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Changing perspectives on the role of the soil seed bank in northern temperate deciduous forests and in tropical lowland rain forests: parallels and contrasts

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Abstract

In the early 1990s a simple view of forest dynamics and the role of the soil seed bank in forests was widely accepted. Plants could be divided into 'pioneers' that need canopy gaps for establishment, and 'non-pioneers' that are able to establish in shade. The species in the persistent seed bank were believed to be 'pioneers', awaiting formation of a gap in the canopy. It was also widely believed that seed bank species need (a) light, and (b) a high red: far-red (R:FR) ratio for germination, and that some need marked diel fluctuation in temperature. We review the changes in perspective during the last 15 years for the two forest-types best studied in this respect: northern temperate deciduous forest (NTDF) and tropical lowland rain forest (TLRF), and concerning NTDF we place especial emphasis on studies in nearly natural stands in the Białowieża Forest in Poland. It is now known that 'pioneers' and 'non-pioneers' merge in the sense that in NTDF there are species that utilize gaps in the herb layer and litter under an intact tree canopy, and in TLRF there are species which need only 'micro-gaps' in the tree canopy caused by the fall of a single branch or of a whole crown a little way off. It is also known that the soil seed bank of both these forest types may contain a substantial number of species that are to a significant degree shade-tolerant; in NTDF there are a few species able to establish in the deepest shade and a greater number able to utilize gaps in the herb layer and litter, while in TLRF there are both species able to establish in the deepest shade and species needing only micro-gaps in the tree canopy. In both forest types a requirement for light and a high R:FR ratio is now seen to be characteristic of the small-seeded canopy-gap-demanding species in the seed bank; small-seeded species able to grow in an appreciable degree of shade do not need a high R:FR for germination. There is emerging evidence that (a) stimulation of germination by diel temperature fluctuation is characteristic of larger-seeded species in the seed bank, and (b) that risk-spreading dormancy is overlain on the dormancy related to awaiting an appropriate signal for germination. TLRF seems to differ from NTDF in that larger-seeded species rather than smaller-seeded last longer in the soil.

Keywords: Deciduous forest; Light requirement; Red:far-red ratio; Seed bank types; Seed mass; Tropical rainforest

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Seek simplicity but distrust it.
(J.L. Lagrange; cf. Grubb, 1992)

If you can look into the seeds of time,
And say which grain will grow, and which will not,
Speak then to me, who neither
beg nor fear
Your favour nor your hate
(*Macbeth* Act 1, Scene iii)

Introduction

In the late 1980s a relatively simple paradigm prevailed in respect of the grouping of forest plants in terms of requirements for establishment, and the role of species found in the soil seed bank of forest soils. In essence, two primary groups were recognized (depending on whether or not they needed canopy gaps for establishment) and the species in the seed bank were all considered to be in the group needing canopy gaps. This review covers the changes in this understanding that have occurred in the last 15 years. It deals mainly with new evidence about the nature of the seed bank, and of the signals needed for germination of the seeds in it, but this has to be considered against the background of changed thinking about the groups of species recognized in terms of requirements for regeneration.

Swaine and Whitmore (1988) presented a simple classification of forest plants into 'pioneers' (establishing only in canopy gaps) and 'non-pioneers' (establishing in canopy shade; however light light-demanding the species might be for onward development). The latter group was later called 'climax' by Whitmore (1989). Various authors have emphasized the continuity between the two groups of species, either on the basis of there being a graded series in the extent of light-requirement for germination (Raich and Gong, 1990) or there being an intermediate group of species needing only 'micro-gaps' in the canopy for establishment – produced by the fall of a branch overhead or the fall of a tree nearby and yielding, say, 2–4% daylight at ground level as opposed to 4–10% in a single-treefall gap (Grubb, 1996; Grubb and Metcalfe, 1996; Metcalfe et al., 1998). There is also evidence for 'pioneers' sensu Swaine and Whitmore (1988) being divisible into those needing only small gaps (usually single tree-falls) and those needing large gaps (usually multiple tree-falls) or forest edges (Grubb and Stevens, 1985; Brokaw, 1987; Putz and Appanah, 1987; Grubb and Metcalfe, 1996; Pearson et al., 2003a). However, these two groups probably inter-grade too (Busing and White, 1997; Dalling and Hubbell, 2002).

In the last 15 years much of the thinking about forest plants in terms of regeneration-requirements has been done in respect of tropical lowland rainforests (TLRF), where the great majority of species are strongly shade-tolerant at the establishment stage. There is a strong contrast with the situation in northern temperate deciduous forests (NTDF) where only a minority of the species of trees, shrubs and herbs is strongly shade-tolerant at the stage of establishment, i.e. able to persist for long periods in 1–2% daylight.

For NTDF the tolerances of tree species have long been expressed on a 5-point scale: by Baker (1945) for North America and by Ellenberg (1963) for Europe. For the most part 'pioneers' sensu Swaine and Whitmore were rated 1, and the categories 2–5 were differentiated by the degree of shade tolerated during onward growth from seedling to adult tree. No species capable of establishing in 'micro-gaps' was explicitly recognized. A scheme which explicitly recognizes differentiation in shade-tolerance at both establishment and onward growth stages has been given by Coomes and Grubb (2000).

For herbs in NTDF in Europe much quantitative work has been done on the degree of shade in which adults of various species can be found (Ellenberg, 1939; Eber, 1972). These observations were used by Ellenberg (1988) in formulating his 9-point scale of tolerance shown in Table 1. His experience in the field enabled him to assign species for which no measurements had been made; for these he knew which species they paralleled most closely among the many for which measurements had been made. The values given are for plants on relatively fertile soils; it is known that on infertile soils many species become much more light-demanding (Ellenberg, 1939) and the explanation is probably that the plants assign much less biomass to leaves when nutrients are in very short supply (Peace and Grubb, 1982). Unfortunately no Ellenberg-type classification of

Table 1. The definitions of the degrees of light-demand recognized in the 9-point scale of Ellenberg (1988) for forest species in Europe

1. Found down to $<1\%$ daylight, rarely in $>30\%$
2. Between 1 and 3
3. Mostly found in $<5\%$, but also in better-lit places
4. Between 3 and 5
5. Rarely in full light, but generally in $>10\%$
6. Between 5 and 7
7. Generally in well lit places but also in partial shade
8. Rarely found in $<40\%$
9. Plants of full daylight, rarely in $<50\%$

These ratings apply to plants found growing on relatively fertile soils, and concern the occurrence of healthy vegetative plants; plants on infertile soils, and flowering plants, commonly need more light. In general, species needing multiple-treefall gaps or comparable gaps made by humans are rated 7–8, while those needing only a single-treefall gap are rated 4–6. Category 4 contains both species needing single-treefall gaps and species able to utilize gaps in the herb and litter layer under the shade of a tree canopy (see text).