 100%*) or reduced by half (*thin line* labeled *Growth 50% : Reproduction 50%*).

weighting or zeroes. When zeroes were omitted, the residuals were normally distributed. The three-dimensional surface plot in figure 2 shows that data points were evenly distributed over the major part of the surface.

The slopes for trees with growth : reproduction ratios of 0% : 100%, 50% : 50%, and 100% : 0% were calculated for a model with unlogged values of Z_{ix} and are shown in figure 3. Under either assumption regarding the effect of reproduction on growth (100% or 50%), the curve of the age-specific costs of reproduction rises from near zero at age 0 to a maximum at age 16 yr and descends steeply to zero at age 23 yr. The maximum of the reproductive cost curve is approximately twice as high under the assumption of no growth as under the assumption of 50% growth.

Discussion

Using serial correlation, we detected positive effects of prior growth on subsequent fecundity as well as growth costs of reproduction. Both effects operated with time lags, and the positive effect implies that reproduction draws on stored resources. Without using serial correlation, the positive effects of prior growth on subsequent reproduction virtually cancelled out the negative effects of reproduction on subsequent growth. Figure 1*A* suggests that the transition from a positive to a negative relationship between

height growth and fecundity occurred about 1 yr before cone initiation. Growth costs in our study were measured in a sample of small, relatively young trees, but such costs have also been found in older trees of *Abies balsamea* (Morris 1951) and *Abies grandis* (Eis et al. 1965). Like Morris (1951), we found that reproduction had a more detectable effect on height growth than on diameter increment. Morris (1951) found that the greatest negative effect of reproduction was on the foliage production of reproductive shoots and that, in years of heavy cone production, vegetative buds could remain completely dormant. We did not measure foliage production, but Morris's observation suggests that a reduction in the production of new leaves and the associated photosynthetic capacity when reproduction occurs could explain why reproduction has a negative impact on subsequent height growth up to 3 yr after cone production.

The complexity of positive and negative correlations between fecundity and growth in different years makes it difficult to quantify the precise growth cost per seed or cone, though the existence of such costs is indisputable given our evidence and that of others. A precise estimate of growth costs is not required to transform growth costs into maximum demographic costs if we make the plausible assumption that reproduction can halt growth for a season. This assumption allowed us to estimate the impact (costs)
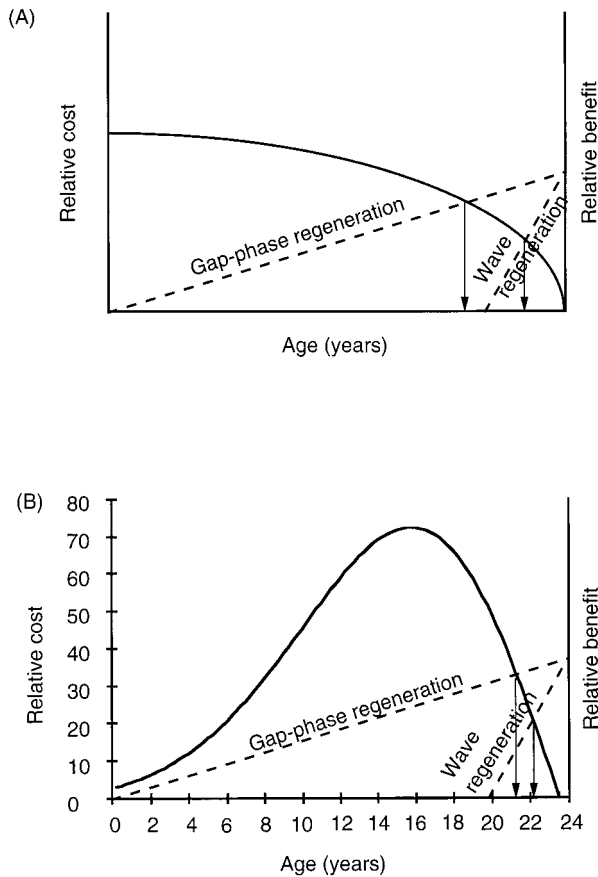
Figure 4: Graphical model of the evolution of age at first reproduction in *Abies balsamea*, based on age-specific patterns of benefit (offspring recruitment, *dashed line*) and cost of reproduction (*solid line*). Reproduction is predicted to begin where the cost and benefit curves intersect (*vertical arrows*). *A*, Graphical model of the hypothesis proposed by Silvertown (1996); *B*, as model *A*, but with the maximum cost curve derived from this study.

of reproduction on partial fitness (Z_{ix}), using the relationship between survival, size, and age (fig. 2) that we inferred from the fir wave chronosequences.

The shape of the cost curve (fig. 3) shows that the demographic costs of reproduction are markedly age specific, with a maximum at age 16 and minima at 0 and 23 yr. The general shape of the cost curve was not sensitive to our assumption that reproduction halts all growth (compare the two heavy lines in fig. 3), though it will be sensitive to a detail of how we gathered our data that can, in principle, be altered in future studies. The minimum at age 0 was a surprise, as we expected reproductive costs to begin high and to decline with age, but we interpret this minimum as an artifact of how we sampled tree size structure. We used nine size classes, chosen in an attempt to achieve numerical equality in sample sizes across the

whole life cycle. With the benefit of hindsight, we see that this resulted in too coarse a classification of the size structure of small trees among which size-dependent mortality was extreme. As a consequence, we underestimated the effect of growth (transition between size classes) on Z_{ix} for young trees. Though the first (0) minimum in the curve is an artifact, we believe that the position (age) of the maximum is realistic because it is determined by age at first reproduction, for which we have accurate estimates (Silvertown and Dodd 1999), and because mortality in the larger size classes is low, making the calculation of Z_{ix} less sensitive to the number of these size classes.

As an illustration of the utility of the age-specific cost curve (fig. 3), we now show how this can be used to resolve a problem in the life-history evolution of *A. balsamea*. Fir waves are natural features in the subalpine forests where they occur and have probably been present at Whiteface Mountain since the colonization of the area by *A. balsamea* at the end of the last glaciation some 12,000 yr ago. Silvertown (1996) suggested that, over this period, wave regeneration should have selected for a delay in the age of first reproduction (α) relative to that in populations regenerating by the normal mechanism of gap-phase replacement. In both types of forest, successful recruitment requires seedlings to colonize a canopy gap. In a normally regenerating forest, such gaps occur haphazardly wherever tall trees are blown down, and this creates a mosaic pattern of tree patches of different ages. In such a population, the recruitment possibilities for the offspring of an individual tree are unpredictable but probably increase steadily with age as trees in surrounding patches grow larger and become more susceptible to blow down. By contrast, recruitment opportunities for the offspring of a tree in a wave-regenerating forest are very predictable and occur only in a narrow window of time and space immediately preceding the death of the parent. A simple cost-benefit model comparing these scenarios in gap phase– and wave-regenerating populations shows that the prediction made by Silvertown (1996) depends (among other things) on the shape of the cost curve at the end of life (fig. 4; Sil-

Table 5: Quadratic multiple regression of log (Z_{ix} + 0.001) on size class i and age x

Term	Coefficient	SE	$t_{(707)}$	P
Constant	.240	.0591	4.06	.00055
Age	−.055	.0098	−5.61	<.00001
Size	.832	.0490	16.98	<.00001
Age^2	−.005	.0005	−10.61	<.00001
Size^2	−.104	.0072	−14.49	<.00001
Age × size	.036	.0029	12.34	<.00001

Note: Data for all four waves combined, $n = 131$, $R = 0.859$. Variance explained = 74%.

vertown and Dodd 1999). According to this model, reproduction should commence at an age when the benefits of reproduction exceed the costs. This point occurs earlier in normal than in wave populations if the decline in the cost curve at the end of life is gradual (fig. 4A) but at similar ages in the two types of population if its decline is steep (fig. 4B).

Silvertown and Dodd (1999) estimated values of α for wave- and gap phase–regenerating populations of *A. balsamea* in the subalpine zone of Whiteface Mountain and found no significant difference between the two. It turns out that this is what is predicted by the very steep decline in the cost curve that we have estimated in this article when reproduction halts all growth (fig. 3). The shape and elevation of the benefit curve for gap-phase regenerating forest shown in figure 4 is not based on any precise information, but our conclusions are robust to a variety of shapes and positions it might take because the cost curve is so steep. Though our existing estimate of the cost curve makes a prediction that is consistent with observed values of α, it is likely that we have overestimated the steepness of the cost curve because we have no quantitative information on how fecundity varies with size and age once reproduction has begun.

Given detailed information on size- and age-specific fecundity that we do not presently have for trees in wave forest, it would be possible to calculate reproductive value (Fisher 1958) instead of Z_{ix} as a measure of fitness and to test the theoretical prediction by Caswell (1982, 1984) that age-specific reproductive costs should be the inverse of reproductive value when fitness is maximized. Reproductive value measures the future expected contribution of individuals to the next generation through their offspring and is especially appropriate for an age-structured population (Fisher 1958; Charlesworth 1994). Equations (1)–(4) can be modified to calculate the reproductive value V_{ix} of individuals of size i at age x quite simply by adding a row matrix $\mathbf{b}_x$, representing size-specific fecundity at age x, to each matrix $\mathbf{P}_i$, and a size class s_0 for seeds to each vector s_r. By setting element $p_{0,0} = 1$ for all the transition matrices, seeds cumulate in s_0 when the model is run. Reproductive value, measured as the cumulative seed production until the end of life for an individual in size class i at age x, is then given by element s_0 of the vector s_q (eq. [4]).

Our method for measuring the age-specific costs of reproduction has potential for use in other stage-structured populations. The four requirements for its use are that survival and/or fecundity should be size dependent (almost universally true for plants); it should be possible to identify discrete cohorts (e.g., those recruited into forest canopy gaps of a particular age) in order to construct a chronosequence; cohorts should have size structure (usual in plants, see Boucher 1997); and that the populations have a stable age structure. Although the spatial structure of fir waves makes these conditions particularly easy to satisfy, they may also be met in normal subalpine *A. balsamea* populations (Moloney 1986) as well as in other species (e.g., Boucher 1997). The structure of a fir wave makes it easy to sample and interpret the chronosequence, but a sampling program that captured the full age range of cohorts from germination to maturity in a forest where cohorts occur in the patches of a mosaic could generate the same kind of data. This method makes it possible to use population structure to estimate age-specific costs in trees and other long-lived perennial plants, reducing the time needed to study the life history of these important organisms from decades to a matter of months.

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