

Are sub-alpine firs evolving towards semelparity?

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Summary

In sub-alpine forests of Northeast America and Japan pure stands of trees in the genus *Abies* exhibit wave regeneration. Opportunities for recruitment in such forests are confined to a window in time and space that coincides with the death of an even-aged cohort of adult trees. I suggest that the coincidence of this recruitment window with the death of adults at a predictable age should select for convergence between age at first reproduction and age at death. Ultimately this would lead to the evolution of semelparity. The available evidence supports this hypothesis for wave-regenerated *Abies* populations in Japan. A field test of the hypothesis is also suggested.

Keywords: *Abies*; semelparity; life history evolution; wave regeneration

Introduction

All plant meristems are semelparous because their growth is terminated when they differentiate into reproduction organs. Since plants are constructed by iterative meristem growth, the fact that reproduction is a terminal act for meristems ought to make the evolutionary transition from iteroparity to semelparity in the whole plant a morphologically simple one (Silvertown, 1989). Yet semelparity at the level of the genet is a relatively rare kind of life history among perennial plants. Although perennial semelparity seems to have evolved repeatedly in a few groups (Silvertown, 1983), it otherwise has a scattered occurrence across many different families (Young and Augspurger, 1991). Besides some palms, only two tree genera (both angiosperms) are known to contain semelparous species (Foster, 1977).

The reproductive effort model (Schaffer and Gadgil, 1975) suggests that semelparity should be selectively favoured when fitness increases and residual reproductive value decreases non-linearly with reproductive effort. A variety of ecological situations may produce a fitness curve with this shape and, so far as the available evidence goes, the model is supported for long-lived semelparous perennials (Schaffer and Schaffer, 1979; Young, 1990; Young and Augspurger, 1991). Another way of looking at the evolution of semelparity is in terms of the coupled evolution of age at first reproduction (α) and length of life. A correlation between α and lifespan is well established in a variety of plant and animal groups (Charnov, 1993).

One may define semelparity as the coincidence of age at first reproduction with the end of life and ask when such a coincidence would be favoured. In plant populations the likeliest occasions are when the death of one generation and its replacement by the next are brought about by the same disturbance event. Tree-killing fires and hurricanes are the commonest examples in forests. Both events are unpredictable and so plants must store up propagules in advance if they are to be represented among the generation that will be recruited after disturbance. In fire-prone habitats such as pine barrens, seeds are stored in the tree canopy inside resin-sealed cones that open after they have been heated by fire. In gap-regenerated forests species such as pin cherry (Marks, 1974) accumulate a soil seed bank that germinates after disturbance. Other species accumulate a bank of seedlings ('advance regeneration') that are released when a gap opens overhead (Grime, 1979).

In all such disturbances any plant which could concentrate its reproductive effort into the season before death would be sowing all its seeds into ploughed earth. Only the unpredictability of disturbance in time and space precludes this semelparous strategy.

If disturbance occurs predictably in time and space semelparity should be a viable strategy. Just such predictable disturbances do occur in sub-alpine wave-regenerated *Abies* forests on mountains in Northeast USA and Japan. Tree death in these forests occurs along a wavefront that typically travels downwind at a steady rate of between 0.4 and 3.4 m per year, depending upon the site (Sato and Iwasa, 1993). A new cohort colonizes the dead zone so that trees of successively older age are found with increasing distance behind the wavefront. Depending upon the population, trees die at between 60 and 100 years of age (Sprugel, 1976; Sato, 1994). Seedlings are found only in the dead zone and just downwind of it and are the offspring of the oldest adult cohorts, including those in the dead zone (Kohyama and Fujita, 1981). It therefore appears that there is a narrow window of opportunity in time and space when offspring can recruit. This coincides with the age of parent trees and is greatest near their age of death. Since seeds produced early in life have little or no chance of success in a wave-regenerating forest, this should favour the convergence of α with age at death. The two should not coincide exactly because some advance regeneration takes place a short distance ahead of the wavefront (Sprugel, 1976; Kohyama and Fujita, 1981; Marchand, 1984).

Methods and results

To test the hypothesis that α is converging with age at death in wave-regenerating *Abies* populations I graphed α against reproductive lifespan for eight non-wave-regenerating species (data from Loehle, 1988) and for three wave-regenerating species (Kohyama, 1982; Sato, 1994). Two of the wave-regenerating species, *Abies veitchii* and *Abies mariesii*, occur sympatrically but they were treated as independent points because they differ significantly in α (Kohyama, 1984). I could find no data value for α in wave-regenerating populations of the American species *Abies balsamea*, so this was included only in the sample of non-wave-regenerating species. I have no published source of data on the life histories of non-wave-regenerating Japanese *Abies* species either, but informal evidence will be mentioned below.

Reproductive lifespan (age at death - α) rather than lifespan was used to achieve independence between x and y variates (Sutherland *et al.*, 1986). Graphed in this way, the vertical axis represents semelparity (reproductive lifespan = 0 for all values of α) and the nearer a species lies to this axis the nearer it approaches semelparity. The relationship between α and reproductive lifespan for non-wave-regenerating species is positive, though the regression is not significant (Fig. 1). Nevertheless it is clear that the wave-regenerating species are extreme outliers from the relationship; they lie much nearer the vertical axis than other species and they have much greater values of α than is to be expected for non-wave-regenerating species with the same reproductive lifespan (Fig. 1).

Discussion

Figure 1 supports the hypothesis that wave regeneration has selected for a convergence between α and age at death. However, the wave-regenerating and the non-wave-regenerating species not only come from different environments, but also come from different continents, so it remains an open question whether the effect shown is the result of a genetic difference or of phenotypic plasticity. Unpublished information on the life histories of two of the Japanese species in non-

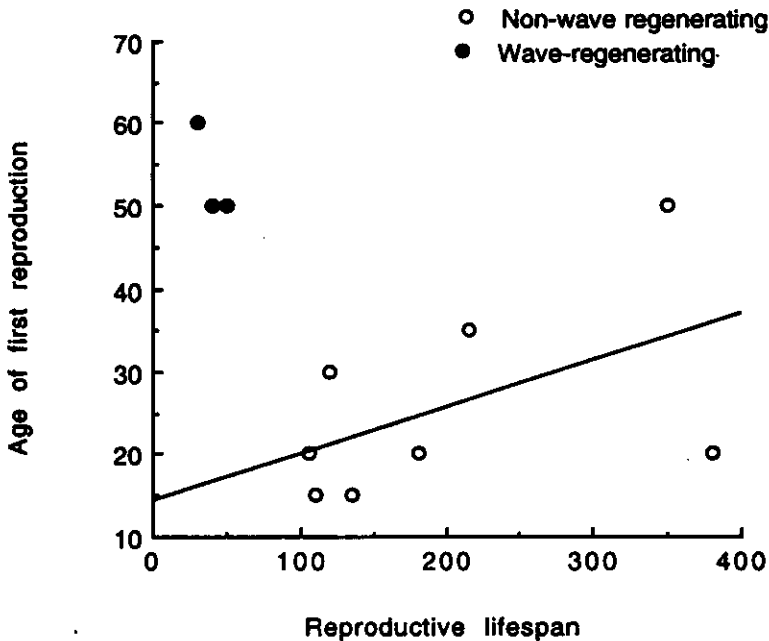


Figure 1. Relationship between age at first reproduction and reproductive lifespan for eight species of non-wave-regenerating *Abies* (*Abies amabilis*, *A. balsamea*, *Abies concolor*, *Abies fraseri*, *Abies grandis*, *Abies lasiocarpa*, *Abies magnifica* and *Abies procera*) shown by open symbols and the regression line, and for three wave-regenerating species (*A. sachalinensis*, *A. veitchii* and *A. mariesii*). The regression line shown ($y = 14.31 + 0.057x$, $R^2 = 0.263$) is indicative, but not significant ($p > 0.05$).

wave-regenerating populations suggest that *Abies sachalinensis* ($\alpha = 40$, reproductive lifespan = 60 – 80) and *A. mariesii* ($\alpha = 50$, reproductive lifespan = 150) lie further away from the vertical axis of Fig. 1 (and hence further away from semelparity) than wave-regenerating populations of these species (T. Kohyama, personal communication).

Comparison in a common garden experiment of α and of reproductive lifespan between individuals drawn from wave-regenerating and non-wave-regenerating populations of the same species would be the ideal test of my hypothesis, but one that would be a long time in producing an answer! A much quicker alternative would be to utilize the differences between fir waves within one locality. Sprugel (1976) found that regeneration waves of *A. balsamea* at his site in New York State differed in wavelength and speed of travel according to local topography and wind direction. This gave rise to differences between waves in age at death, in the range of 41–75 years. Because each wave travelled at a consistent speed, differences in age at death in the forest as a whole are likely to be site-specific and consistent on a very local scale. If the value of α is selected for convergence with age at death, then α should also vary site-specifically and it should be correlated with age at death when waves are compared. Since gymnosperms tend to be highly outcrossing gene-flow between sites might swamp local selection, but not if that selection is very strong. Such a test would not only throw light upon the evolutionary relationship between age at first reproduction and lifespan in *Abies*, but would have more general relevance for this question too. It may be better to think of semelparity and iteroparity as the opposite ends of a continuum of life history variation rather than as a simple dichotomy.

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