

SILVICULTURE AND STAND DYNAMICS IN SCOTS PINE FORESTS IN GREAT BRITAIN; IMPLICATIONS FOR BIODIVERSITY

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SUMMARY

There are 241,000 hectares of Scots pine forest in Great Britain or about 10 percent of the total forest area. Traditionally, a distinction has been drawn between a small area of native pinewoods with high conservation value in northern Scotland and the younger plantations of Scots pine to be found in many parts of Britain. The latter have been primarily managed for timber although they are now expected to meet multipurpose objectives including enhanced biodiversity. Silvicultural practices in the plantations are based upon a system of clear felling and artificial regeneration. However, older plantation stands can be colonised by rare species previously thought to be confined to the native pinewoods. The structure of Scots pine stands of different ages is examined using modern concepts of stand dynamics. The analysis highlights that the native pinewood stands have features characteristic of «old-growth» such as: a lower stocking density; more large trees; greater variation in diameter; a clumped distribution of stems; and appreciable quantities of standing deadwood. By contrast, most plantation stands have higher stocking densities, less variation in diameter, more uniform spacing and limited amounts of deadwood. By quantifying these structures it becomes possible to propose thinning regimes which can be introduced into plantations to accelerate the development of old-growth conditions without undue sacrifice of timber values. Natural disturbance histories in British pinewoods indicate a return period for stand replacing events (fire, windthrow) of once every 100 years which suggests that a maximum of 10 per cent of the pine resource should be managed as old growth stands. The age structure of some remnant pinewoods shows a lack of younger age classes and the desired old-growth habitat will diminish over time unless suitable plantation stands are managed as potential old-growth habitat. The maintenance of biodiversity in British pinewoods requires an integrated approach that applies to both the native pinewoods and the plantation stands.

KEY WORDS: Scots pine
Silviculture
Stand dynamics
Old-growth
Stand structure

INTRODUCTION

Scots pine (*Pinus sylvestris* L.) is the most widespread conifer in the world (Nikolov and Helmisaari, 1992) and is the only pine indigenous to Great Britain (Bennett, 1995).

Its natural range stretches from Spain to Norway, and from Scotland to Siberia. After the last ice age, the species recolonised Britain about 10,000 years ago primarily via the landbridge from mainland Europe although part of the Scottish population may have originated from a refugium located to the west of Ireland (Bennett, 1995). Over much of Britain as far north as southern Scotland, pine was displaced by species such as oak and alder. However in northern Scotland, by some 5,000 years ago the species had become the major constituent of the natural forest which covered an area estimated at around 1.5M ha (McVean and Ratcliffe, 1962). Since then, the area of natural pine forest has been reduced to about one per cent of that original estimate because of: climatic changes, the indirect effects of human activity (e.g. overgrazing by cattle, sheep and deer, and possibly reduction of fire frequencies), plus unsustainable exploitation for timber, most notably in the seventeenth to the nineteenth centuries (Steven and Carlisle, 1959).

However, from the start of plantation forestry in Britain in the seventeenth century, Scots pine was commonly planted because of its rapid early growth, tolerance of transplant shock, good timber properties and adaptability to a range of site conditions. Although in the last two centuries a range of introduced species (e.g. Sitka spruce *Picea sitchensis*; larches *Larix* spp.; Corsican pine *Pinus nigra* var. *maritima*) have proved more productive over much of Britain (Mason, 1996b), Scots pine is still widely favoured particularly in north-eastern Scotland.

As a consequence of this history, two categories of Scots pine forest are distinguished (see Table 1).

TABLE 1

ESTIMATED AREA OF SCOTS PINE FOREST IN THE UNITED KINGDOM AND DISTRIBUTION BY TYPE AND BY NATION. NOTE THAT «NATIVE» COMBINES «NATIVE» AND «SEMI-NATURAL» CATEGORIES

Superficie estimada de bosques de Pino silvestre en el Reino Unido, y distribución por tipo y por nación (señalar que «nativo» combina las categorías «nativo» y «seminatural»)

	Total area of Scots pine ('000 ha)	Area of native Scots pine ('000 ha)	Area of planted Scots pine ('000 ha)
United Kingdom	241.0	19.8	221.2
England	91.1	0.0	91.1
Northern Ireland	7.0	0.0	7.0
Scotland	137.3	19.8	117.5
Wales	5.6	0.0	5.6

Source: Forestry Commission Woodland Surveys Branch (1999).

Native («Caledonian») pinewoods are found only in northern Scotland and cover an estimated 16,000 ha occurring in 84 different sites. These pinewoods are recognised as a priority habitat under the European Commission's Habitat Directive (Forestry Commission, 1994). There is a smaller area of semi-natural pinewoods that occur within the natu-

ral range of Scots pine in Scotland and are believed to result from natural regeneration from planted stands of trees of native origin. For the purposes of this paper, they will be classed with the native pinewoods.

Planted forests of Scots pine occur widely throughout Great Britain as a result of the plantations established since the 1600's, e.g. on heathland soils in lowland England and northeastern Scotland. Some 214,000 ha (~92 %) of Scots pine forest falls into this category (see Table 1). The combined area of both categories of Scots pine forest amounts to about 10 per cent of the total forest area, making this the second most important type after Sitka spruce forests. The age-class distribution of the planted forests is shown in Table 2

TABLE 2
PERCENTAGE AGE-CLASS DISTRIBUTION OF THE PLANTED SCOTS PINE FOREST TYPE AND THEIR CLASSIFICATION BY STAND DEVELOPMENT STAGE

Porcentaje por clase de edad de la distribución de los tipos de bosques de Pino silvestre plantados y su clasificación por etapa de desarrollo del rodal

Age-class	Percentage of area	Stand development stage ¹
1981-1990	4	Stand initiation
1971-1980	6	Stem exclusion
1961-1970	19	Stem exclusion
1951-1960	27	Stem exclusion
1941-1950	12	Stem exclusion
1931-1940	9	Stem exclusion
1921-1930	12	Stem exclusion
1911-1920	3	Understorey reinitiation
1901-1910	2	Understorey reinitiation
1861-1900	4	Understorey reinitiation
Before 1861	2	Old growth

Source; Forestry Commission Woodland Surveys Branch (1997).

¹ See Table 3 for definition of stand development stages.

highlighting that nearly 60 per cent of stands fall in the 30-60 years old age range.

The purpose of this paper is to describe current silvicultural practice in both categories of British pine forests in relation to stand dynamics, to consider the relationship with biodiversity, and to make recommendations for future management.

ECOLOGICAL CLASSIFICATION OF BRITISH SCOTS PINE FORESTS

Native

Areas of indigenous pinewood are only found in the Highlands of Scotland. They typically occur on infertile lithologies with strongly leached podsollic soils. In eastern Scotland where the rainfall varies between 800-1,000 mm the pine forests are composed of extensive pure stands, but in western Scotland where rainfall can be 1,500-2,000 mm or more, pine generally occurs on morainic knolls in a mosaic with broadleaves. All native pinewoods have been influenced by man to varying degrees; grazing by deer, sheep and cattle, and extensive felling have simplified the structure and species composition.

The Scottish pinewoods are classed by Rodwell (1991) as *Pinus* - *Hylocomium splendens* woodlands, which are dominated by Scots pine but have associated tree species of silver and downy birch (*Betula pendula* and *B. pubescens*) with rowan (*Sorbus aucuparia*) and juniper (*Juniperus communis*). The ground flora has three constant elements which are a grass sward of *Deschampsia flexuosa*, a low shrub layer of ericaceous species such as *Calluna vulgaris* and to a lesser extent *Vaccinium* spp, together with a carpet of bryophytes. These woodlands have close links with the heathy acid pinewoods of northern Europe and in particular with those of Scandinavia and western Norway beyond the natural range of Norway spruce (*Picea abies*) (Rodwell and Cooper, 1995).

Planted

Planted forests of Scots pine fall into two broad categories,

- a) those which are likely to develop in a similar manner to the native forests and;
- b) those which are precursors to the development of a mixed forest composed of a range of species of which Scots pine is only a minor component.

Studies of 20-40 years old planted stands of Scots pine on nutrient-poor soils in different parts of northern Scotland indicated that the vegetation communities showed a close affinity to those found in the natural pine forests (Humphrey *et al.*, 1995; Malcolm and Mason, 1999). There are notable examples of planted pine forests on nutrient poor soils outside the accepted range of native Scots pine developing a ground flora with a number of pinewood specialists (e.g. Culbin forest near Forres in north-east Scotland; Pitkin *et al.*, 1995).

In southern Britain, vegetation development was studied in a chronosequence of Scots pine stands ranging from a dense 3m tall stand arising from natural regeneration to a mature stand reduced to 30-40 trees per ha following a seed tree felling (Ferris-Kaan *et al.*, 1998). The closest links were either with natural heathland vegetation or with an acid oak woodland, depending upon stand age.

MANAGEMENT GOALS

The main management objectives in all British forests are the sustainable management of the existing forests coupled with the steady expansion of the forest area to provide multi-purpose benefits. These goals are expanded in the UK Forestry Standard (Forestry Authority, 1998) which outlines a number of principles of management for conifer plantations (e.g. including planted Scots pine stands) with little structural diversity. These include: felling areas at different times to increase age diversity, use of alternative silvicultural systems to clearfelling on windfirm sites, retaining trees beyond financial rotation to provide habitat features characteristic of older stands, ensuring the shape of felling areas conforms to the aesthetics of the land form, and providing wind stable edges to felling areas.

A specific subset of management goals for the native pinewoods in northern Scotland has been developed over the last two decades (e.g. Forestry Commission, 1994) including maintaining the genetic integrity of recognised subpopulations of native pine (Forrest, 1980). These aims are developed in the following four main objectives (Anon., 1995):

- maintain remnant native pinewood areas listed on the Caledonian Pinewood Inventory (Tuley, 1995) and restore their natural diversity of composition and structure;
- regenerate and expand a total of 35 % of the current wooded area of remnant native pinewoods (16,046 ha) by 2005, predominantly by natural regeneration within the core and regeneration zones.
- create the conditions by 2005 for a further 35 % of the current area to be naturally regenerated over the following 20 years, mainly by the removal of non-native planted species and/or genotypes and the control of browsing levels;
- establish new native pinewoods over a cumulative total area of 25,000 ha by 2005 (equivalent to 155 % of the existing remnant pinewood area). They should be planted, or naturally colonised where possible, on suitable sites within the natural range of native pinewood.

SILVICULTURE OF SCOTS PINE

The following section is based primarily upon the planted forests since, at present, most of the native pinewoods are managed primarily for conservation with limited active manipulation of stand structure and composition.

Planting

Although there are a number of reports of natural regeneration in native and planted Scots pine forests (e.g. Jones, 1947), it is estimated that over 80 per cent of all Scots pine forests are regenerated through planting. Normal planting spacing is at 2m by 2m to give a target density of 2,500 stems per ha. Both bare-root and containerised plant types are used with the former accounting for about 70 per cent of all Scots pine planting. Bare-root plants are normally produced as two-years-old stock either as transplants or as precision

sown undercuts; such plants will be around 15-25 cm tall at time of planting. Containerised seedlings are normally 12-18 months at time of planting and around 10-15 cm tall. This type of planting stock has been favoured in schemes to restore the native pinewoods where specific seed sources have to be used and maximum outturn achieved from limited supplies of seed. Outwith the native pinewoods, increased use is being made of genetically improved seed origins which offer an estimated 8 per cent improvement in growth and form over unimproved material (Lee, 1999).

Site preparation and other establishment operations

On the freely draining mineral soils (acidic brown earths, podsoles) where Scots pine is normally grown, the limiting site factors to establishment are the presence of competitive weed species such as *Calluna vulgaris* or *Deschampsia flexuosa*. On some sites, ironpan formations cause a perched water table and/or prevent satisfactory rooting. The normal prescription for these sites is surface scarification to provide a weed-free planting position plus ripping where necessary to break up a compacted horizon (Paterson and Mason, 1999). The benefits of cultivation can last well beyond the establishment phase since Mason (1996a) showed improved growth of Scots pine in response to cultivation 30 years after planting on a podsol soil in northern Scotland. On afforestation sites, phosphate fertiliser is normally applied at planting at around c 60 kg element ha⁻¹ (Taylor, 1991) but the benefits from this vary according to the nutritional quality of the site (Zehetmayr, 1960). There are no benefits to be found from the use of fertiliser on restocking sites.

Thinning and other stand management operations

Published yield tables for Scots pine in Britain (e.g. Hamilton and Christie, 1971) show productivity (Yield Class) ranging from 4 to 14 m³ ha⁻¹ yr⁻¹ according to site and climatic region. The average for Scots pine stands in Britain is around 8.6 with higher values in southern England and lower ones in northern Scotland (Mason, 1996b). This range of productivity corresponds to ages at first thinning of 20 to 40 years respectively. The normal practice is for low thinning at about a C/D grade intensity (ie removal of suppressed and intermediate trees) with a thinning cycle of 4-10 years with the greater interval corresponding to less fertile sites. There are no reports of any influence of thinning grade upon timber quality outturn. Recently, attempts have been made by one conservation agency to use a variable thinning intensity to foster a more irregular stand structure. This involves removing around 60 per cent of stems at first thinning and a further 50 per cent of the remaining trees at second thinning while ensuring that all broadleaves are favoured (Taylor, 1995).

Extensive fertiliser trials were carried out to look at the possibility of improving growth rates in pole stage (ie stem exclusion) stands through the use of fertilisers (McIntosh, 1984). These showed a positive response to nitrogen application in stands on the more nutrient deficient lithologies. However, the financial benefits have not been attractive and, in practice, no fertiliser applications are made to Scots pine stands once they have closed canopy.

Most stands where Scots pine is intended as the final crop are managed as pure species stands for the whole rotation. One exception is in parts of north-eastern Scotland where Scots pine was often grown in a mixture with larch and Norway spruce with the latter species planted where there is local improvement in soil moisture or fertility. There are also areas where spontaneous mixtures of birch and Scots pine have developed and there is some attempt to manage these as mixed stands. However, recent results from planted mixtures (Malcolm and Mason, 1999) suggest that, in the absence of thinning, birch: birchipine mixtures will tend to develop to pure pine stands. On nitrogen deficient heathland soils, Scots pine is often planted as a sacrificial nurse to more productive species (Morgan *et al.*, 1992). On such sites the pine provides improved nutritional conditions for the early growth of the nursed species so that both enter the canopy together, but thereafter the slower growing pine is gradually suppressed.

Rotation age and timber properties

The yield tables (Hamilton and Christie, 1971) suggest an age of maximum mean annual volume increment of 65 to 90 years according to declining productivity. Yields vary from 450 to 200 m³ ha⁻¹ according to declining site quality corresponding to top heights of 27 to 17 m and mean diameters of 45 to 20 cm. Both planted and native stands are capable of producing quality timber with good strength properties that can provide a higher value outturn than Sitka spruce. The main constraints are the presence of knots and poor straightness, particularly when trees are planted at wide spacing (Petty, 1995; Thornton, 1995).

Silvicultural system

The main silvicultural system is clear felling followed by artificial regeneration. Coupe sizes range from less than 1 ha to 25 ha or more depending upon location and the visibility of the site. In good seed years, the felling site can be colonised by natural seedlings at densities of 5000 stems ha⁻¹ or greater, and, where this occurs, natural regeneration will be accepted in preference to planting on grounds of lower cost. In some private woodlands, particularly in northern Scotland, there is a tradition of using seed tree or shelterwood systems to promote natural regeneration on the felled site. The distinction between these 2 regeneration systems is based primarily upon the number of retained trees, around 25-50 ha⁻¹ in the seed tree and 100-150 ha⁻¹ in the shelter wood. The retained trees are removed in one stage in the former and in 2 or more stages in the latter.

STAND DYNAMICS IN BRITISH SCOTS PINE FORESTS

Forests can be considered as spatial mosaics of four key structural stages (Table 3; after Oliver and Larson, 1996) changing with time through dynamic processes. In all forests there is a cycle initiated by disturbance with stages *b*, *c* and *d* reverting back to *a*. Disturbance can range in size from small, transient gaps arising through the death of a single tree filled by lateral ingrowth of surrounding branches (Whitmore, 1989), to large areas created by clear felling or a catastrophic fire which may need planting to aid recolonisation of the site (Spies and Franklin, 1989).

TABLE 3
THE FOUR KEY STAGES IN STAND DEVELOPMENT
(AFTER OLIVER AND LARSON, 1996).
(IN ITALIC STAGE NAMES INDICATE THOSE USED IN THE TEXT)

Las cuatro etapas principales en el desarrollo del rodal (después de Oliver y Larson, 1996). (En cursiva los nombres de las etapas utilizadas en el texto)

Stage	Stage name	Age	Stage description
<i>a</i>	<i>stand initiation;</i> <i>pre-thicket</i>	0-20	colonisation; planting; establishment; stand pattern largely determined in this stage
<i>b</i>	<i>stem exclusion;</i> <i>closed canopy</i>	20-75	no further establishment; thicket stage with some individuals gaining dominance over others; low light levels on forest floor; self-thinning begins
<i>c</i>	<i>understorey reinitiation;</i> <i>mature</i>	75-150	herbs, shrubs and advance regeneration invades forest floor as amount of light increases through self-thinning
<i>d</i>	<i>old growth;</i> <i>overmature</i>	>150	senescence; death of large canopy trees forms gaps allowing small patch scale establishment and stand initiation; decay of dominant trees; more light in patches; relative abundance of standing and fallen dead wood

Characteristics of these stages in British pine forests

There have been no previous attempts to define these stages quantitatively for British pine forests. Therefore, in an attempt to discriminate between these stages, selected data are presented in Table 4 from a range of planted and natural pine stands of different ages in Britain and in Sweden.

TABLE 4
SAMPLE MEASURES OF STAND STRUCTURE FROM A RANGE OF BRITISH AND SWEDISH SCOTS PINE STANDS (ND = no data; N/A = not applicable)
Muestra de las mediciones de la estructura del rodal de un conjunto de rodales de Pino silvestre británicos y suecos (ND: sin datos; N/A: no aplicable)

Location	Plot or experiment number	Age	Trees ha ⁻¹	Top height (m)	Yield Class (m ³ ha ⁻¹ yr ⁻¹)	Basal area (m ² ha ⁻¹)	Mean dbh	Maximum dbh	Number of trees >50 cm dbh	Standard deviation	Coefficient of variation (%)	Comments
British planted stands												
Teindland	81	45	3400	16.0	8	62.1	14.7	23.0	0	4.2	28.6	unthinned
	81	45	1550	15.5		49.7	19.8	27.8	0	4.1	20.7	thinned
	1103	62	689	22.6	12	40.6	26.8	42.4	0	5.7	21.3	thinned
	1103	107	291	29.1		44.2	43.3	59.0	67	8.0	18.5	
New Forest	1104	64	637	25.1	12	60.1	34.2	52.6	5	5.9	17.3	unthinned
	1104	109	475	29.7		79.9	45.6	67.5	151	7.7	16.9	
	1104	135	334	34.5		70.1	50.5	72.7	183	8.6	17.0	
	3015	36	3435	11.6	8	36.6	11.2	19.4	0	3.0	26.8	unthinned
Glen Dye	3015	96	1051	24.0		60.1	26.5	43.6	0	5.2	19.6	
	3016	36	2807	11.9	8	34.5	12.2	22.6	0	2.9	23.8	thinned
	3016	96	224	22.8		24.0	36.6	47.6	0	5.1	13.9	
	3029	35	2273	13.3	10	39.4	14.5	24.3	0	3.7	25.5	unthinned
Balmoral	3029	105	770	27.6		70.6	33.4	56.7	9	7.3	21.9	
	3114	60	1720	12.2	2	32.8	15.2	24.3	0	3.3	21.7	thinned
	3114	116	573	15.5		31.5	27.5	39.3	0	5.0	18.2	
	1.3	100	328	23.5	8	38.3	37.9	59.0	12	7.7	20.3	biodiversity plot
Glen Affric	2.3	65	1238	15.5	6	46.9	21.7	31.1	0	4.1	18.9	biodiversity plot
Native British pinewoods												
Glen Affric	1.4	N/A	102	20.9	N/A	15.2	56.0	81.5	72	12.3	22.0	biodiversity plot
Glen More	2.4	N/A	152	18.5	N/A	22.0	40.5	80.3	30	14.1	34.8	biodiversity plot
Glen More	14/61	20-230	261	22.0	N/A	22.5	28.6	100.0	46	19.4	67.8	pinewood reserve
Glen Affric	2/97	140-280	88		N/A	18.3	49.9	76.0	40	11.0	22.0	pinewood reserve
Rannoch	4	23-270	165	27.0	N/A	28.2	42.8	118.0	45	19.0	44.4	pinewood reserve
	7	20-150	242	23.8	N/A	18.6	30.0	85.0	31	17.0	56.7	pinewood reserve
Abemethy (Bognacruie)		65-210	356	17.9	N/A	45.6	37.9	90.0	84	14.0	36.9	
Swedish 'old growth' stands												
Gertsbacken		10-380	400	12.9	N/A	6.6	30.3	61	8	10.3	34.0	Zackrisson <i>et al.</i> (1995)
Deliken		10-435	392	14.1	N/A	5.3	24.3	43	0	7.8	32.1	
Vuomavare		20-340	145	15.6	N/A	9.4	25.0	47	0	11.6	46.4	
Stora Sjöfallet		20-380	326	12.7	N/A	10	36.3	71	25	12.1	33.3	
Tometrask		20-220	334	11.2	N/A	9.6	22.7	53	2	12.8	56.4	
Ovre Soppero		10-270	403	10.2	N/A	5.4	19.1	61	7	13.7	71.7	

Stands in the planted category are a mixture of experimental trials and sample plots managed for mensurational information. They span a range of productivity from two very fast growing stands in the New Forest in southern England to a very slow growing one at Culbin in northern Scotland. Where available, data are presented for more than one point in time as well as for thinned and unthinned stands. All thinning regimes have been based upon low thinnings to standard yield table prescriptions (Hamilton and Christie, 1971). The semi-natural category is made up of a range of six long-term non-intervention reserves (0.8-1.0 ha in size) in different native pinewoods (Edwards and Nixon, 1999) plus a smaller (0.25 ha) temporary sample plot in the Abernethy pinewood (Edwards and Oyen, 1996). For comparison, data are presented from six «old-growth» stands in northern Sweden that have not been subjected to disturbance by fire, wind, or timber cutting (Zackrisson *et al.*, 1995).

The parameters used to classify the stands are tree based measures that could be collected during a normal inventory. These follow those used successfully by Spies and Franklin (1991) to discriminate between structural stages in forests of Douglas fir (*Pseudotsuga menziesii*) in north-west America. Of particular importance are the following;

1. the number of trees >7 cm diameter ha⁻¹;
2. the number of large trees >50 cm diameter ha⁻¹;
3. the mean diameter of the trees in the stand;
4. the standard deviation of tree diameter.

The only difference from the American study was that they defined large trees as being more than 100 cm diameter, whereas in British Scots pine stands such sizes are very rare (e.g. Goodier and Bunce, 1977; their Fig. 1) and 50 cm seemed a more appropriate cut-off.

a - stand initiation

This stage lasts for up to 10 years in plantations but may be up to 20 years or longer in natural regeneration because of the greater length of time it takes for seedlings to become established. It is the easiest to define because it persists only until the crowns begin to interlock when the trees are between 5 and 10 metres in height. No values for this stage are presented in Table 4 because of its comparative simplicity. The difference between planted sites and natural regeneration is largely a function of the greater regularity of spacing and uniformity of growth in the former and the occurrence of other regenerating species besides Scots pine in the latter. Attempts are sometimes made to plant trees in clumps with a variable spacing in the belief that this will simulate a more natural pattern and that stands created in this way will not develop the regular structure characteristic of the stem exclusion phase. However, this practice overlooks the general rule for stands to move towards a regular distribution of dominant stems in the late stem exclusion phase as a consequence of differential self-thinning (Oliver and Larson, 1996). Eventually, in the later stages the regular pattern will break up due to disturbance and/or mortality and a more clumped pattern will develop.

b - stem exclusion

This corresponds with the period between around 20 years up to about 75 years of age where there is complete canopy closure of Scots pine with trees of a height from 10 to

perhaps 20 m. Except on the most fertile sites, stocking densities in the absence of thinning are generally between 1000-3000 stems ha^{-1} and basal areas of 30-40 $\text{m}^2 \text{ha}^{-1}$. The site is characterised by low light levels under the canopy so that regeneration is absent while suppressed trees in the lower canopy die because of inter-tree competition unless removed in thinning. As well as increasing the mean diameter of the stand by reducing stocking densities below 1000 stems ha^{-1} , the weight and frequency of thinning can accelerate the speed with which understorey shrubs begin to colonise the site. Thus Humphrey (1996) reported that characteristic pinewood species such as *Vaccinium myrtillus* showed greater growth in thinned 35 year old stands of Scots pine in northern Scotland compared to unthinned controls. There is comparatively little variation in the diameter size distribution and this decreases over time because of the mortality of the smaller trees (see coefficients of variation in Table 4). There are no big trees present at this stage.

c - understorey reinitiation

The exact transition between the previous stage and this one is not easy to determine. Although there is still a substantial canopy cover, gaps begin to occur as the trees grow taller and light levels under the canopy are higher than in the previous stage with ground vegetation being more extensive. The presence of advance regeneration and other understorey shrubs is generally considered as one of the defining features of this stage but heavy browsing or vegetation competition can limit regeneration success. In this phase the stand height is 15-25 m or more and the trees are aged 75 to perhaps 150 years. Stand densities are normally between 200 and 750 stems ha^{-1} depending upon fertility and thinning history. The older stands in the New Forest, Balmoral and Glen Affric (Table 4) have features characteristic of this stage. There is still limited variability in diameter size distribution reflecting the largely intact canopy. However, in older stands in this stage, or in those that have been well thinned, there can be appreciable numbers of big trees. This is the stage when one of the regular silvicultural systems such as uniform shelterwood or seed tree is introduced. Stands managed under the latter systems will tend to have a higher percentage of older trees than those managed under the clear fell system.

There is little published information about stands in this stage, especially about the development towards structures more typical of «old-growth» pine stands. However, comparison with values for the «old-growth» native pinewood sites suggest that this transition must involve progressive canopy break-up due to disturbance and mortality. The age at which the transition occurs is uncertain but is around 150 years based upon figures in Table 4, although there will be considerable variation between sites.

d - old growth

The characteristic appearance of pine stands at this stage is of canopy break-up with groups of deep crowned old trees scattered through the stand as well as areas with smaller trees or open ground. The height of the mature trees can be 20-25 m and more, with ages well in excess of 200 years (Table 4). Findings on other sites show that many trees exceed 300 years and individuals of over 550 years have been reported (Nixon and Edwards, 1997). However, similarities in structure can mask appreciable variation in age class dis-

tribution due to differences in management history. Thus at Rannoch 4 the majority of the trees were between 80 and 150 years of age (Fig. 1) but the occasional much older and some younger trees reflected intermittent selective harvesting of larger trees over a period of 300 years. There was also evidence of a reduction in browsing pressure in recent decades (Arkle and Nixon, 1996). In Glenmore 14 there was a bimodal distribution with one group of trees between 160 and 230 years of age and a much younger cohort around 50 to 60 years old (Fig. 2). This reflects a history of extensive felling in the 1800's followed by heavy browsing pressure and finally regeneration during the 1930's as a consequence of site disturbance.

Despite the variation in age-class distribution between sites, there appear to be certain typical structural features of these «old-growth» stands. Basal area values are typically 50-70 per cent of those found in the previous two stages, there are much higher numbers of big trees ha^{-1} , total numbers of trees ha^{-1} are generally low (e.g. 100-250 stems ha^{-1}) and measures of diameter variability are also much higher. The understorey may either be absent where there is heavy grazing pressure or may have a range of shrub species and young saplings if grazing is controlled. An additional feature of such stands is the occurrence of appreciable amounts of both standing and fallen deadwood. As many older trees have been left to biological maturity, dead boughs and broken crowns are more abundant compared to stands in the earlier stages. Between 40 and 55 $\text{m}^3 \text{ha}^{-1}$ of fallen and standing dead wood was found in Scottish old growth stands which was nearly 5 times that present in stands in the late stem exclusion or early understorey reinitiation phases (Reid *et al.*, 1996).

The stand at Abernethy offers an interesting contrast to the other 6 semi-natural stands in that it has both a higher number of stems ha^{-1} and a greater basal area ha^{-1} while still having a large number of big trees and a variable dbh distribution (Fig. 3). This plot also had quite a high deadwood component, estimated at 52.4 $\text{m}^3 \text{ha}^{-1}$. Much of this was recent mortality with little decay, probably due to competition during self-thinning (Edwards and Oylen, 1996). The age class distribution suggests that this stand is the product of 2 different cohorts: the older being a population that originated between 150 and 200 years ago, while the second was a consequence of regeneration about 75-100 years ago. It is unclear whether the second cohort occurred following a seeding felling or because of a sudden reduction in the grazing pressure. It is possible that this stand is moving towards a more typical old-growth structure with inter-tree competition creating a «pulse» of mortality in both cohorts with consequent benefits to the deadwood habitat.

The Swedish stands have smaller trees than those in Britain which reflects their northerly location (65-68° N compared with 56-58° N in Britain). However, the measures of diameter variability are similar to those for the British semi-natural pinewoods. Since the Swedish stands are known to have developed without disturbance (Zackrisson *et al.*, 1995), it suggests that these measures may offer a useful model for defining target structure in stands being managed for old-growth habitat

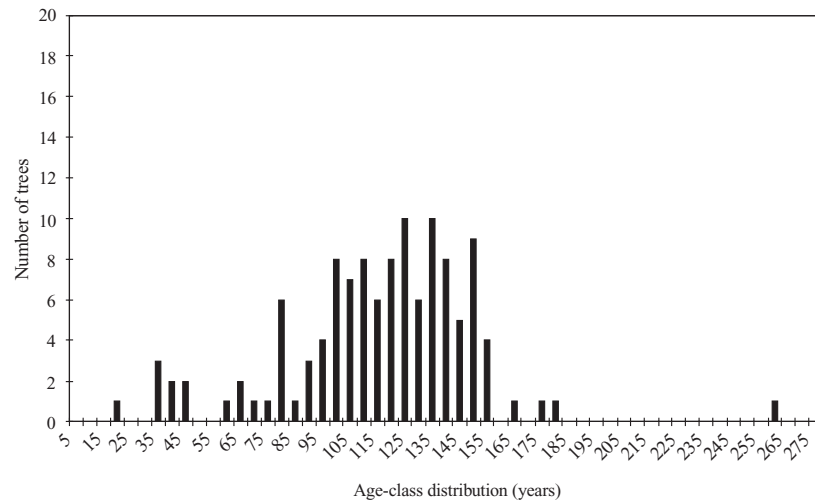


Fig. 1.—Age class distribution of all trees >10 cm diameter on the Rannoch 4 plot

Distribución, por clase de edad, de todos los árboles de diámetro >10 cm en la parcela 4 de Rannoch

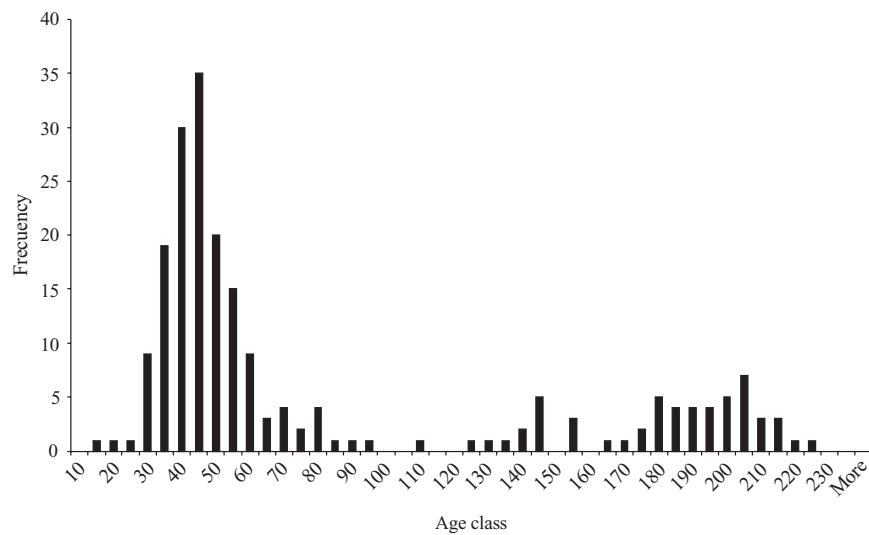


Fig. 2.—Age class distribution of all trees >10 cm diameter on the Glenmore 14 plot

Distribución, por clase de edad, de todos los árboles con diámetro >10 cm en la parcela 14 de Glenmore

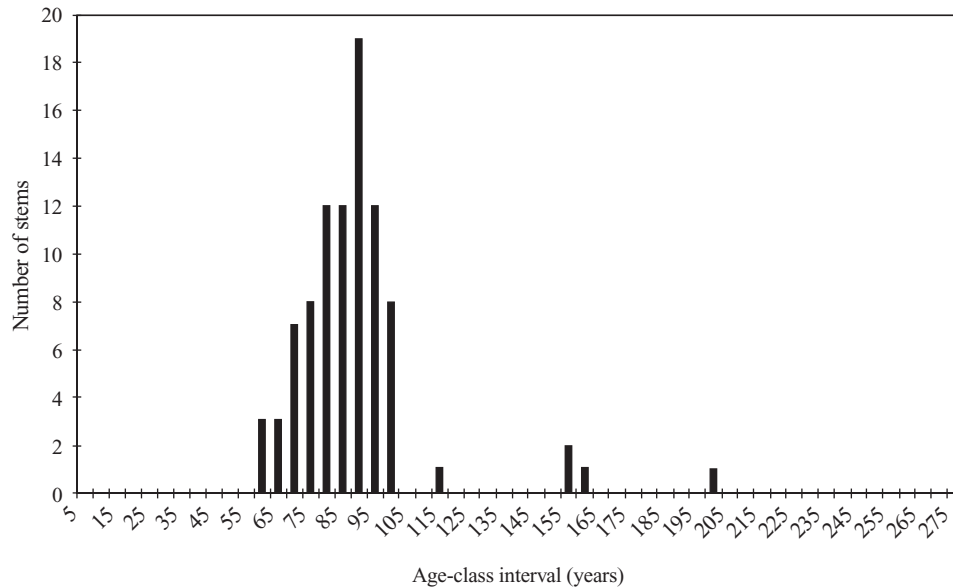


Fig. 3.—Age class distribution of all trees >10 cm diameter on the Abernethy plot
Distribución, por clase de edad, de todos los árboles con diámetro >10 cm en la parcela de Abernethy

Comparison with other structural classifications of British pine forests

Picozzi *et al.* (1992) attempted to classify forest structure in 15 different forests in Scotland which included at least 3 native pinewoods plus a number of Scots pine plantations. The objective was to provide an index of habitat suitability for capercaillie (*Tetrao urogallus*) based upon features of stand form and vegetation. Using principal components analysis, they were able to distinguish between a structure characterised by open spaced stands with clumps of mature, well branched trees plus a good field layer of dwarf shrubs (GRANNY), and one characterised by dense, regularly spaced stands with little understorey vegetation (PLANTATION). The density of male capercaillie at lek (display) sites was positively related to the GRANNY score for the forest surrounding the site. Based upon the above, they developed a key for classifying stands which included measures of vegetation type, depth of crown, regularity of spacing within the stand, and degree of canopy overlap as well as height and diameter. However, inspection of their results (e.g. their Fig. 1a) suggests that these features are simply a function of the different stages of stand development ie a high GRANNY score is equivalent to old-growth conditions whereas a high PLANTATION score is found in the stem exclusion or understorey reinitiation stage. Given that their classification distinguishes some 20 different stand types and requires measures of crown depth and branch interlock as well as conventional parameters, it does not seem to provide the simplicity of a classification based upon Oliver and Larson's four stages.

SUCCESSION AND DISTURBANCE MECHANISMS

Successional development within British pinewoods varies according to site fertility. Three broad categories of site can be distinguished based upon differences in soil nutrient regime (SNR) identified in the Ecological Site Classification (ESC) (Pyatt and Suárez, 1997).

Firstly, there are those areas throughout Britain where Scots pine plantations have been planted upon comparatively fertile soils («poor-medium» or better in SNR). These are likely to be colonised by a range of species more adapted to the site which regenerate under the shade of the maturing pine stand. Lust *et al.* (1998) have described how pine plantations on podsolic soils in Flanders are colonised by broadleaved species such as *Quercus robur* and *Q. rubra* and pine regeneration only occurs after site disturbance by cultivation or fire. One would anticipate that, in Britain, Scots pine on such sites would gradually die out without human intervention or catastrophic disturbance. Second are those stands, including the native pinewood zone, where Scots pine is found upon nutrient poor soils («very poor» to «poor» in SNR terms). Here Scots pine will remain a dominant component of the stands, but the spatial structure will depend upon the frequency and severity of wind disturbance. Humphrey (in press) has proposed for Glen Affric a continuous variation between intimate mosaics of small clumps of trees of different ages in more sheltered areas to a coarser structure of regular patches in exposed sites where single cohorts of seedlings have regenerated following stand replacing disturbances. One aspect that is poorly understood is the degree of broadleaved species involvement in the succession on these sites. Recent results from a fenced enclosure on a moderately sheltered site in the Glen Garry pinewood show that, 60 years after thinning a pine stand and site disturbance, the understorey was 85 per cent broadleaved (predominantly *Betula pubescens* and *Sorbus aucuparia*). However there was also a small percentage of pine saplings that seemed likely to outcompete the broadleaved understorey in due course (Edwards and Nixon, 1999). Similar results have been reported from other pinewood areas where deer have been excluded through fencing or by rigorous culling.

There is a third, intermediate category comprising those stands on sites of «poor» SNR where one can envisage a mixed species stand developing over time containing both Scots pine and other more demanding species. The latter could be either native broadleaves such as birch and oak or could be introduced conifers like Sitka spruce or European larch. In either case, the pine would remain as a long-term component of the mixed stand because of the beneficial effect of its mycorrhizal associates upon the nutrient dynamics of the stand (Morgan *et al.*, 1992).

The two major disturbance mechanisms that have affected Scots pine forests in Britain are wind and fire. Scots pine plantations in the stem exclusion and early understorey reinitiation phases suffered catastrophic damage from windstorms in north-eastern Scotland in 1953 and in southern England in 1987. It is likely that such damage can be expected to recur with a return period of perhaps once in every 100 to 300 years depending upon location within Britain. There is much less historical evidence of catastrophic wind damage to older stands in the old growth stage which have less regular structures, but all such stands typically show evidence of small scale damage from wind where a group of trees has blown over in a winter gale (Peterken, 1996). It is possible that past harvesting may have broken up any extensive areas of mature timber so that only the smaller scale pattern persists. The fire record is even more uncertain. Records from the most easterly native pinewood (e.g. with the most continental climate) in Glen Tanar suggest a fire return period of 1 in every

80-100 years since 1600 (Ross, 1995). There are records of severe fires in most pinewoods, but there has been no published analysis of fire incidence in British pinewoods. Current prevention measures would ensure that any fire that occurred was not likely to exceed 5-10 ha so that this is at present a comparatively small-scale disturbance mechanism. Other climatic factors that damage stands (e.g. snow breakage) are very rare and are only serious when combined with wind. Trees can be killed by fungal attack (e.g. top dying due to *Peridermium pini*) or insect pests but these tend to affect only a group of trees.

Thus, it appears that the prevailing disturbance mechanisms in British pine forests operate at a fine grained «gap phase» scale, but, in the past, when the pine forests were more extensive, catastrophic disturbances may have been more important. The latter can be expected to cause severe damage in the future if the area of pine forest is increased, particularly to stands in the stem exclusion and understorey reinitiation phases. The amount of «old-growth» would depend upon the frequency of disturbance and the age at which old-growth conditions develop.

A feature of the natural pine forest cycle in Scotland may have been an alternation between the closed forest and open heathland, particularly where low intensity fires were used to open the understorey for grazing. Such fires can also cause the death of damaged mature overstorey trees by burning these out from the inside as shown recently in northern Sweden (Linder, 1998). Under this scenario, intermittent exploitation combined with low intensity fires to promote grazing would be sufficient to ensure that mature stands reverted to heath whilst the confinement of grazing animals to a different part of the forest could allow regeneration to recolonise open land.

SCOTS PINE FORESTS: LINKS BETWEEN STRUCTURAL STAGES AND BIODIVERSITY

Until recently, studies of pinewood biodiversity tended to focus upon the native pinewoods because of their specialised flora and fauna and there have been fewer investigations in planted pinewoods. There are no reports on Scots pine stands that are being colonised by trees representative of another woodland type.

There are no mammal species specifically associated with Scots pine in Britain. However, Scots pine is a favoured habitat for the red squirrel (*Sciurus vulgaris*) where stands in the late stem exclusion and understorey reinitiation phase growing at a density of ca. 500 trees ha⁻¹ allow free movement through the canopy without having to come to the ground. Trees of this size also provide larger cones than the smaller ones associated with the older trees in mature pinewoods (Summers *et al.*, 1995). Grazing pressure from red deer (*Cervus elaphus*) influences the development and structure of many pinewoods. The impact of typical population densities (e.g. > 10 animals per 100 ha) is to limit the establishment of tree regeneration through repeated browsing, and to reduce or alter the vegetation. Heavier grazing results in more grass cover and less *Calluna vulgaris*, less *Vaccinium myrtillus* and fewer insect larvae; chicks of key pinewood bird species, such as the capercaillie, depend upon *Vaccinium* and lepidopterous larvae. Studies at Abernethy indicate that red deer populations consistently maintained below the level of 5 animals km⁻² allows natural regeneration of pine to occur (Beaumont *et al.*, 1995).

Pine stands in the early stem exclusion stage have some 16-20 breeding bird species and there are about 30 breeding species in the transition to understorey reinitiation. These figures compare with some 45 species breeding in the «old-growth» native pinewood habitat and the three key pinewood bird species, capercaillie, crested tit (*Parus cristatus*) and Scottish crossbill (*Loxia scotica*) are found most regularly in this stage. Capercaillie populations are generally higher in native pinewoods than in younger planted stands (17-24 birds km⁻² against 8 km⁻²; Summers *et al.*, 1995) where the limiting factor appears to be a suitable chick habitat (Moss and Picozzi, 1994). The crested tit, with a current population estimated at 900 pairs (Summers *et al.*, 1995), favour native pinewoods with rotten stumps and a diverse field layer but have also been recorded breeding in Scots pine plantations of 20 years and older. The Scottish crossbill has a world population estimated to be 1000-1250 pairs and breeds almost exclusively in native pinewoods where they frequent the older more open stands, often in trees 160-200 or more years old. Limiting factors to the spread of this species into younger natural forest or plantations include tree age, density, and cone size.

Many invertebrate species in native pinewoods also occur in Scots pine plantations including many common and vagrant species also found in other habitats. Using comparative data from unmanaged semi-natural Scots pine sites and plantations, Humphrey *et al.* (1999) found no differences in species richness or diversity for both syrphids (hoverflies) and carabids (ground beetles). Of the measured habitat variables, vertical stand structure showed the best correlation with species richness and diversity of both carabids and syrphids; richness and diversity was greatest in young stands with a high field layer vegetation. However, the rare invertebrate species tend to be associated with the deadwood habitat and open structure characteristic of the «old-growth» stage. For example, three rare species of wood ant (*Formica lugubris*, *F. aquilonia*, *F. sanguinea*) depend upon an open woodland structure as sunlight is needed to warm their nests to help mature the brood. They are commonest in the old-growth native pinewoods but are also found in younger Scots pine plantations although here they are restricted to the sunny margins of stands. They are very susceptible to clear felling which removes their food supply and nest building materials.

The most characteristic plant species of native pinewoods are *Goodyera repens*, *Linnaea borealis* and *Moneses uniflora* (Pitkin *et al.*, 1995). They are dependent on an intact field and shrub layer and have all been found in mature, undisturbed Scots pine plantations in the understorey reinitiation phase. These plants are potentially vulnerable to disturbance through forestry operations or natural catastrophe. Disturbance caused through clearfelling, heavy thinning, intensive soil cultivation, and herbicide applications of large areas can damage the viability of plant populations. A key aspect in the survival of such plant species would be to maintain tracts of mature, undisturbed woodland and to provide connectivity to areas where new pinewoods are developing. Similar conclusions apply to the bryophyte, lichen and fungal communities associated with British pinewoods.

Thus, while native Scots pine stands appear to have distinctive communities compared to plantations, a number of rare species, once thought to be restricted to native pinewoods, occur in plantations in the later stages of stand development. This suggests that the structural features of a pine forest such as the amount and distribution of deadwood are critical features for the pine ecosystem biodiversity and that the presence of key species is a function of development stage and site type rather than of pinewood category. However, most of the notable species are critically dependent upon the «old growth» structure that is such a feature of the native pinewoods. Therefore ensuring an adequate

and continuing supply of stands with this structure is critical for maintaining and enhancing the biodiversity of pinewoods in Britain. Measures taken in the last two decades will ensure the future of many of the forests by fostering young stands in the stand initiation stage, but these are unlikely to provide key habitat features for perhaps the next 200 years. If we accept that provision of old growth structures should be a major objective of future pinewood management, then the key questions are how much old growth should there be and how should we manipulate younger stands to achieve desired structures so that the old growth habitat can be maintained over time?

AREA OF PINE FORESTS IN DIFFERENT STRUCTURAL STAGES

The age-class distribution of the planted pine forests (Table 2) suggests that there is perhaps 4 per cent of the planted forest type in stand initiation, 85 per cent in stem exclusion, 9 per cent in understorey reinitiation, and 2 per cent may have old growth conditions. In addition, there are about 19,000 ha of native pinewood which consist largely of old trees (>100 years old) with a few younger specimens (Goodier and Bunce, 1977). Although not all this area will be old-growth, these estimates suggest a total of slightly under 15,000 ha of old-growth Scots pine forest in Britain at the present time (all in northern Scotland) or about six per cent of the pine forest area. There is considerable local variation in the incidence of old-growth stands. For example, a recent study in the largest native pinewood at Abernethy, suggested that 26 per cent of the forest could be classed as old-growth, compared with 12 per cent in understorey reinitiation, 40 per cent in stem exclusion, and 22 per cent in stand initiation (Summers *et al.*, 1997; their Table 3). By contrast in lowland pine forests, there are no known examples of old-growth structures (Ferris-Kaan, *et al.*, 1998).

As shown by Seymour and Hunter (1999), one can adapt a model of natural disturbance regimes (in their case fire frequency) to calculate an anticipated distribution of stand structures under natural conditions for a given disturbance frequency. This model is based upon the equation;

$$A(x) = p \exp(-px)$$

where $A(x)$ is the area of stands of age x , and p is the disturbance cycle (the inverse of disturbance frequency), while an equal probability of disturbance amongst age classes is assumed. For British pine forests where old-growth develops at 150 years and the stand replacement disturbance frequency is perhaps between 1 in 100 and 1 in 300 years, then the anticipated percentage of old-growth would vary from 5 per cent to perhaps 10 per cent of the forest. These figures are gross simplifications of a complex reality since they do not allow for any possibility of partial disturbances and gap phase dynamics within pinewoods. This estimate is broadly in agreement with the figure for the current amount of old-growth given in the previous paragraph, but that is almost entirely dependant upon the old growth stands in the native pinewoods. If the desired area of old-growth Scots pine forest in northern Scotland is around 25,000 ha (Anon., 1995), then the total area of pine forest required to sustain this habitat in that region is about 250,000 ha which is more than twice the current plantation area.

SILVICULTURAL OPTIONS FOR PROMOTING OLD GROWTH HABITAT

It should be clear from the preceding sections that managing the existing old-growth stands in isolation from the other parts of the pinewood resource is doomed to failure in the long-term. Many trees in the old stands are near biological maturity, there has been limited regeneration, and the stands themselves may be vulnerable to catastrophic damage at some point in the future. Therefore a percentage of planted stands in the stem exclusion and understorey reinitiation phases need to be identified and managed as future old-growth habitats. These stands need to be of a sufficient scale to provide the desired habitat, i.e. they need to be identified at the scale of tens or even hundreds of hectares rather than reserved at the level of a hectare or less. The main means of developing the desired features will be through thinning to speed the progress through the understorey reinitiation stage. Bailey and Tappeiner (1998) reported how operational thinning in coastal Douglas fir stands in North America hastened the development of multi-storied stands with features resembling old-growth.

A suitable method and intensity of thinning to promote old growth in pinewoods has not been well defined. Traditionally, pine stands managed for timber production have been thinned from below to a constant density. There is little evidence (e.g. Table 4) to suggest that variable density thinning in younger stands will hasten the establishment of desired structures and some concern that this may reduce the timber value of the residual stand. There have been no studies of crown thinning regimes as a means of promoting a more variable stand structure, but the light demanding nature of the species and the limited response of crowns after opening up suggests that this may not be a practical proposition. A more effective approach may be to maintain standard thinning practice until the stand is well beyond 100 years of age and starts to show signs of break-up. At that stage thinning should favour clumps of large trees with wide spaces between the clumps which will form the framework of the future old-growth habitat. Once this transition stage has been reached, then any attempt at systematic timber production would be foregone, but until break-up pine stands should be managed to produce high quality and high value timber. The other critical aspect of thinning practice in designated old-growth stands is to make sure that dead and dying trees are not removed but are left as biological legacies to initiate the continuity of deadwood habitat.

While these recommendations are based upon experience in northern pinewoods, they would seem reasonably applicable to equivalent stands in southern Britain. The main issue outwith the native pinewood zone is to accept that a small percentage of the pine resource should be managed upon much longer rotations to enhance biodiversity (UKWAS, 2000). In areas where the successional process is likely to result in the replacement of pine by other, less profitable species, a certain level of disturbance may be required to ensure that some regeneration of pine is achieved to maintain pine as an economic component of the system.

CONCLUSIONS

A major argument of this paper is that the distinction traditionally drawn between the native pinewoods and the plantation pinewood resource in Britain is artificial. The high conservation value of the native stands is a function of their old-growth structure that provides a rare habitat in what is otherwise a comparatively young forest area. Planted stands managed on conventional clear felling regimes are managed on comparatively short rotations (<100 years) so that they show a very simple stand structure. However, the presence of a range of pinewood specialist species in older plantation stands indicates that, with appropriate management, old growth structures and habitat can be developed in plantations. Old-growth stands have a number of characteristic structures compared to younger plantations including lower stocking, more deadwood, more variable diameter distributions and the presence of large trees; these structures can be favoured by thinning regimes once the stand begins to break up after some 100 years of age. Since many of the trees in old-growth stands in the native pinewoods are nearing biological maturity, maintaining the continuity of the old-growth habitat is dependant upon suitable plantation stands being identified and managed as designate old-growth.

Consideration of prevailing disturbance regimes and their frequency of occurrence can give a guide to the relative amounts of different structural stages that can be found in a pine dominated landscape. Under the once in 100 years return period proposed for catastrophic disturbance in much of the northern pinewood zone in Britain, it seems unlikely that old growth stands ever amounted to more than 10 per cent of the pinewood ecosystem. However, it is important that any retained stands are on a sufficiently large enough scale to allow continuity of habitat: mere retention of a few old trees beyond financial maturity is not equivalent to old-growth condition although they may provide useful links between such habitats.

Over the course of the twentieth century, prevailing silvicultural regimes based upon the maximisation of wood production over time have simplified pinewoods in Britain by reducing the extent of older stands in the understorey reinitiation and old-growth stages. Those older stands that remain survived only because of their high conservation and cultural value. However, the integration of timber production with enhanced biodiversity does not require the abandonment of existing silvicultural practices but rather an acceptance that relatively small percentage of the pinewood stands should be managed upon much longer rotations than those which prevailed when timber production was the sole objective.

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RESUMEN

Selvicultura y dinámica de las masas de Pino silvestre en Gran Bretaña: implicaciones para la biodiversidad

En Gran Bretaña existen 241.000 ha de Pino silvestre, lo que representa sobre el 10 % de la superficie forestal total. Tradicionalmente, se ha realizado una distinción entre una superficie pequeña de pinares nativos con un alto valor de conservación en el norte de Escocia y las plantaciones más jóvenes de Pino silvestre que se encuentran en muchas partes de Gran Bretaña. Las plantaciones se han gestionado principalmente para producción de madera aunque actualmente se espera que cumplan objetivos múltiples incluyendo el aumento de la biodiversidad. Las técnicas selvícolas de las plantaciones se basan en un sistema de cortas a hecho y regeneración artificial. Sin embargo, las plantaciones más adultas pueden colonizarse por especies raras previamente confinadas a los pinares nativos. Se examina la estructura de las masas de Pino silvestre de distintas edades utilizando conceptos modernos de la dinámica de las masas. El análisis resalta que los pinares nativos tienen rasgos característicos de «crecimiento viejo» como: menor densidad de existencias, mayor variación en diámetro, una distribución de pies en grupos, y apreciables cantidades de madera muerta en pie. En contraste, la mayoría de las plantaciones tienen mayor densidad de existencias, menor variación en diámetro, un espaciamiento más uniforme, y una limitada cantidad de madera muerta. Para cuantificar estas estructuras es posible proponer regímenes de claras que pueden introducirse en las plantaciones para acelerar el desarrollo de condiciones de crecimiento viejo sin un sacrificio excesivo de la producción de madera. La historia de las perturbaciones naturales de los pinares Británicos indican un período de retorno para los sucesos que reemplazan el rodal (fuego, apeo por viento) de una vez cada 100 años que sugiere que se puede gestionar como rodales de crecimiento viejo un máximo del 10 % de los recursos de los pinares. La estructura de edad de algunos pinares residuales muestra una falta de las clases de edad más jóvenes y el hábitat deseado de crecimiento viejo disminuirá con el tiempo a menos que las plantaciones adecuadas se gestionen como hábitats potenciales de crecimiento viejo. El mantenimiento de la biodiversidad en los pinares Británicos requiere una aproximación integrada que se aplica tanto a los pinares nativos como a las plantaciones.

PALABRAS CLAVE: Pino silvestre
Selvicultura
Dinámica del rodal
Crecimiento viejo
Estructura del rodal

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