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8. THE RECOVERY OF GROUND VEGETATION IN COPPICE WOOD: THE SIGNIFICANCE OF BURIED SEED

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Many of the ancient woods of lowland England have been managed as coppice for hundreds of years. These coppice woods have distinctive, diverse, and ecologically interesting assemblages of plants, some being more-or-less confined to these habitats, eg *Carex pendula, Galeobdolon luteum* and *Oxalis acetosella* (Peterken, 1974). The relatively frequent alternation of light and shade, as a result of coppicing, has favoured the development of a shade flora (including, for example, *Anemone nemorosa, Endymion non-scriptus* and *Mercurialis perennis*), which persists for the whole coppice cycle, and a marginal flora, whose light-demanding species persist in rides and glades. Species of the marginal flora (such as *Cirsium palustre, Lysimachia nemorum* and *Stachys sylvatica*) also recolonise the 'body' of the wood for the first few years after coppicing before being eliminated as shading again intensifies. Salisbury (1924) wrote:

> "The story of the Coppice woods is thus a continual rise and fall in the vigour of the shade flora accompanied by an ebb and flow of the marginal flora. At each coppicing, the latter, as it were, floods the sparsely occupied ground and then, as the shade increases, flows back to its original position".

Because of changing economic and social conditions many coppices have been neglected or have been planted with conifers. As a result, the diversity of the ground flora has decreased, with losses of up to 70% occurring (Table 12), the losses being less in neglected coppice than in woodlands planted with conifers (Brown & Pearce, 1976).

However, to what extent are these changes reversible? It has, for long, been recognised that some recovery of the ground vegetation occurs when neglected coppice is felled; similarly, ground vegetation diversifies as conifer stands age and are thinned, and especially after clear-felling. To what extent does this vegetation represent the original flora? Where do the plants come from? Some will undoubtedly be attributable to the few remaining shade tolerant plants, and others may have immigrated from elsewhere. However, the existence of a seed-bank in the soil might also be of some importance.

1. Experimental observations

It is well known that weed seeds in agricultural soils can persist in a dormant but viable condition for many years (eg Roberts, 1970) or even for centuries (Odum, 1965). Much less is known about dormant seed populations in forest and woodland soils, and most published information refers to North America (eg Kellman, 1970). To gain an insight into the situation in the UK, 27 soil samples were examined from 5 overgrown, neglected coppice woodlands in East Anglia whose current

TABLE 12 Mean numbers, per 200 m^2, of different types of ground flora species found in 11 differently managed East Anglian woods.

Species type	System of managment Worked Coppice	 Neglected Coppice	 Coppice planted with conifers
Shade	11.0	8.3 *(75%)*	5.5 *(50%)*
Marginal	13.5	6.3 *(47%)*	3.9 *(29%)*
Woody seedlings	3.6	2.6 *(72%)*	2.5 *(69%)*
Others	1.9	0.8	0.1
Total	30.0	18.0 *(60%)*	12.0 *(40%)*
Species indicative of ancient woodland	3.4	2.5 *(74%)*	1.0 *(29%)*

(Percentages refer to comparisons with worked coppice) vegetation had already been surveyed. Samples were taken at random from heavily shaded areas in which ground cover was either absent or consisted of *Endymion non-scriptus* or *Mercurialis perennis* and occasional *Rubus fruticosus, Anemone nemorosa* or *Lonicera periclymenum.* Litter and humus layers were discarded from each 30 cm x 30 cm sample area, before collecting the underlying soil, separated into 2 horizons, 0-5 and 5-15 cm below ground level. Subsequently, the soils were transferred to plastic seed-trays in an unheated glasshouse, allowing germination and hence the subsequent identification, of the buried seeds. Although the trays were retained for 30 months, most seedlings had emerged within 2-3 months. Mean numbers of seedlings per tray ranged from 130 to 178 at Chalkney/Weeley and Felsham respectively (Plate 9).

In total, 68 different plant species germinated. For individual woods, numbers averaged 31 with 24 and 23 occurring in the 0-5 and 5-15 cm soil layers respectively (Table 14).

The seedlings that emerged were classified into 3 categories (i) light-demanding species, and those tolerant of (ii) some or (iii) heavy shade, accounting for 87%, 6% and 7% respectively of the total of 8073 (Table 15). The viable seeds were not representative of the current ground flora of neglected coppice which consists predominantly of deep-shade species, with a few marginal species. In contrast, the soil seed-bank contains mainly marginal species, but very few species of deep-

TABLE 13 Mean numbers of seedlings germinating in 2 horizons of soil taken from neglected coppices at 5 sites in East Anglia

Name of Wood	Nos. of replicate samples at each site	Soil horizons, cm below ground level 0-5 cm	5-15 cm
		(numbers of seedlings per 4,500 cm^3 of soil)	
Chalkney	6	178	83
Weeley	7	104	155
Felsham	4	181	174
Groton	4	185	128
Parkhall	6	203	133
Combined Woods	27	166	133

Some seedlings emerged in all trays, numbers in surface (0-5 cm) soil averaging 166, equivalent to 1844 m^{-2} or 18.4 million ha^{-1} compared with 133 per tray at a depth of 5-15 cm (Table 13).

TABLE 14 Total numbers of plant species emerging from different soil horizons taken from 5 neglected coppices in East Anglia.

Name of Wood	Soil horizons, cm below ground level 0-5 cm	5-15 cm	0-15 cm ie the 2 horizons combined
Chalkney	32	31	41
Weeley	23	20	28
Felsham	19	24	27
Groton	23	13	26
Parkhall	24	27	34
Total nos. of species for all woods, combined	61	57	68
Average no. of species per wood	24	23	31

TABLE 15 Numbers of seedlings of different species (grouped according to shade tolerance) emerging after keeping soil samples from 5 neglected coppices in East Anglia for 2 years in an unheated glasshouse.
(Nos. of seedlings from 27 replicate 30 cm x 30 cm samples)

	No. of seedlings		No. of seedlings
	Light-demanding species		
Agrostis canina	113	*Plantago major*	1
Agrostis stolonifera	327	*Polygonum aviculare*	1
Anthoxanthum odoratum	105	*Polygonum convolvulus*	23
Betula sp	1335	*Polygonum lapathifolium*	1
Carex pallescens	71	*Polygonum nodusum*	2
Carex pilulifera	50	*Polygonum persicaria*	1
Centaurium erythraea	11	*Ranunculus flammula*	6
Chenopodium album	39	*Rumex obtusifolius*	26
Cirsium palustre	28	*Sagina procumbens*	11
Digitalis purpurea	276	*Salix* sp	4
Epilobium adenocaulon	42	*Sarothamnus scoparius*	2
Epilobium sp	10	*Solanum nigrum*	34
Festuca sp	34	*Trifolium* sp	1
Gnaphalium uliginosum	1	*Tripleurospermum maritimum inodorum*	1
Hypericum hirsutum	3	*Veronica chamaedrys*	6
Hypericum humifusum	34	*Veronica officinalis*	60
Hypericum pulchrum	20	*Veronica serpyllifolia*	7
Hypericum tetrapterum	54		
Isolepis setacea	68		
Juncus bufonius	139		
Juncus effusus	4205		
Lotus corniculatus	15		
	Species tolerant of some shade		
Carex pendula	10	*Ranunculus repens*	8
Deschampsia cespitosa	2	*Rosa* sp	1
Euphorbia amygdaloides	1	*Rubus idaeus*	9
Fragaria vesca	3	*Sambucus nigra*	11
Holcus lanatus	26	*Scrophularia nodosa*	4
Luzula pilosa	19	*Silene dioica*	18
Lysimachia nemorum	57	*Solidago virgaurea*	1
Poa nemoralis	5	*Stachys sylvatica*	1
Poa trivialis	27	*Stellaria media*	1
Potentilla sterillis	8	*Veronica montana*	45
	Species tolerant of heavy shade		
Ajuga reptans	32	*Primula vulgaris*	3
Carex remota	14	*Rubus caesius*	1
Carex sylvatica	1	*Rubus fruticosus*	446
Corydalis claviculata	13	*Viola* sp	16
Moehringia trinervia	33		

shade; *Endymion non-scriptus*, *Anemone nemorosa*, *Lonicera periclymenum*, *Circaea lutetiana* and *Mercurialis perennis* are notable absentees.

This lack of correspondence between the buried seeds and the current composition of the vegetation is not unusual (eg Harper, 1977). However, it calls into question the origin of the seed-banks: have they survived from the vegetation of an earlier more open phase, or have they immigrated from elsewhere? The evidence supports the former alternative, with some seeds remaining viable for the 30 or 40 years since the woods were last coppiced. Seeds of many species of open, unshaded habitats have (or acquire) a requirement for light in order to germinate—thus remaining dormant while buried. In contrast, seeds of species of closed vegetation (including the shade species of forests), although possibly requiring a chilling or other pre-treatment, seem to germinate equally readily in light or dark conditions (Grime & Jarvis, 1975), and are therefore not incorporated into the seed-bank. The paucity of shade species in seed-banks in coppice woods matches observations on North American (Leavitt, 1963; Kellman, 1974) and on Russian forest soils (Karpov, 1960).

2. Implications

Traditionally, it has been considered that the marginal flora of coppice woodlands would reinvade freshly cut areas by its spread from rides and glades (Salisbury, 1924; Rackham, 1975). However, there is increasing evidence (Brown & Oosterhuis, 1981) that this ebb and flow, in the sense of retreating to, and re-invading from, open areas is of less importance than the buried seed-bank. If this is an effective mechanism where trees are coppiced, there seems to be no immediate reason why it should not also apply when old coppice is converted to conifers, although the longer rotation of conifers (50 yr), compared with the coppice cycle of say 15 years, may well eventually reduce seed survival. Preliminary studies indicate that seeds of a similar range of species survive in soils of 20 year old coniferous plantations (Brown, 1979).

In contrast, not only do the deep-shade species seem to be absent from the soil seed-bank, but other evidence (Webb, 1966) suggests that their migration from elsewhere is likely to be slow; they tend to produce relatively few but heavy seeds which remain close to parent plants (Salisbury, 1942), unless spread by animals such as ants (Ridley, 1931; Fahn & Werker, 1972).

In summary, it seems that:

(i) marginal species and species of less extreme shade are able to survive in soil-borne seed-banks for periods of 30 years or more, and thus have the potential to recover, and (ii) species of deep-shade, if lost because of extreme conditions, eg the seasonally unvarying intense shade in evergreen coniferous plantations (compared with the seasonally variable shade in stands of deciduous trees), will only be re-established with difficulty, if at all.

References

Brown, A.H.F. 1979. *Management effects in lowland coppice woods. Viable seed content of soils of conifer-planted areas in ancient coppice woods.* Natural Environment Research Council contract report to the Nature Conservancy Council. Grange-over-Sands: Institute of Terrestrial Ecology. (Unpublished).

Brown, A.H.F. & Oosterhuis, L. 1981. The role of buried seed in coppice woods. *Biol Consvn.* **21**, 19-38.

Brown, A.H.F. & Pearce, N.J. 1976. Ecological effects of management in coppice woodlands: progress report. Natural Environment Research Council contract report to the Nature Conservancy Council. Grange-over-Sands: Institute of Terrestrial Ecology. (Unpublished).

Fahn, A. & Werker, E. 1972. Anatomical mechanisms of seed dispersal. In: *Seed biology* Vol 1, edited by T.T. Kozlowski, 151-221. New York; London: Academic Press.

Grime, J.P. & Jarvis, B.C. 1975. Shade avoidance and shade tolerance in flowering plants. II. Effects of light on the germination of species of contrasted ecology. In: *Light as an ecological factor: II,* edited by G.C. Evans, R. Bainbridge and O. Rackham, 525-532. Oxford: Blackwell Scientific.

Harper, J.L. 1977. *Population biology of plants.* London: Academic Press.

Karpov, V.G. 1960. (On the quantity and species composition of viable seed in the soil of spruce forests with a *Vaccinium* shrub layer). Translation from: *Trudŷ mosk. Obshch. ispŷt. Prir.,* 3, 131-140.

Kellman, M.C. 1970. The viable seed content of some forest soils in coastal British Columbia. *Can. J. Bot.,* **48,** 1383-85.

Kellman, M.C. 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. *J. Biogeogr.,* **1**, 123-133.

Leavitt, T.P. 1963. *Presence and viability of seeds in forest soils as related to depth, time and land-use history.* Hons. Thesis, Amhest College, Massachusetts.

Odum, S. 1965. Germination of ancient seeds. Floristical observations and experiments with archaeologically dated soil samples. *Dansk. bot. Ark.,* **24**, 1-70.

Peterken, G.F. 1974. A method for assessing woodland flora for conservation using indicator species. *Biol. Conserv.* **6**, 239-245.

Rackham, O. 1975. *Hayley Wood—its history and ecology.* Cambridge: Cambridgeshire and Isle of Ely Naturalists Trust Limited.

Ridley, H.N. 1931. *The dispersal of plants throughout the world.* Ashford: Reeve.

Roberts, H.A. 1970. Viable weed seeds in cultivated soils. *Rep. natn. Veg. Res. Stn 1969,* 25-38.

Salisbury, E.J. 1924. The effects of coppicing as illustrated by the woods of Hertfordshire. *Trans. Herts. nat. Hist. Soc. Fld Club,* **18**, 1-21.

Salisbury, E.J. 1942. *The reproductive capacity of plants.* London: Bell.

Webb, D.A. 1966. Dispersal and establishment: what do we really know? In: *Reproductive biology and taxonomy of vascular plants,* edited by J.G. Hawkes, 93-102. Oxford: Pergamon, for the Botanical Society of the British Isles.