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Authors:	Birks, H.J.B. Birks, Hilary H.
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PALEOECOLOGY

The Rise and Fall of Forests

After a catastrophic disruption to an ecosystem, or at the beginning of an interglacial period, there is a phase of ecological development that results in soil changes and increases in productivity, biomass, and nutrient availability. Later during the interglacial period, this early primary successional phase is followed by a phase of retrogressive succession during which ecosystem productivity and plant biomass decrease. Although the mechanisms underpinning early primary succession are well established, those underlying retrogressive succession are not. On page 509 of this issue, Wardle et al. (1) provide insights into the ecological processes contributing to the long-term decline of a variety of forest ecosystems during retrogressive succession in different interglacial periods.

The retrogressive succession of forests (2) is a characteristic of the later phases of interglacial periods, and, according to pollen analyses, has taken place during several interglacials including the present one, the Holocene (3, 4). Interpretation of Holocene forest history is complicated by human impact on the landscape since the mid-Holocene (5000 to 6000 years ago), but the successions that took place in earlier interglacials in the absence of any human impact are unambiguous (2).

The retrogressive phase of long-term vegetational succession is part of the glacial-interglacial cycle first proposed for northwestern Europe by Iversen (5) and developed by Andersen and Birks (3, 4, 6). A long cryocratic or glacial stage, with a cold, dry climate and open treeless vegetation growing on immature base-rich soils, alternates with an interglacial stage that usually lasts about 10,000 to 30,000 years (see the figure). The interglacial comprises four phases: a protocratic or pioneer phase (with rising temperatures and the development of diverse light-demanding vegetation and unleached soils), a mesocratic phase (with high temperatures and development of closed forest and fertile soils), an oligocratic phase (with decreasing forest cover and deteriorating soils), and a final telocratic phase (with declining temperatures, increasingly open vegetation, and infertile soils) (3-6). The processes influencing succession during interglacial cycles include changes in climate, soil, and biotic interactions (3, 4, 7). Soil changes during the later phases of primary succession may be due to leaching and a decline in the nutrient base with associated changes in soil biota and humus type (2-4, 6, 8, 9).

Ecologists have intensively studied the early stages of primary succession along a variety of chronosequences. A chronosequence is a series of sites — for example, glacier forelands, volcanic lava flows, sand dunes, recently formed islands (10, 11) — of different but known ages. These studies show that after initial colonization there is a phase of maximum biomass development following predictable increases in productivity, biomass, nutrient availability, and changes in soil composition (10, 11). Ecologically speaking, these phases resemble the protocratic (pioneer) and the mesocratic (maximum biomass) phases of the interglacial cycle (see the figure). Ecologists, however, have paid scant attention to the later phases of primary succession (in the absence of a catastrophic disturbance) corresponding to the oligocratic and telocratic phases of the interglacial cycle during which biomass and productivity decline.

This is where Wardle et al. (1) come in. They have studied six chronosequences in Australia, Sweden, Alaska, Hawaii, and New Zealand, covering a time range from 6000 years ago (Sweden) to >600,000 years ago (Australia) and even 4 million years ago (Hawaii) — the sorts of time scales studied by Quaternary paleoecologists. They take advantage of a technique called "space-for-time" substitution, which allows them to study modern vegetation and soils on surfaces of different but known ages, and hence to infer what changes in ecology and soils took place over time. The application of space-for-time substitution to the study of ecosystem dynamics requires that assumptions be made, for example, that external factors remain constant and there are no major disturbances (10, 11). Assumptions aside, the six chronosequences selected by Wardle et al. represent a unique "natural experiment" for determining consistent ecological features in the retrogressive phase of vegetational succession in temperate, tropical, and boreal vegetation.

These investigators report a unimodal response of tree basal area (a surrogate measure of tree biomass) over time. The tree basal area declines within 1000 to 10,000 years after the onset of primary succession. There is also an increase in the nitrogen to phosphorus (N:P) and carbon to phosphorus (C:P) ratios in humus in all six chronosequences, accompanied by a marked increase in the N:P ratio of litter in four of the chronosequences. These results imply that during retrogressive succession, P becomes limiting relative to N in the humus layer, followed by reduced P concentrations in the litter produced by vegetation in four of the chronosequences. Thus, unlike N, which is biologically renewable, P is not and is leached from soils over time, leading to a phosphorus-depeleted ecosystem.

As the authors demonstrate, declining tree biomass is often accompanied by reductions in litter decomposition rates and release of P from litter, as well as decreased activity of microbial decomposers. The proportion of fungi relative to bacteria increases as retrogressive succession proceeds. Fungal-based soil food webs retain nutrients better than do bacterial-based food webs, which suggests that during forest decline, nutrient cycling becomes more closed and nutrients become less available. The overall picture provided by Wardle et al. is that (in the absence of a major disturbance) there is a long-term decline in biomass accompanied by increasing P limitation relative to N, reduced rates of P release in decomposing litter, and reductions in litter decomposition, soil respiration, microbial biomass, and the ratio of bacterial to fungal biomass.

These findings, and the ecological processes proposed to explain them, provide an elegant model for the onset of the oligocratic phase of an interglacial, namely that tree biomass declines as P becomes increasingly limiting. Reductions in litter decomposition rates and changes in soil microbial assemblages may also occur. Paleoecologists have suggested that such changes may explain the long-term switch from forest soils composed of mull humus to those composed of mor humus (2, 8, 9). Given recent developments in paleoecology, paleolimnology, and stable-isotope analysis (12-14), paleoecologists now have tools to test directly some of the ideas proposed by Wardle and co-workers.

DIAGRAM: The effects of a glacial-interglacial cycle on a long-term ecosystem. Depicted are the likely changes in biomass and soil that take place during the glacial (cryocratic) stage and interglacial (1). The four phases of the interglacial — protocratic, mesocratic, oligocratic, and telocratic — are shown. The largest changes in temperature occur at glacial-interglacial transitions, that is, at the beginning and end of the cryocratic phase. [Modified from (6)]

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By H.J.B. Birks and Hilary H. Birks
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