Scale of mast-seeding and tree-ring growth

The synchronous production of large seed crops by a population of plants[1,2], known as mast-seeding, and synchronous tree-ring growth[3,4] within sites are well known phenomena among trees in the temperate zone. But information about the geographic or taxonomic extent of such synchronous growth or reproduction, or about the geographic extent of switching between them, is sparse. We have detected synchrony in growth and reproduction, both within and among genera of Northern Hemisphere boreal trees, across geographical areas almost the size of a continent. Furthermore, we found a significant negative correlation between seed production and tree-ring growth at sites up to 1,000 kilometres apart, implying that there are trade-offs between them. This discovery suggests that mast-seeding is an evolved strategy that occurs on a geographic scale far larger than previously suspected[5].

Annual seed or cone production values were obtained from the literature and standardized so that data acquired using different scales and methodologies could be combined. We used 298 data sets from seven genera of boreal coniferous trees (*Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja* and *Tsuga*) containing a minimum of four years of data (mean, 12.4 years). As a proxy of vegetative growth, we used dendrochronologies obtained from the International Tree-Ring Data Bank (version 2.2), a repository of more than 1,200 site-standardized chronologies from around the world.

Both data sets consisted of annual site means. Analyses included within-genus comparisons of sites measuring congeners and among-genera comparisons performed by pairing different genera. This latter analysis included firs (*Abies*), larches (*Larix*),

spruces (*Picea*), Douglas-firs (*Pseudotsuga*), cedars (*Thuja*) and hemlocks (*Tsuga*), but excluded pines (*Pinus*), which require more than a year to mature cones. Spatial autocorrelations and cross-correlations were calculated using a modified correlogram procedure[6].

Our results reveal statistically significant spatial autocorrelation over large areas. Synchrony in the production of seeds and cones was detectable between sites from 500 km apart (*Abies*) up to 2,500 km apart (*Pinus*) (Fig. 1a). Synchrony in tree-ring growth was found between sites from 500 km apart (*Abies*) up to 5,000 km apart (*Larix*) (Fig. 1b). Assuming a circular area with a diameter corresponding to these distances, this indicates that detectable synchrony in cone production occurs over areas of 0.2–4.9 × 10^6 km^2, and tree-ring growth patterns over areas of 0.2–19.6 × 10^6 km^2. For comparison, the approximate land area of the North American continent is 24.3 × 10^6 km^2, so reproduction and radial growth of conifers are statistically synchronous over subcontinent- to continent-wide areas.

Cone production and tree-ring growth patterns are both generally correlated with climatic factors, such as temperature or rainfall[3,4,7]. If the large-scale patterns of variable growth and reproduction are positively correlated with climate, they may involve only environmental tracking and require no further evolutionary explanation. Alternatively, mast-seeding may be an evolved strategy, conferring fitness advantages by means of economies of scale involving seed predation, seed dispersal, or wind pollination[8,9]. The critical prediction, given these alternatives, is that there must be a trade-off between vegetative and reproductive growth on a population scale[1].

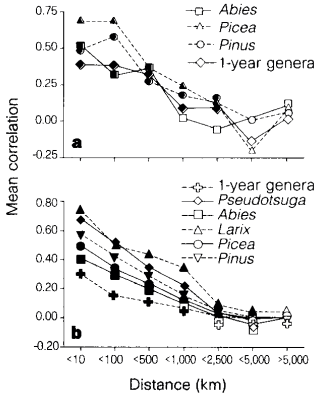

Figure 1 Correlations between synchronous activity of Northern Hemisphere coniferous trees depending on the geographical distance between sites. **a**, Mean annual seed or cone crop; **b**, mean annual tree-ring growth. Within-genus comparisons (*Abies*, *Larix*, *Picea*, *Pseudotsuga* and *Pinus*) include all sites measuring any species within the genus. The one-year genera category involves among-genera correlations using *Abies*, *Larix*, *Picea*, *Pseudotsuga*, *Thuja* and *Tsuga*, and excluded all within-genus comparisons. Filled symbols are significant at $P < 0.05$ by randomization tests.

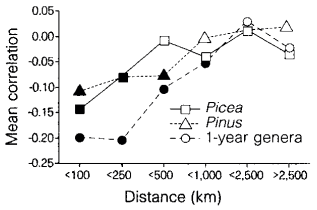

Figure 2 Cross-correlation between mean annual seed or cone crops and mean annual tree-ring growth of Northern Hemisphere coniferous trees depending on the geographical distance between sites. Within- and between-genus comparisons are as for Fig. 1; only *Picea* and *Pinus* had sufficient data to be tested individually. Filled symbols are significant at $P < 0.05$ by randomization tests.

We tested for such trade-offs by using cross-correlation analyses between the tree-ring and seed-production data sets. These yielded a negative relation between growth and reproduction for sites up to 250 km apart for spruces, 500 km apart for pines, and 1,000 km apart for one-year genera combined (Fig. 2). These inverse correlations between growth and reproduction, which are indicative of resource switching, are detectable within genera across areas of up to 196,000 km^2 and between genera across areas of up to 785,000 km^2.

Our results show that mast-seeding involving switching of resources between growth and reproduction is characteristic of Northern Hemisphere conifers on a large geographic scale. Furthermore, in conifers, mast-seeding is detectable both between species and between genera, at least when restricted to genera requiring a single year to mature cone crops. They also show that patterns of seed production are sufficiently broad, both taxonomically and geographically, to affect the populations of seed predators over large areas. For example, our results support the hypothesis that the synchronized invasion of boreal seed-eating birds into southern latitudes could be the result of geographically widespread seed-crop failures[10]. Similarly, resident populations of birds and mammals that depend on conifer seeds for food are likely to be affected synchronously over large geographic areas by both bumper crops and widespread crop failures.

The many potential effects of such large-scale ecological phenomena on ecosystem function and biodiversity[11] remain to be investigated. Furthermore, because broad climatic patterns almost certainly correlate with the large-scale synchrony, global climate change[12,13] may affect ecosystems in previously unanticipated ways.

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