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Plant Communities and Soil Seedbanks in Broadleaved-Conifer Mixtures on Ancient Woodland Sites in Lowland Britain

INFORMATION NOTE

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SUMMARY

A survey of the groundflora in lowland plantations on ancient woodland sites highlighted its impoverished nature in the majority of stands compared to ancient semi-natural woodlands (ASNW) on similar site types. Within all sites, the crop species and planting arrangement significantly affected the composition and extent of the ground- and field-layer vegetation. The survey concentrated on broadleaved-conifer mixtures; the most frequent being row mixtures of oak/Norway spruce and beech/pine. Within these stands the conifer component differed in its effect on the ground vegetation; Norway spruce tending to reduce the cover-abundance of vascular plants and pine tending to increase it. Moss cover was richer and more extensive in stands with Norway spruce, but only where these stands were thinned. Lower stand stem density was most consistently related to a diverse, extensive groundflora, highlighting the importance of rigorous thinning regimes in mixed stands. The buried seedbank cannot be relied on to replenish the vegetation after a rotation, as seeds of woodland groundflora were rarely detected in seedbank analysis.

INTRODUCTION

1. Between 1938 and the early 1980s over one-third of ancient semi-natural woodlands (ASNW) were converted to plantation, mainly composed of introduced tree species (Kirby *et al*., 1984). After the conservation importance of ASNW was fully realised, this process was stopped in 1985. Since then conservation and sympathetic management of the remaining ASNW has been encouraged as part of forestry policy (Forestry Commission 1994, 1998).

2. Restoration to a semi-natural type of woodland has also been recognised as a potential conservation objective for the areas which have been converted to plantation stands (Forestry Commission, 1994), and *The UK Forestry Standard* encourages this where significant features characteristic of ASNW remain (Forestry Commission, 1998). One of the main situations where this is thought likely is where broadleaved-conifer mixtures were planted, a practice which was widespread in lowland areas during the 1950s and 1960s.

3. Recently, the Habitat Action Plans for native woodlands have set UK-wide targets for the restoration of native woodland on ancient woodland sites, ideally to be targeted at the sites where the most benefits may result. The UK Woodland Assurance Scheme has also set out a framework for deciding future management of plantations on ancient woodland sites, for woodlands covered by the scheme.

4. A Forestry Commission Practice Guide is being prepared to give guidance on where and how best to restore native woodlands from plantations on ancient woodland sites. This Note supports that Guide by reporting the results of research to investigate the ecological effects of planting broadleaved-conifer mixtures to replace semi-natural stands on ancient woodland sites. The implications for future management options will be discussed.

SURVEY OBJECTIVES

5. This survey was initiated to examine the impact of planted mixtures of conifers and broadleaves on ancient woodland groundflora. It aimed to investigate in detail the species composition and relative abundance of the plant communities found and to relate the findings to crop, site and management factors, and compare these with established plantations and undisturbed ASNW on the same site types.

METHODS

6. Twenty sites across lowland England and Wales were selected for survey from Forestry Commission and private woodland records, on the basis that they were on ancient woodland sites, contained broadleaved-conifer mixtures and had pure stands of broadleaf and conifer components on nearby ancient woodland sites.

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7. Three replicate 300 m² plots were randomly located at a minimum of 15 m into the stand to avoid edge effects. The crop age, planting pattern, height and diameter at breast height (dbh) were measured for each plot (see Table 1 for site details), and all natural regeneration and shrub species recorded. The summer groundflora of vascular plants and mosses was assessed in each plot within six 1 m x 5 m transects placed centrally, where possible, across the interface between two different crop species. The transects were divided into metre squares in which the percentage cover of each species was recorded.

8. In the autumn, 20 soil samples were taken from each plot (to a maximum depth of 15 cm) to determine soil pH and assess the buried seedbank. In 12 of the sites the organic horizon was also sampled. In mixed stands the location of the samples was noted with respect to the canopy overhead, and only samples from under the same canopy were bulked. The buried seed was germinated in an unheated polytunnel over an 8-month period, by spreading the samples out in seedtrays. Emergent seedlings were removed in four harvests between April and July.

RESULTS

Ground vegetation

9. **Soil factors**

- Surface soil acidification under Norway spruce was shown to be strongly negatively correlated with both cover-abundance and species richness of vascular flora. Similar results were found for pine/beech mixtures, with a strong positive correlation between soil acidity and cover-abundance of mosses. Vascular plant cover-abundance increased with higher pH values.

- Increased litter depth and levels of soil organic carbon were found to be significant factors reducing cover-abundance of vascular flora.

10. **Stand factors**

- Thinned broadleaved-conifer mixtures contained a more extensive and species-rich groundflora than unthinned mixed stands (e.g. Figure 1). Thinning led to significantly greater cover of bramble (*Rubus fruticosus* agg.) and, to a lesser extent, honeysuckle (*Lonicera periclymenum*), compared to unthinned mixtures.

- Stem density was the crop factor most closely negatively correlated with the extent and richness of the ground vegetation (Table 2). The shade-casting species had the strongest effect in mixed stands, with a high density of Norway spruce stems particularly detrimental to the cover of the vascular groundflora. In mixtures this effect was reduced by early thinning and the use of at least 50% oak in the crop.

- Stands containing pine tended to support a particularly rich groundflora if they were thinned.

- Stands containing Norway spruce supported a rich moss flora, composed mainly of acid loving species benefiting from an increase in substrate variety, e.g. different humus forms.

- Exclusive use of species with light-transmitting canopies, e.g. oak and pine, invariably led to the dominance of bramble (*Rubus fruticosus* agg.) at the expense of other groundflora species.

Figure 1 Mean species number and mean percent cover per square metre in different woodland types

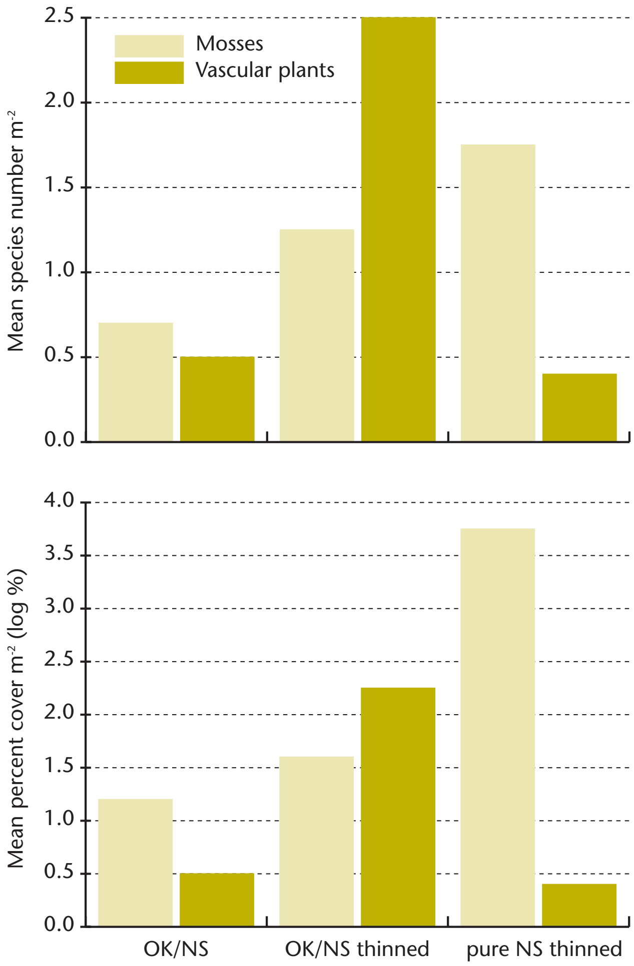

Table 1 Details of sites at which sub-compartments were surveyed

Location	Crop	Planting year	NVC community	Soil type	Planting pattern
Kings Wood, Kent	DF/BE SP/BE	1956 1942	W10	paleo-argillic brown earth	3:3 2:4
Denge Wood, Kent	NS/BE	1964	W14	brown rendzina	3:3
Shipbourne, Kent	NS/OK	1953	W10	typical stagnogley	3:3
Ampfield Wood, Hampshire	NS/OK NS/OK	1959 1959	W10	pelo-stagnogley	3:2 3:2
West & Crab Woods, Hampshire	CP/BE DF/BE	1956 1955	W12	brown rendzina	3:3 3:3
Parnholt, Hampshire	EL/BE	1916	W14	typical brown earth	-
Stoughton Down, West Sussex	CP/BE CP/BE	1954 1954	W14	stagnogley -argillic brown earth	3:3 1:1
Chawton Park & Bushy Leaze, Hampshire	NS/OK CP/BE DF/BE EL/BE	1953 1953 1951 1954	W10	typical brown calcareous earth	3:3 3:3 3:3 3:3
Homefield Wood, Buckinghamshire	DF/BE NS/BE CP/BE	1955 1960 1958	W10	stagnogley paleo -argillic brown earth	3:3 3:3 4:2
Wendover, Buckinghamshire	NS/BE SP/BE CP/BE	1934-6 1934 1951	W12	grey rendzina	1:1 1:1 2:2
Salcey Forest, Northamptonshire	NS/OK NS/OK SP/OK	1908 1945 1915	W8	stagnogley	- 3:6 -
Bernwood, Oxfordshire	NS/OK NS/(OK)	1956 1956	W10	pelo-stagnogley	3:3 3:3
Flaxley, Forest of Dean, Gloucestershire	EL/OK	1958-62	W10	-	3:3
Rougham Estate, Suffolk	DF/NS/OK NS/OK EL/SP/BE	1954	W10	-	1:4:3 group of 7 oak 3:2
Ashridge, Buckinghamshire	EL/SC/OK/BE SP/BE (NS)/OK OK/EL/BE SP/NS/BE NS/EL/SP/OK SP/BE	1934	W10	-	 group of 9 beech
Ragley, Warwickshire	HL/AH/BI EL/(NS)/AH EL/SC EL/NS/OK NS/OK	1930 1948 1937 1953 1970	W10	-	
Whitfield Estate, Herefordshire	EL/AH/OK EL/NS/OK NS/OK OK/TH TH/OK NS/(TH)/OK/AH	1961 1963 1966 1966 1963	W10		 group of 9 TH group of 9 oak
Ebworth Estate, Gloucestershire	EL/BE EL/BE/SYC (EL)/BE/AH (EL)/BE	 1936	W12	-	1:1
Boughton Estate, Northamptonshire	EL/OK EL/BE/AH EL/NS/OK	 1960	W8	-	-

Table 2a Significant positive and negative correlations of ground flora mean species number and percentage cover per square metre with crop stocking in mixed stands of oak/Norway spruce

	Mosses		Vascular plants	
	mean % cover m^{-2}	mean no. species m^{-2}	mean % cover m^{-2} (ln)	mean no. species m^{-2}
Oak				
Basal area (m^2 ha^{-1})	-*		+ **	
Stem number ha^{-1}	- *			
Top height (m)	- *		+ ***	+ ***
Yield class (m^3 ha^{-1} yr^{-1})	- *		+ *	
Norway spruce				
Basal area (m^2 ha^{-1})	+ *		- **	
Stem number ha^{-1}	+ **		- ***	- ***
Top height (m)				
Yield class (m^3 ha^{-1} yr^{-1})			- **	
% spruce basal area	+ **	+ *	- ***	

_ = trees > 7 cm diameter

* P <0.05, ** P <0.01, *** P <0.001 (degree of significance)

Table 2b Significant positive and negative correlations of ground flora mean species number and percentage cover per square metre with crop stocking in mixed stands of beech/pine

	Mosses		Vascular plants	
	mean % cover m^{-2}	mean no. species m^{-2}	mean % cover m^{-2} (ln)	mean no. species m^{-2}
Beech				
Basal area (m^2 ha^{-1})		- *	- ***	- ***
Stem number ha^{-1}	- **	- ***	- ***	- ***
Top height (m)	- *	- **	- **	- ***
Yield class (m^3 ha^{-1} yr^{-1})	- *	- **	- *	- ***
Pine				
Basal area (m^2 ha^{-1})			+ *	+ **
Stem number ha^{-1}				+ *
% pine basal area		+ *	+ **	+ **

_ = trees > 7 cm diameter

* P <0.05, ** P <0.01, *** P <0.001 (degree of significance)

Table 3 Species occurring in at least 15% of soil samples from 1988 sites. Seedbank strategies from Thompson and Grime (1979)

Species	Latin name	% frequency of species in samples		No. sites at which species recorded (max. = 12)		Seed bank strategy
		Soil	Organic horizon	Soil	Organic horizon	
Bramble	*Rubus fruticosus*	64	20	12	11	IV
Soft rush	*Juncus effusus*	51	21	11	7	IV
St. John's wort	*Hypericum* spp.	56	9	9	9	IV
Willowherb	*Epilobium* spp.	46	45	12	12	III?
Foxglove	*Digitalis purpurea*	32	13	10	7	III
Birch	*Betula* spp.	25	33	10	7	III
Figwort	*Scrophularia nodosa*	27	4	7	4	-
Tufted hair grass	*Deschampsia cespitosa*	19	14	9	7	III
Wood sedge	*Carex sylvatica**	25	8	10	6	-
Creeping bent	*Agrostis stolonifera*	21	12	12	8	III
Common nettle	*Urtica dioica*	19	10	5	6	IV
Three-veined sandwort	*Moehringia trinervia*	16	4	9	3	III?
Hairy wood-rush	*Luzula pilosa**	16	1	8	2	III or IV
Wood sage	*Teucrium scorodonia*	15	0	8	0	II - IV?

I Species with transient seed banks present during the summer.
II Species with transient seed banks present during the winter.
III Species with persistent seed banks in which a proportion of seeds germinate soon after they are released (i.e. function as Type I seed bank).
IV Species with large persistent seed banks.
* Ancient Woodland Indicator species.

Soil seedbanks

11. • Frequently, species found in the seedbank were not represented in the above-ground vegetation, although increased overall seed density occurred under stands with more vascular vegetation.

- The commonest seedbank species were bramble and soft rush (*Juncus effusus*), followed by St. John's wort (*Hypericum* spp.) and willowherb species (Table 3). Most seedlings identified were from species with a persistent seedbank (see Thompson and Grime, 1979); few were ancient woodland indicator species.

Table 4 Correlation of seed density in the soil with vegetation and plot factors in oak/Norway spruce and beech/pine stands

Factor	Number of seeds m^{-2} soil: Oak/Norway spruce	Beech/ pine
Mean % cover vascular species	+ *	+ *
Mean no. vascular species	+ *	
Conifer factors:		
Basal area (m^2 ha^{-1})	- *	+ *
Stem number ha^{-1}	- *	
% conifer basal area	- *	+ *
Conifer top height (m)		+ *
Broadleaf factors:		
Stem number ha^{-1}		- *
Broadleaf yield class (m^3 ha^{-1} yr^{-1})	+ *	
Basal area (m^2 ha^{-1})		- *
Broadleaf top height (m)	+*	

Table 5 Seedbank density in thinned oak, Norway spruce and mixed stands in Shipbourne Forest, Kent

Crop	Planting year	Species number	Seed density m^{-2}
Oak (pure)	1951	12	9097
Norway spruce (pure)	1951	9	2682
Oak/spruce mixture	1953		
i) oak rows		18	9053
ii) spruce rows		14	12978
	Grand mean		**8452**
	Standard error of mean		**2109**
	LSD ($P = 0.05$)		**7297**
	Variance ratio		**4.09**

- The organic horizon contained fewer seedbank species than the soil. Birch (*Betula*) and willowherb (*Epilobium*) species were most frequent in the organic horizon, having light, wind-dispersed seed (Table 3).

- Seedbank densities tended to be in excess of 2000 seeds m^{-2}, although lower densities were found in soil under shade-casting canopies, e.g. pure, unthinned stands of beech or spruce. Increasing the proportion of Norway spruce in an oak/Norway spruce mixture was negatively correlated with the soil seed density. A similar relationship was found for beech in beech/pine mixtures (Table 4).

- There was significantly more seed under oak rows in thinned oak/Norway spruce stands than in pure Norway spruce (Table 5), demonstrating the beneficial effects of Norway spruce canopy removal in enabling vascular flora to establish and recharge their seedbank reserves.

DISCUSSION

12. Most mixed stands sampled dated from the 1950s and were in the thicket or pole stage, where they would be expected to exert maximum effect on the ground vegetation (Ovington, 1955; Page, 1968). Thinning was particularly significant in its beneficial effect on the vascular groundflora, leading to an increase in the number of vascular plant species recorded when the shade-casting canopy component was removed, e.g. spruce in oak/Norway spruce stands, or beech in mixtures with pine. However, the reduced light conditions and consequent reduction in vascular flora under Norway spruce stands supported a greater number of mosses, mainly acidophilous species such as *Mnium hornum*, *Pseudoscleropodium purum*, *Hypnum cupressiforme*, *Dicranella heteromalla* and *Thuidium tamariscinum*.

13. Seedbanks were influenced by the broadleaf and conifer mixture components in much the same way as for the groundflora; the shade-casting trees reducing the seedbank density due to earlier decline of establishment-phase groundflora species. Larger seedbanks under stands with more above-ground vascular vegetation could not be related solely to the current vegetation. With the exception of ubiquitous bramble, species in the seedbank were often absent from the above-ground vegetation. Instead, the seedbank was dominated by light-demanding species, e.g. foxglove (*Digitalis purpurea*), typical of the disturbed conditions of a plantation after establishment or thinning.

14. Few ancient woodland groundflora species contributed significantly to the seedbank, and this could have consequences for their survival. For example, the limited seedbank of grasses typical of ancient woodland, such as wood millet (*Milium effusum*) and wood meadow-grass (*Poa nemoralis*), may result in replacement by species such as rough meadow-grass (*Poa trivialis*) and Yorkshire fog (*Holcus lanatus*), once they are lost from the above-ground vegetation. Where ancient woodland species have already been lost, recolonisation rates are slow, of the order of around 1m per year for lowland woods, and considerably less for some species, e.g. wood sorrel (*Oxalis acetosella*): 10 cm per year; wood anemone (*Anemone nemorosa*): 13 cm per year (Grime *et al*., 1988). Increasing distance from a source patch of propagules can lead to impoverishment of target woodland patches (e.g. Grashof-Bokdam and Geertsema, 1998). This emphasises the importance of taking early remedial action (i.e. the gradual removal of the conifer component from mixed stands on ancient woodland sites) to allow their survival.

15. The majority of stands surveyed in the present study were between 30–40 years old, planted as 3:3 row mixtures. These are suitable for line thinnings, which may allow some sensitive ancient woodland species sufficient periods of growth and flowering to carry them through the rotation. Since distances between rows are relatively short, it is also possible for barren rows (i.e. under Norway spruce or beech) to become colonised. However, three broadleaved rows may be insufficient to preserve some vestige of ancient woodland flora. Reducing the proportion of conifers to at least half that of the broadleaved component would be beneficial to the groundflora.

16. Similar points may be made concerning group mixtures, in which the minimum patch size needs to provide sufficiently long gradients of microclimate, with a varied pattern of light and litter. Small broadleaved patches have only a limited capacity to act as reservoirs for ancient woodland species. However, if patches are larger, and the conifer element is allowed to eliminate the ground vegetation, these may only partially recolonise from adjacent sources when conditions improve (Simmons, 1992).

17. Complete restoration to semi-natural broadleaved woodland may be appropriate on some planted ancient woodland sites, depending upon criteria such as ecological context at a landscape scale, nature conservation designations (including adjoining sites), the regional scarcity or importance of the woodland type, the potential size of the restored woodland, and importance for BAP species. Further research concerning methods for restoration and possible problems associated with these is required.

MANAGEMENT IMPLICATIONS

Loss of ancient woodland plants

18. Few ancient woodland species form significant components of the seedbank, and so their regeneration is dependent upon vegetative propagation and spread or immediate seed dispersal to suitable sites. Their reduction in planted ancient woodland sites is mirrored by an increase in abundance of more competitive or ephemeral species, often resulting from the disturbed conditions following silvicultural operations. In order to restore these ancient woodland species, a reduction in the conifer component is likely to be required, thereby increasing light transmission and reducing the depth of the litter and humus layers. However, control of competing vegetation may be required in order to aid recolonisation.

Species composition

19. Thicket stage beech or Norway spruce has a detrimental effect on the groundflora, even in row mixtures. In contrast, pine and oak tend to allow greater persistence of the groundflora, either through increased light levels or by virtue of the deciduous habit.

Natural regeneration

20. The basal area of naturally-regenerated broadleaves sometimes accounted for 10% of a stand in the current survey. This proportion can benefit the groundflora, especially if it occurs in an otherwise pure stand, by providing variation in the light environment.

Cleaning

21. In stands dominated by oak in which the shrub layer has been removed, the canopy tends to be too light and invasive species such as bramble dominate.

Planting arrangements

22. Where replanting with non-native species is deemed appropriate on an ancient woodland site (i.e. where they are already present and if the site is not to be completely restored to native woodland) the following points should be considered in defining planting arrangement, so that further losses in biodiversity can be minimised or avoided:

23. **Intimate** planting arrangements are inherently unstable if one or more crop species is subordinate to another, leading to both changes in the ground conditions (light, litter and soil) and to difficult choices at thinning. Line thinning is not appropriate in these types of mixture.

24. Intimate mixtures of two or three species tend to provide minimal variation between the crowns of adjacent young trees. The ‘averaging’ of conditions created by such a composite canopy tends to produce uniformity in the ground vegetation.

25. **Group** mixtures create longer ecological gradients across the forest floor and a more patchy environment of light and litterfall, which may encourage greater numbers of groundflora species. Later thinning may increase this patchiness.

26. However, if one species component tends to eliminate the vegetation underneath it, the denuded area may only partially recolonise from adjacent vegetation sources when conditions improve. Stem density critically affects the groundflora, and initial wide spacing or early thinning may be very beneficial on sensitive sites.

27. Small groups have a limited capacity to act as reservoirs for groundflora species, and the distance between such groups is crucial. Groups may be from 7–12 m apart, but the shorter distance would be preferable if groups were in a spruce matrix. An edge effect will also be found in group plantings, and so groups should be large enough (a minimum of 9 trees, and preferably >20) for at least one final crop tree to survive.

28. **Row** mixtures have a number of advantages not shared by either intimate or group mixtures. The rows are eminently suitable for line thinnings, which may allow some sensitive groundflora species sufficient periods of growth and flowering to carry them through the rest of the rotation. Barren rows under species such as Norway spruce and beech also appear to colonise rapidly, as the distances across species bands are relatively short. However, for the same reason, the gap sizes created by line thinning may be insufficient to favour the ephemeral species which form large, persistent seedbanks. A minimum of three adjacent rows of broadleaf, as in the common 3 row : 3 row mixture, is necessary to preserve some vestige of the ancient woodland groundflora. A 50% proportion at planting of a shade-casting conifer invariably dominated most stands surveyed (at approximately 30 years plus), and reducing this would benefit the groundflora.

29. Opportunities should be considered to encourage natural regeneration or coppice regrowth of native species, to enhance the semi-natural component of the wood instead of planting (Forestry Commission, 1994).

Thinning

30. Although failure to thin a crop may not be financially damaging in the long term, it can be highly detrimental to the woodland groundflora, and early thinning is one of the most effective ways of assisting its survival.

31. Line thinnings could be made earlier and more intensive by routinely removing both outer rows of the conifer nurse crop in 3 row : 3 row mixtures, before the risk of instability. Removal of the nurse crops needs to be planned so as to create the maximum opportunities for recolonisation by groundflora species. Gradual thinning may be used to minimise disturbance and possible colonisation by dominant species such as bramble, and provide opportunities for vegetative spread and for new propagules to be added into the seedbank. Early thinning and felling may be suitable for the conservation of light-demanding species without a persistent seedbank. The retention of some stems to maturity in order to promote structural variation in the canopy may also be beneficial if it does not conflict with the restoration of groundflora communities.

CONCLUSIONS

- Phased removal of conifers can prevent abrupt changes to the light regime resulting in the often rapid spread of species typical of disturbed conditions, e.g. bramble. The reduction from 50% to 30-40% of the Norway spruce component in oak-spruce mixtures in this survey led to an increase in cover-abundance of groundflora in plots with six oak rows to every three Norway spruce rows.

- In existing mixed stands, the future of the groundflora depends on the frequency and intensity of thinning; lower stem densities having been shown to allow the spread of vascular groundflora. However, even where thinning has occurred as recommended, the more restricted ancient woodland flora is likely to be at a competitive disadvantage compared with those species able to exploit disturbed conditions with rapid growth, e.g.Yorkshire fog (*Holcus lanatus*).

- The species which were observed to survive in broadleaved-conifer plantations possessed most of the following characteristics: stoloniferous growth, tolerance of heavy shade, seeds which germinate in leaf litter, seedlings which can penetrate leaf litter, and a tolerance of litter deposition and decomposition. Prominent examples included bramble, rough meadow-grass, and three-veined sandwort (*Moehringia trinervia*). The expansion of these common species is likely to be at the expense of more restricted species such as yellow archangel (*Lamiastrum galeobdolon*) and primrose (*Primula vulgaris*).

- The soil seedbank cannot be depended upon to restore the majority of ancient woodland plant species to a stand once they are lost from the above-ground vegetation. Ancient woodland plants are largely lost following a reduction in light transmission, due to canopy closure, and the build up of a conifer or conifer/broadleaved litter layer, in which fewer species persist. The combination of these two factors results in the elimination of ancient woodland species after canopy closure plus approximately 15–25 years, depending upon silvicultural treatment and site type.

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