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# Evolution of life history in balsam fir (*Abies balsamea*) in subalpine forests

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Subalpine forests in North America and Japan dominated by *Abies* spp. show an unusual pattern of regeneration in which recruitment is confined to a narrow window in time and space that just precedes the death of the largest trees. Previously, Silvertown suggested that selection in such forests should favour delayed reproduction. A graphical model supporting this prediction also suggests that trees in 'normal' forests should benefit from precocious reproduction when they are taller than their neighbours, while trees in wave populations should not. Here, we present a field test of the two hypotheses based upon a comparison of the life history of trees in adjacent wave and non-wave populations at Whiteface Mountain, New York. The results show that reproduction commences at a similar age in both kinds of forest, and that trees in the subalpine zone reproduce later and die earlier than conspecifics in lowland forests. The failure of the first hypothesis can be explained by modifying our original assumptions about how reproductive costs and benefits vary with age in the model. In our test of the second hypothesis, we find that the reproductive behaviour of individual trees in the two kinds of forest is different and consistent with our prediction. Phenotypic plasticity for age at first reproduction appears to be present only in the population where it is adaptive.

**Keywords:** *Abies balsamea*; life-history evolution; wave regeneration; age at first reproduction; phenotypic plasticity; subalpine

## 1. INTRODUCTION

In iteroparous organisms, age at first reproduction ( $\alpha$ ) is generally expected to occur relatively early in life (Sibly & Calow 1986), and only in semelparous species is a prolonged delay expected. Indeed, it has been proposed that in iteroparous species the ratio of age at first reproduction to mean reproductive life span ( $\alpha/E_\alpha$ ) is an invariant within broadly defined taxonomic groups such as angiosperms or gymnosperms (Charnov 1993; Franco & Silvertown 1996). Silvertown (1996) pointed out that subalpine, wave-regenerating populations of *Abies* spp. may be an exception to this rule among iteroparous species.

Recruitment in wave-regenerating populations is confined to a narrow window of time and space, which occurs just in advance of the arrival of the mortality waves that pass at a constant rate across the landscape, killing mature trees (Sprugel 1976). The canopy gap created by a mortality wave is colonized by an even-aged cohort of seedlings. As the wave passes through the forest, it leaves in its wake a series of cohorts that increase monotonically in age with distance behind the wavefront. Silvertown (1996) suggested that this unusual situation, where recruitment of the offspring generation narrowly precedes the near-synchronous death of the parent generation, should result in age at first reproduction converging with age at death. Subalpine firs might therefore be evolving towards semelparity.

The hypothesis is shown in graphical form in figure 1. We assume the cost of reproduction (as measured by the effect of current reproduction upon residual reproductive

value) declines and that the benefits (as measured by offspring recruited) increase with age. Reproduction is predicted to begin when benefits exceed costs. We make the parsimonious assumption that wave and non-wave populations have identical cost curves (figure 1). Benefit curves, which represent the probability of successful recruitment of offspring, increase with age in both types of population because age and size are closely correlated and fecundity is assumed to be size dependent. However, the intercepts of the benefit curves on the age axis differ between population types because successful recruitment can only occur in a canopy gap, and these gaps have different temporal (as well as spatial) distributions in the two cases. Normal populations are composed of a haphazard mosaic of even-aged patches (Moloney 1986), and gaps created by tree-falls can occur at any time. By contrast, in wave-regenerating populations, canopy gaps only occur when the mortality wave defoliates the oldest trees, which die while still standing. Because cohorts are lined up ahead of a wave in strictly decreasing order of age away from the advancing wavefront, the immediate neighbours of the canopy gap, which are the individuals with the greatest chance of colonizing it with their offspring, are the oldest surviving trees in the population. This causes the benefit curve to be zero until near the age at death (figure 1), leading to the prediction that  $\alpha$  should occur very late in life.

At the time this hypothesis was proposed, the only evidence available to test it came from a comparison of life-history parameters in wave-regenerating populations of three *Abies* species in Japan with normally regenerating *Abies* forests of eight other species in North America

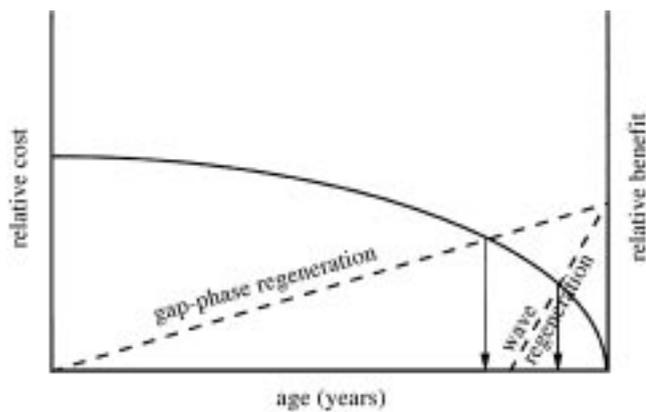


Figure 1. Hypothetical age-specific costs (solid line) and benefits (dashed lines) of reproduction in a normal population of *Abies balsamea* and in a wave-regenerating population.

(Silvertown 1996). This comparison supported the hypothesis, showing the wave-regenerating Japanese populations to delay reproduction relative to age at death. Unfortunately, no published information could be found to permit an intraspecific comparison of the relevant life-history parameters for wave-regenerating and non-wave-regenerating forests occurring at the same altitude as each other. The question was therefore left open as to whether the relatively high value of  $\alpha/E_\alpha$  found in wave-regenerating stands was a consequence of wave regeneration itself (in agreement with the hypothesis), a characteristic of all firs in subalpine environments, or indeed just peculiar to Japanese subalpine firs. In this paper we report the results of a field test of the hypothesis that is free of the confounding effects of species, altitude and provenance, because it compares life-history parameters for wave-regenerating and normal populations of balsam fir (*Abies balsamea*), both growing in the subalpine zone of the same mountain in North America.

The cost–benefit model (figure 1) also suggests that there may be selection for another difference between normal and wave-regenerating populations, due to the difference in their benefit curves. The cost curve in the model represents a mean for a population, but consider how the predictions of the model are altered for an individual tree that happens to have an age-specific cost lower than the population mean. For a tree in a normal forest, a lower cost will favour earlier reproduction by that individual because the cost curve will intersect the benefit curve earlier. However, for a tree in ‘wave forest’, a lower than average cost of reproduction will not affect the predicted value of  $\alpha$  unless the reduction occurs late in life when benefits become non-zero (figure 1). Even then, a unit decrease in the elevation of the cost curve will lower the predicted value of  $\alpha$  less for a tree in a wave population than for one in a normal population, because the benefit curve for the former has a steeper slope than that of the latter. If the costs of reproduction vary between individuals, and if trees can predict to some degree what these costs will be, then there should be selection for plasticity in  $\alpha$  in normal populations, but no such plasticity should be seen in wave populations.

Silvertown & Dodd (1999) have shown that reproduction in small trees of *A. balsamea* in the subalpine zone incurs a measurable cost in height growth, which translates into

lowered chances of survival because there is intense density-dependent mortality (self-thinning) in both normal and wave-regenerating stands of *A. balsamea* (Mohler *et al.* 1978). In such situations the largest trees invariably survive at the expense of smaller neighbours, which suffer strongly in asymmetrical competition for light (Weiner 1990). For an individual tree in a self-thinning stand, the degree of shading by neighbours provides a reliable cue to the potential costs of reproduction. This argument, concerning how the costs of reproduction will vary for individuals depending upon their height relative to neighbours, applies with equal force to trees in either type of population, but the evolutionary consequences will be different in the two types if, as we propose, the age-dependent benefits are different between them (figure 1). The argument suggests that young trees that are bigger than their neighbours, and thus unlikely to be overtopped by them, can benefit from precocious reproduction in normal populations but not in wave populations. We therefore predict that the age of commencing reproduction ( $\alpha$ ) will be sensitive to the height of neighbours in normal populations, but not in wave populations. This hypothesis is also tested here.

## 2. METHODS

### (a) Sites

Fieldwork was conducted at the best-studied and most accessible site of fir waves in North America at Whiteface Mountain in New York State (44° 22' N, 73° 54' W). Sprugel (1976) describes the site in detail. Five fir waves were studied on the slopes of Mount Esther and Mount Lookout between an altitude of 1128 m and 1227 m. *A. balsamea* was virtually the only canopy tree at all sites, with only a very few individuals of *Betula papyrifera* and *Picea rubens* encountered during sampling.

One normally regenerating stand of *A. balsamea*, located within 100 m horizontal and 50 m vertical distance of the nearest fir wave, was chosen for study. This site is described in detail by Moloney (1986). Other non-wave areas of *Abies* forest occur at Whiteface Mountain, but all are on hazardous terrain. We used data from the forestry literature to estimate life-history parameters for low-altitude *A. balsamea*, as did Silvertown (1996).

### (b) Sampling

Sampling was conducted in July and August 1997 along transects laid perpendicular to wavefronts by using compass bearings or (in the normal forest) approximately along contours. The normal forest was sampled along three transects to provide some (albeit pseudo-) replication. All sampling locations were referenced using a global positioning system to both a base map and aerial photographs taken in 1995.

In each metre or alternate metre section of the transect we recorded the number of stems falling in each of four size classes: class 1, seedlings  $\leq 0.5$  m tall; class 2, saplings  $> 0.5$  m tall and  $< 1$  cm in diameter at breast height (DBH); class 3, stems  $> 1$  cm DBH and  $< 4.8$  cm DBH; class 4, stems  $\geq 4.8$  cm DBH. Stem density and stem diameter were negatively correlated across classes, so sampling areas of different sizes were used for each class in order to achieve comparable sampling intensities. Class 4 stems were recorded 2.5 m either side of a tape running the length of the transect, class 3 stems were recorded 1 m either side of the tape, class 2 stems were recorded 0.5 m either side of the tape, and class 1 stems were recorded within a 0.2 m  $\times$  0.2 m quadrat. Stem densities in each class were later standardized to numbers  $m^{-2}$ .

Diameter at breast height (1.4 m) was measured for all living stems in classes 3 and 4, and for standing dead trees in class 4. Dead stems in classes 1–3 were not recorded.

### (c) Age and life-table estimation

The main trunk and branches of *A. balsamea* both 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. Additionally, a sample of class 2 stems was sectioned near ground level to obtain ring counts, and up to three class 3 stems per recorded metre of transect were cored 25 cm from the base with an increment borer for the same purpose. All class 4 stems encountered were cored 25 cm from the base for age estimation. A sample of standing dead trees was cored and age at death was estimated where the heartwood was sound. Annual rings were clearly visible in virtually all cores, and were counted under a hand-lens in the field or in the laboratory soon after coring. A sample of age estimates was cross-checked by different workers to identify and eliminate systematic counting errors.

Since the population is at equilibrium, its age structure may be interpreted directly to give a static life table and survivorship curve (Kohyama & Fujita 1981) by graphing standardized stem densities per unit area against mean age of stems per quadrat (or transect section). Having established the median value of  $\alpha$  for a population (see below), the median value of  $E_\alpha$  can then be calculated from the survivorship curve as the age by which half of the individuals that reached age  $a$  are dead (or the median age of trees older than  $\alpha$ ).

### (d) Reproduction

Cone rachises persist on branches for decades after seeds have been shed, and can therefore be used to estimate retrospectively when a tree began reproduction. New female cones in *Abies* occur only on the penultimate-branch whorls towards the top of the tree. Binoculars were used to score their presence or absence and the location of cones and rachises on branches. Age at first reproduction was estimated by counting the number of whorls ( $b$ ) from the top down to the oldest whorl carrying cones or rachises on its branches, and then counting the number of whorls ( $c$ ) along a branch outwards from the trunk to the first evidence of past reproduction. If the age of the tree is  $a$ , then age at first reproduction is  $(a - b) + c$ .

In the normal population and in three out of the five wave populations we estimated the interference from neighbours experienced by each tree in size classes 3 and 4 as follows. Starting from the leader shoot we counted whorls down the main stem until we reached the first whorl the branches of which were overlapped by those of a neighbour. The number of 'interference-free' whorls above this point was recorded. Logistic regression of reproduction (started or not started) on stem DBH, tree age and the number of interference-free whorls was used to determine the degree to which the commencement of reproduction for individual trees depended upon age, size (DBH) and height relative to neighbours.

## 3. RESULTS

### (a) Age at first reproduction and expectation of life

Ratios ( $\alpha/E_\alpha$ ) were logged to normalize them, and are compared for subalpine normally regenerating, wave-regenerating, and lowland-forest populations of *A. balsamea*

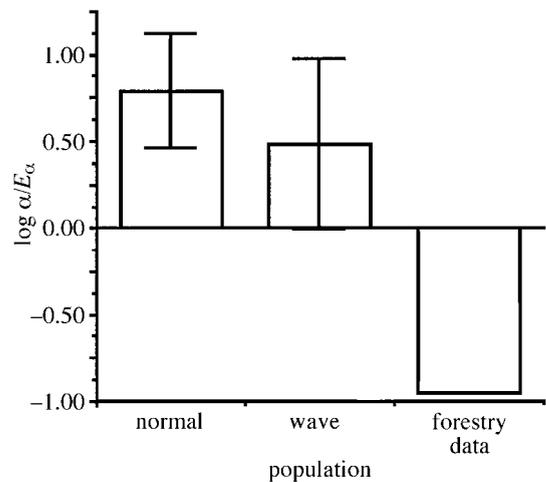


Figure 2. Comparison of  $\log \alpha/E_\alpha$  for normal subalpine, wave and low-altitude normal populations of *Abies balsamea*. Confidence limits (95%) of  $\log \alpha/E_\alpha$  are shown for normal and wave populations.

in figure 2. The data from non-wave-regenerating stands at low altitude come from the forestry literature, which report  $\alpha = 15$  years and longevity = 150 years (hence  $E_\alpha \approx 135$ ) (Loehle 1988). Mean values across samples for  $\alpha$  and  $E_\alpha$  were, respectively, 33.5 years and 5.5 years for the normal forest, and 32.2 years and 10.8 years for the fir waves. Two points are apparent from figure 2: (i) the subalpine populations with different modes of regeneration do not differ from each other, and (ii) both have higher ages at the first reproduction with respect to age at death than lowland-forest populations.

### (b) Commencement of reproduction in relation to age, size and competition

Regression statistics for the relationship between the commencement of reproduction, tree size, age and the number of whorls free from interference by neighbours are given in table 1. The relationship with size (DBH) was significant in all populations, and the relationship with age, which was highly correlated with DBH, was significant in two of the three waves. Freedom from interference did not significantly influence whether or not trees in wave populations had commenced reproduction, but it had a highly significant effect upon this in the non-wave population. The coefficient of variation in number of whorls free was similar in wave and non-wave populations, so the difference between them was not an artefact caused by greater uniformity of tree height in wave populations than in normal populations.

The effects of interference on the probability that a tree of a given size had started reproduction in the non-wave population is shown in figure 3.

## 4. DISCUSSION

The original hypothesis of Silvertown (1996) has been proved incorrect, since the ratio of age at first reproduction to expectation of life ( $\alpha/E_\alpha$ ) did not vary between wave-regenerating and normal populations of *A. balsamea* growing at similar altitude. However,  $\alpha/E_\alpha$  did vary between populations at different altitudes, and appeared to be significantly higher in subalpine than in lowland

Table 1. *Logistical regression of reproduction (started or not started) on tree size (DBH), interference-free whorls and age for three wave populations and the non-wave population*

(Standard errors (s.e.) are shown in brackets.)

population	n (started)	constant (s.e.)	regression term DBH (s.e.)	interference (s.e.)	age (s.e.)
wave 1	203 (47)	-3.221 (0.597)***	0.052 (0.012)***	0.032 (0.041)	-0.027 (0.030)
wave 5	105 (22)	-4.103 (0.978)***	0.093 (0.025)***	-0.077 (0.136)	-0.137 (0.060)*
wave 6	93 (28)	-5.446 (1.612)**	0.175 (0.040)***	0.031 (0.044)	-0.149 (0.056)**
non-wave	383 (68)	-6.162 (0.724)***	0.029 (0.009)**	0.515 (0.090)***	0.026 (0.020)

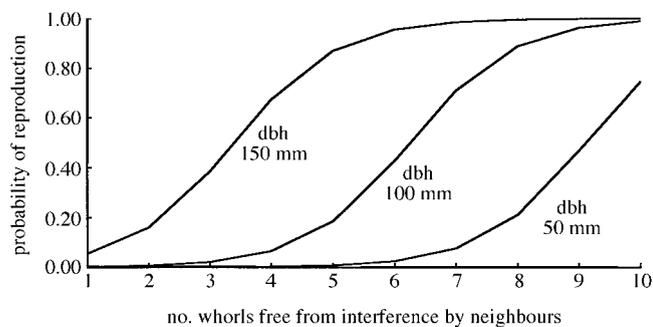
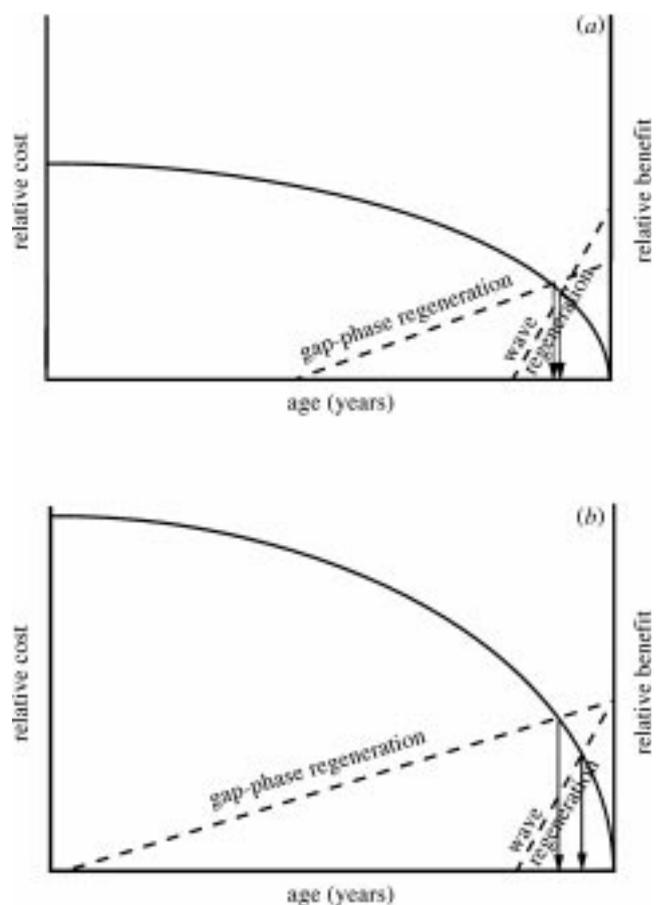
\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

Figure 3. The dependence of reproduction upon size (DBH) and interference in the normal population.

populations (figure 2). Trees in subalpine populations of *A. balsamea* reproduce later and die earlier than lowland conspecifics. Our second hypothesis, which predicted that the onset of reproduction should depend upon tree height relative to neighbours only in non-wave forests, was confirmed. Precocious reproduction by trees that were taller than their neighbours was observed in the normal forest, but not in the wave forest. It is surprising that this difference did not result in a lower overall median age of first reproduction in the normal forest than in the wave forest.

There are three possible reasons why the first hypothesis proved to be incorrect: (i)  $\alpha$  is not heritable; (ii) gene flow between the population types swamps the effects of local selection; and (iii) selection regimes do not differ between the population types as expected. Taking the first explanation, unfortunately we do not have any data on the heritability of  $\alpha$ , but it seems unlikely that there would be no heritable variation for this trait since provenance trials show that conifers in general, and *A. balsamea* in particular, show geographically and elevationally correlated genetic variation for most measurements made (Fryer & Ledig 1972; Marty *et al.* 1983). Regarding the second explanation, we have no direct information on gene flow, although it is known that local selection often leads to genetic divergence between closely adjacent plant populations, even when these are outcrossing (Linhart & Grant 1996).

Perhaps the third explanation for the rejection of the hypothesis is the most likely, because the hypothesis is sensitive to assumptions about the configuration of the cost and benefit curves (figure 1). Either lowering the elevation of the benefit curve for the normal population (figure 4a) or raising the slope of the cost curve

Figure 4. The effect, which should be compared with figure 1, of (a) lowering the benefit curve for normal populations (dashed line) and (b) a steeper cost curve (solid line) on the expected value of  $\alpha$  in normal and wave-regenerating populations.

(figure 4b) will cause the  $\alpha$  values for the two types of population to converge relative to the situation shown in figure 1. The shape and elevation of the benefit curves is conjectural and in practice very difficult to estimate for a normal population because all a tree's offspring need to be identified. The cost curve can be estimated more easily, although the procedure is complex. Silvertown & Dodd (1999) used a method of estimation based on translating observed negative effects of reproduction upon growth into the consequences for survival. Growth and survival are linked because there is heavy density-dependent mortality (self-thinning) in stands of *A. balsamea* (Mohler *et al.* 1978). The self-thinning process is driven by

strongly asymmetrical competition for light, which soon after germination gives rise to a skewed distribution of tree size, consisting of many small and a few large individuals. As self-thinning proceeds, mortality selectively takes its toll of small individuals, and only the largest trees in a cohort survive to reproduce. The consequences of reproduction for subsequent survival can thus be estimated from the effect of reproduction on growth. Using this approach, Silvertown & Dodd (1999) found that the cost curve for reproduction in fir waves declined steeply around the age of first reproduction, consistent with the pattern shown in figure 4b.

Although we found that the median age at first reproduction does not differ between wave and non-wave populations, the confirmation of our second hypothesis demonstrates a difference in how the onset of reproduction was controlled in the two types of population. Size and age controlled this in wave populations, but size and interference from competitors did so in the normal population. Morris (1951) found that the presence and quantity of cones on trees of *A. balsamea* was positively correlated with freedom from crowding in a non-wave population in New Brunswick, so neighbour sensitivity of reproduction should be considered the 'norm' in *A. balsamea* and neighbour insensitivity may be an adaptation to the selection regime created by wave regeneration.

Interactions among plants are largely confined to those among neighbours, and how plants respond to crowding is a major manifestation of their phenotypic plasticity, with consequences for adaptation to local conditions (Schmitt & Wulff 1993). However, phenotypic plasticity may have costs as well as benefits (DeWitt *et al.* 1998) and wave populations of *A. balsamea* may be a case where the plasticity found in normal populations has been lost because its costs outweigh any benefits.

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