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***Pinus sylvestris* L.**

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A large genus within the family Pinaceae (sub-family Abietineae) consisting of evergreen trees and shrubs. Native to Europe, Asia, North America, Central America, North Africa and nearby islands (Dallimore & Jackson 1948). *Pinus sylvestris* L. is the only species of this genus which is indigenous to Britain. It is a two-needled pine, with the leaf-bases surrounded by a common sheath. A tree of monopodial growth, the branches are produced in whorls, with no lateral buds between the whorls. The monopodial growth is not as marked as in *Picea abies*, and the habit varies from narrow spire-like crowns to bushy trees with no definite main axes. Bark in upper part of stem thin, papery and bright orange or reddish-brown; bark of lower part of stem thick, dark brown and fissured in young trees; thinner, pale grey-brown with shallow fissures in old trees. Shoots green to green-brown in first season, maturing to greyish-brown, and later to orange or red-brown. Buds up to 12 mm long, oblong ovoid, resinous, generally red-grey-brown, rarely red. Each adult leaf pair arises on a short shoot; leaf bases enclosed in a common 5–10 mm long sheath, white at first, becoming grey-brown and finally dark brown at maturity. The needle-shaped leaves are 3–8 (–10) cm long, 1–2 mm wide; summer colour grey or blue-green; winter colour dark grey-green, or yellow, or reddish-green; finely serrulate; persistent 2–4 (–6) years. The leaf has xeromorphic characters, with a thick-walled epidermis and a well-developed collenchymatous hypodermis; two vascular bundles are within the leaf stele, separated by thick-walled tissue. Resin canals generally five to ten, usually marginal and in contact with the hypodermis, but medial canals surrounded by the parenchyma of the mesophyll frequently occur (Carlisle 1954). Monoecious. The male inflorescences occur in clusters at the base of the current season's growth. Colour immediately prior to anthesis usually yellow or violet-yellow, occasionally pink or violet-red (Carlisle 1954; Nekrasova 1959). Pollen round or elliptic, diameter of body 44.2–52.0 μ , two winged, exine reticulated with small ridge at base of wings (Carlisle 1954, 1958; Steven & Carlisle 1959). Female inflorescence or cone borne at end of current year's growth; young cone about 5–7 mm long, red or red-brown, consisting of circular bract scales and shorter, fleshy, seminiferous scales with red, pointed tips. Mature female inflorescence a woody cone consisting of a main axis with small bracts, in the axils of which arise woody ovuliferous scales. On the adaxial surface of each ovuliferous scale are two integumental ovules; each ripens to a winged seed after fertilization. Seeds 3.5–5.5 mm long; colour dark grey, grey-brown, brown, pale brown or yellow, sometimes mottled; seed wing 15–20 mm long, variable in shape from short and broad to long and narrow, colour pale brown, brown, pink-brown, dark brown or dark red-brown, sometimes

longitudinally striped (Steven & Carlisle 1959; Carlisle 1954, 1958). Stem sapwood yellowish-white, heartwood pale brown or reddish; medullary rays low, some (with a circular resin canal) more than one cell wide, others (with no canal) one cell wide; ray tracheids dentate; difficult to distinguish from *Pinus densiflora*, *P. nigra* and *P. resinosa* (Anon. 1960c; Boulton & Jay 1946; Phillips 1949; Rol 1932). Timber density and tracheid length vary with the provenance (Echols 1958).

A great many subspecies, varieties and forms of *P. sylvestris* L. have been recorded in the literature, many of them being of doubtful validity; they are described by Steven and Carlisle (1959), Carlisle (1958), Beissner & Fitschen (1930) and Pravdin (1964). The indigenous Scots pine of Britain is generally called var. *scotica* Schott, although some authors regard it as a subspecies. The indigenous pine in Britain is geographically isolated, but there is insufficient evidence to show whether or not it is morphologically distinguishable from the Scots pine in other geographic regions. Little is known about the occurrence of variants and their frequency in natural Scots pine populations other than those of Scotland and Sweden which have been studied in some detail (Steven & Carlisle 1959; Sylven 1916). The Scots pine of Scotland is morphologically and anatomically heterogeneous, and the variation appears to be continuous. The variants (habit, bark, leaf colour, leaf length, cone form, etc.) recorded in Scotland (Steven & Carlisle 1959) occur in other populations throughout the range of the species, and are not unique. The frequency with which the variants occur, however, appears to vary from one geographic region to another. Until more is known, it is valid to refer to the indigenous Scots pine of Britain as var. *scotica* Schott.

Scots pine exhibits variation in its physiological characteristics of time of flushing, leaf retention and tolerance to extreme conditions of soil and climate. On the basis of provenance trials, attempts have been made to distinguish 'geographic ecotypes' (Wright & Baldwin 1957), but Langlet (1959) points out that there is no evidence of discontinuity in the variability which is continuous and correlated with environmental factors.

I. Geographical and altitudinal distribution. (a) *Geographical distribution.* All the pinewoods of undoubted natural and native origin in Britain, which have descended from one generation to another by natural means, are located in Scotland between the latitudes of 57°57'N and 56°22'N and the longitudes of 2°53'W and 5°38'W (Fig. 1). There are also Scots pines on bogs in England which are of reputed natural native origin, but there is a distinct possibility that, although the present stands have arisen naturally, the parent trees could have been planted or originated from planted trees. In the absence of reliable documentary and other evidence, therefore, the natural, indigenous pinewoods of Britain should be regarded as confined to Scotland. Scots pine has been widely planted in the British Isles, and a map of the distribution is given by Perring & Walters (1962).

The northern limit (Fig. 2) of Scots pine is at 70°29'N in Norway (Enquist 1933; Steven & Carlisle 1959); the southern limit at 37°N in southern Spain and the western limit at 7°W in north-west Spain (Vazquez 1947), but there are pine woodlands of unknown status further west in northern Portugal (Eliseu 1942); eastern limit at about 138° E, with a few trees further east, reaching the Pacific coast (Malev 1955). The Scots pine of Scotland at 5°38'W is near the western limit of the species. A more detailed description of the distribution of *P. sylvestris* is given by Steven & Carlisle (1959).

(b) *Altitudinal distribution.* In Scotland the native Scots pine occur in woodland communities between sea level in the north-west and 625 m in the Cairngorm Mountains of central Scotland. The altitudinal limit is higher in east and central Scotland than in the

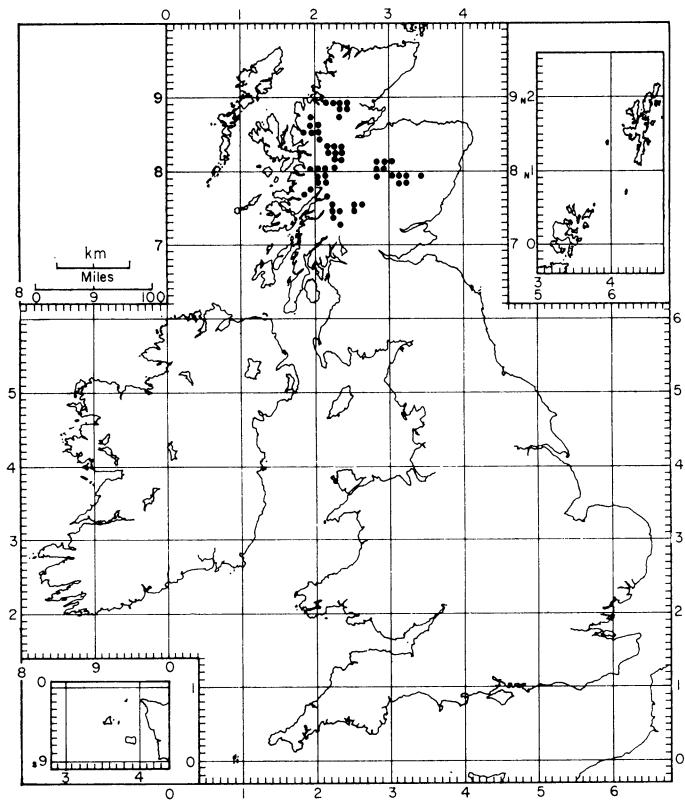


FIG. 1. The distribution of *Pinus sylvestris* L. woodlands of undoubted natural and native origin in the British Isles (after Steven & Carlisle 1959).

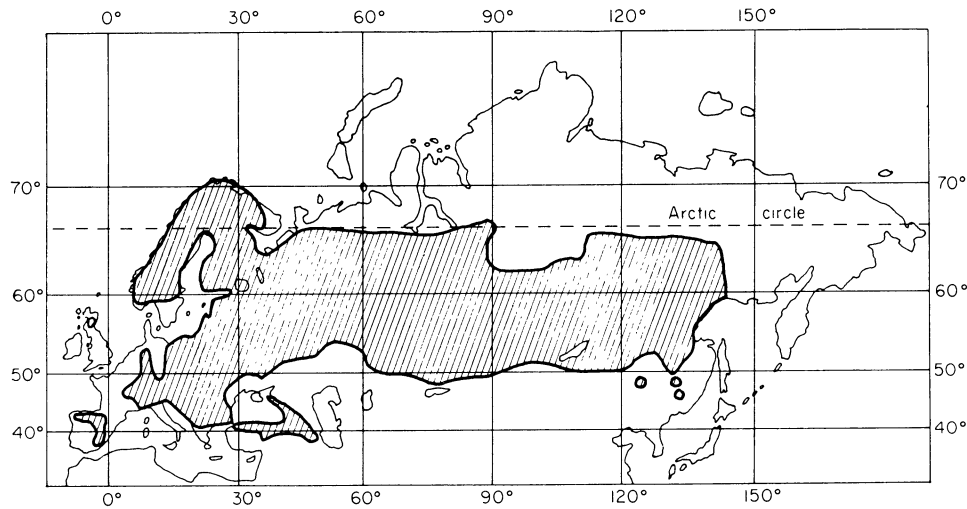


FIG. 2. The world distribution of indigenous *Pinus sylvestris* L. woodlands (after Steven & Carlisle 1959).

Table 1. Profile descriptions of soils beneath Pinus sylvestris in indigenous pinewoods in eastern, central and western Scotland (after Manley 1961)

Profile 1		Profile 2	
Ballochbuie Forest, Aberdeenshire		Rothiemurchus, Inverness-shire	
Rainfall: 88.9 cm/annum		Rainfall: 114.3 cm/annum	
Tree cover: Pinus sylvestris		Tree cover: Pinus sylvestris	
Ground vegetation: Calluna vulgaris/Vaccinium myrtillus		Ground vegetation: Calluna vulgaris, Vaccinium myrtillus and Arctostaphylos uva-ursi	
Parent material:	Granite, with glacial drift consisting of granite, diorite and schist	Parent material:	Glacial and fluvioglacial materials consisting of micaceous schists, siliceous granulates and granite
Soil drainage:	Free	Soil drainage:	Free
Taxonomic unit:	Humus iron podsol	Taxonomic unit:	Humus iron podsol
0-11.4 cm	Reddish-brown raw humus, well-decomposed and compacted; numerous woody roots	0-7.6 cm	Loose litter only slightly decomposed, much moss remains, with woody roots
11.4-15.2 cm	Pinkish-grey (7.5 YR 6/2) sandy loam; mainly bleached quartz grains	7.6-11.4 cm	Reddish-brown well-decomposed and compacted raw humus with numerous roots
15.2-29.2 cm	Blotched medium and dark brown (7.5 YR 5/8 and 7.5 YR 4/4) sandy loam; grains coated with iron and humic material; more or less compacted; few roots	11.4-16.5 cm	Dark red-brown humified and compacted organic matter with roots
29.2- cm	Medium brown (10 YR 5/6) well-compacted sandy loam	16.5-19.0 cm	Humified organic matter mixed with charcoal fragments and bleached mineral grains
		19.0-25.4 cm	Dark grey-brown (10 YR 4/2) highly leached coarse sand slightly coloured with black organic material
		25.4-35.6 cm	Greyish (10 YR 6/2) bleached sand
		35.6-43.2 cm	Bleached sand with appreciable dark organic matter

Profile 3		Profile 4	
Strathfarrar, Inverness-shire		Loch Maree (Beinn Eighe), Wester Ross	
Rainfall: 177.8 cm/annum		Rainfall: 177.8–203.2 cm/annum	
Tree cover: <i>Pinus sylvestris</i> and <i>Betula</i> sp.		Tree cover: <i>Pinus sylvestris</i> , <i>Betula</i> sp. and <i>Sorbus aucuparia</i>	
Ground vegetation: <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , and <i>Arctostaphylos uva-ursi</i>		Ground vegetation: <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , and a well-developed layer of mosses	
Parent material:	Glacial and fluvio-glacial well-weathered micaceous, bright orange sand, with some schist	Parent material:	Lower Cambrian quartzites covered with morainic and scree material (almost pure quartzite)
Soil drainage:	Free	Soil drainage:	Very free
Taxonomic unit:	Humus iron podsol		Loose, slightly decomposed litter layer with numerous roots
0–2.5 cm	Loose litter only slightly decomposed with recognizable moss remains	10.2–15.2 cm	Reddish-brown slightly compacted amorphous organic matter; wet and sticky; charcoal remains
2.5–22.9 cm	Compacted, reddish-brown amorphous raw humus with numerous fibrous and woody roots	15.2–53.3 cm	Almost white (10 YR 7/2) bleached quartzite sandy; occasional pale yellow blotching
22.9–25.4 cm	Black organic matter with charcoal fragments and bleached mineral grains	53.3–91.4 cm	Light brown (10 YR 5/3) sand; few roots
25.4–30.5 cm	Pinkish-grey (7.5 YR 5/2) bleached micaceous sandy loam with a few roots		
30.5– cm	Blotched, brown (7.5 YR 5/6) material		

Note: Munsell colour code in parentheses.

Table 2. Mechanical and chemical analyses of soils beneath Pinus sylvestris in indigenous woodlands in eastern and western Scotland

Horizon	Munsell colour in parentheses	Colour theses	Sample depths (cm)	% H ₂ O	% loss on ignition	Mechanical analysis				Exchangeable cations m-eq./100 g							Organic fraction				Phosphorus	
						% Sand	% Silt	% Clay	Ca	Mg	Na	K	H	Total	% Base saturation	pH	% C	% N	C/N	% O.M.	Total mg/100/g	Acetic mg/100/g
(a) Humus iron podsol: Allachy Wood, Glentanar, Aberdeenshire. Rainfall 89 cm/annum; granitic till. <i>Pinus sylvestris</i> , <i>Vaccinium myrtillus</i> , <i>Calluna vulgaris</i>																						
L	Dark reddish-brown (5YR2/2)		12.7-11.4	10.69	69.00	N.D.	N.D.	N.D.	10.30	3.49	0.25	1.05	77.82	92.91	16.2	4.10	38.86	1.103	36.1	68.4	155	11.9
F	Dark reddish-brown (5YR2/2)		11.4-6.4	14.20	86.00	N.D.	N.D.	N.D.	16.06	7.83	0.52	1.62	131.89	157.92	16.5	3.75	52.52	1.618	32.5	90.27	170	18.1
H	Dark reddish-brown mor humus (5YR2/2)		5.1-0.0	14.87	90.00	N.D.	N.D.	N.D.	13.39	9.19	0.61	1.83	148.01	173.03	14.5	3.61	55.68	1.609	34.6	95.74	167	24.3
A ₂	Reddish-grey loamy sand (5YR5/2)		2.5-10.2	0.84	4.59	76.5	10.5	10.7	0.13	0.14	0.04	0.17	9.13	9.61	5.0	3.79	N.D.	N.D.	N.D.	N.D.	24	Nil
B ₂	Dark reddish-brown sandy loam (5YR3/3)		15.2-25.4	7.71	17.89	74.7	6.5	5.4	Nil	0.13	0.08	0.15	39.98	40.34	0.9	4.09	N.D.	N.D.	N.D.	N.D.	89	Nil
B ₃	Dark reddish-brown sandy loam (5YR3/3)		35.6-43.2	8.00	17.70	75.0	6.3	5.4	Nil	0.05	0.08	0.11	38.91	39.15	0.6	4.20	N.D.	N.D.	N.D.	N.D.	102	Nil
B ₃	Reddish-yellow loamy coarse sand (5YR6/6)		45.7-55.9	1.01	0.22	74.7	13.8	11.5	0.13	Nil	0.02	0.04	5.66	5.87	3.2	4.24	N.D.	N.D.	N.D.	N.D.	38	1.4
C	Light reddish-brown to reddish-yellow loamy coarse sandy loam (5YR6/4-6/6)		63.5-76.2 91.4-121.9	0.92 0.97	1.53 1.41	76.8 73.6	12.3 12.7	10.9 13.7	0.13 Nil	Nil Nil	0.04 0.04	0.08 0.04	3.91 4.11	4.16 4.19	6.0 1.9	4.49 4.31	N.D. N.D.	N.D. N.D.	N.D. N.D.	N.D. N.D.	25 26	1.8 0.4
(b) Humus iron podsol: Beinn Eighe Pinewood, Loch Maree, W. Ross. Rainfall 178-203 cm/annum. <i>Pinus sylvestris</i> , <i>Calluna vulgaris</i> , thick moss carpet																						
L	<i>Sphagnum</i> and other moss litter with pine needles		0-5.1	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
F	Matted and felty Black greasy humus with charcoal		5.1-20.3	16.30	96.50	N.D.	N.D.	N.D.	7.53	20.80	4.38	1.29	94.50	128.50	26.4	4.28	48.20	1.000	48.2	82.90	91	12.3
H	Yellow grey 'cheesy' material with marbled streaks of black and high wax content		22.9-30.5	10.31	69.60	N.D.	N.D.	N.D.	0.33	16.36	4.08	0.40	92.10	113.27	18.6	4.30	26.40	0.582	45.4	45.50	47	5.8
A ₂	White loamy sand		30.5-33.0	6.21	51.60	N.D.	N.D.	N.D.	1.60	13.88	1.90	0.25	56.60	74.23	23.8	4.45	25.00	0.281	89.0	43.00	35	1.9
B ₁	Diffuse banding of black-dark brown humus		33.0-45.7	0.26	0.87	84.5	8.6	6.0	Nil	0.50	0.10	0.05	1.50	2.15	30.2	4.86	N.D.	N.D.	N.D.	N.D.	17	0.8
B ₂	Yellow-orange stony fine sandy loam		53.3-63.5	3.67	8.29	84.4	5.4	6.0	Nil	1.00	0.31	0.09	18.20	19.60	7.2	4.95	N.D.	N.D.	N.D.	N.D.	39	0.7
C	Yellow gravelly loamy sand		71.1-78.7 116.8-142.2	6.47 1.05	12.79 1.58	80.8 89.3	8.3 3.0	4.5 6.1	Nil Nil	0.22 0.08	0.36 0.06	Nil 0.03	14.97 2.33	15.55 2.50	3.7 6.8	5.12 5.39	N.D. N.D.	N.D. N.D.	N.D. N.D.	N.D. N.D.	68 38	0.5 0.4

Analyses kindly supplied by Soil Survey of Scotland, Macaulay Institute for Soil Research, Aberdeen. Methods as described in Glentworth & Muir (1963). N.D. = Not analysed; O.M. = Organic matter.

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more oceanic west. Throughout its range the altitudinal limits of Scots pine are from sea level to 2438 m above sea level, the limit being higher in the southern than in the northern parts of its distribution (Steven & Carlisle 1959).

II. *Habitat.* (a) *Climatic and topographic limitations.* Scots pine tolerates a wide range of climatic conditions, from the severe cold of northern Siberia to the Mediterranean climate of southern Spain and the foothills of the Ligurian Alps; and from the wet, oceanic climate of the west coast of Scotland to the dry continental climate of central Europe and Asia. The western limit is determined by the barrier of the Atlantic, and the eastern limit by the Pacific except in north-eastern Russia where the Verkhoyansk Mountains effectively prevent eastward migration. The northern limit of Scots pine is probably determined by temperature, although at what stage in the life cycle of the tree this operates is not clear. Scots pine is able to withstand winter temperatures as low as -26.7°C (Parker 1961). It is possible that the northern distribution of *P. sylvestris* is limited by low temperatures during either pollination or fertilization, preventing the pollen tubes from reaching the ovules (Salisbury 1939). Mikola (1962) states that Scots pine needs mean temperatures of $+10.5^{\circ}\text{C}$ and $+8.5^{\circ}\text{C}$ in 4 summer months to ripen the seed and produce vegetative growth respectively. The factors determining the southern boundary of the distribution of Scots pine are also not clear, but Scots pine does not occur naturally where the mean summer (July) temperature is more than 26.7°C . Printz (1933) suggests that the southern limit of Scots pine may be determined by an unfavourable balance between photosynthesis and respiration at high temperatures. The altitudinal limit of Scots pine is probably determined by a combination of temperature and exposure to wind blast, but little information is available on this point.

Scots pine is a light demanding species and will not tolerate heavy shading by other trees. There is a tendency for the native pine woodlands of Scotland to be located on north-facing slopes; how far this applies to other regions is not known.

(b) *Substratum.* *P. sylvestris* has been planted on a wide range of soil types in Britain. It prefers light, non-calcareous freely-drained soils and is particularly successful on heaths, where it occupies more than half of the area of the latter sites planted by the Forestry Commission (Zehetmayr 1960). It grows well on these heaths where thin peat overlies coarse sand, but is less successful on thicker peats where a hard pan overlies compact gravels. The indigenous pinewoods of Scotland occur on glacial and fluvioglacial deposits, mainly over schists, gneisses and granites, but locally on quartzite and Torridonian sandstone. The soils are of low base status and are generally humus iron podsols. The humus layer is well-developed, often black or reddish-brown, and generally a mor; most profiles show marked leaching and charcoal fragments are common (Manley 1961); there are no earthworms. Profile descriptions (Manley 1961) for soils under indigenous pine in a range of rainfall conditions are given in Table 1; mechanical and chemical analyses in Table 2. Further information is available in the theses of Stewart (1958) and Manley (1961). Scots pine has also been planted on deep peats, but has generally been a failure on wet peats on exposed, elevated sites. It is widespread in a semi-natural condition on lowland peats where it grows moderately well on waterlogged sites provided conditions are not reducing (Eh at pH5 < 350 mV) in the rooting zone (Brown, Carlisle & White 1966) (see VIe). On deep peats Scots pine often suffers from phosphorus deficiency unless given a suitable fertilizer. Potassium is sometimes deficient on deep peats (Goor 1961; Brown *et al.* 1964), but is generally sufficient to support growth for the first 20–30 years (Binns 1959). At high (549 m) elevations, however,

potassium deficiency can seriously limit growth on blanket peat even though these peats have a higher potassium content than peats on lower sites where Scots pine growth is normal (Brown *et al.* 1964). Scots pine will also reach maturity and regenerate on calcareous sites (e.g. shallow mulls over Carboniferous limestone in north Lancashire) but is sometimes chlorotic on limestone sites (Peace 1962). The optimum nutrient levels, deficiency levels and the deficiency symptoms are described in VI(e).

The mean total litter fall (leaves, twigs, etc.) for Scots pine stands studied in Europe (Bray & Gorham 1964) is 2.8 metric tons/ha/annum on an oven dry (100° C) basis, ranging from 0.6–6.0 metric tons/ha/annum (Levina 1960; Krutzsch 1869). On fertile sites the litter production is as much as three times that on poor sites (Bray & Gorham 1964). Ebermayer (1876) found that litter production tended to be highest on sites least exposed to the heating and drying effects of insolation. Viro (1955) estimated that leaves, fruit, branch, bark and other litter were 69, 2, 12, 11 and 6% of the total litter fall respectively. Small quantities of Scots pine litter fall throughout the year, but there is a peak in the later summer–autumn period (in England from mid July–mid September), unlike *Picea sitchensis* (Bong.) Carr. and *P. abies* (L.) Karst. which drop appreciable quantities of litter throughout the year (Viro 1955; Kendrick 1959; Owen 1954; Wright 1957). Litter fall may vary considerably from year to year; in seven woodlands in Germany the maximum/minimum litter fall ratio was 2.2 (Bray & Gorham 1964). The nutrient content of the total annual litter fall in Scots pine forests in Finland (Viro 1955) was (kg/ha) 11.19 nitrogen, 0.89 phosphorus, 2.08 potassium, 10.01 calcium, 2.03 magnesium, 0.50 sodium and 32.1 ash; the leaf litter accounted for 68–79% of these elements. The C/N ratio of Scots pine litter ranges from 66–91 (Duvigneaud & Denaeyer-de Smet 1964); litter calorific values (kcal/g on oven dry basis) are leaves 4.99–5.22 (mean 5.12), branches 4.88–4.99 (mean 4.93) and cones 4.66–4.85 (mean 4.79) (Ovington 1961). The pH of pine leaf litter is generally 4.0–4.2 (Hesselman 1925; Mattson & Koutler-Andersson 1941); it has a titratable acidity of 33.9 m-eq/100 g dry matter and titratable base content of 43.2 m-eq/100 g dry matter which is within the range of mull-forming species, but the ratio of titratable bases/titratable acidity is lower than for any of the latter (Mattson & Koutler-Andersson 1941). Ten amino acids (glutamic acid, leucine, valine, α -alanine, serine, threonine, glycine, aspartic acid, lysine and arginine) have been recorded in aqueous extracts of the leaf litter and these all disappeared after 4 days aerobic decomposition *in vitro*. The main sugars present in these aqueous extracts were glucose (6.1% of the extract) and fructose (1.5%), and these also disappeared after 4 days decomposition (Nykqvist 1959, 1963). Arabinose, xylose, galactose and ribose have also been identified in the free state in aqueous extracts of the leaf litter (Alvsaker & Michelson 1957). Aliphatic acids in the aqueous extracts are malic acid (0.9% of extract), citric acid (1.8%), phosphoric acid (0.6%) and small amounts of lactic + succinic acid and fumaric acid. After decomposition for 4 days *in vitro* these all disappeared except citric and phosphoric acid (Nykqvist 1963). Aqueous extracts of Scots pine litter are capable of causing non-biological solution of ferric and aluminium oxides and reducing the ferric iron to the ferrous state, thereby inducing podsolization (Bloomfield 1953). Acid solutions formed in the litter/humus layers of 20–60 year Scots pinewoods in Russia leached 3–7 kg/ha/annum of iron and 0.5–1.5 kg/ha/annum of aluminium from the upper part of the soil horizon (Smirnova & Suhanova 1964). The litter is a mor-forming material, and breaks down relatively slowly on the more acid sites. Kendrick (1959) found that it took 10 years for the leaf litter to be completely reduced to the material of the H layer; twig and cone litter took longer. The cellulose of pine needle

litter is relatively resistant to decomposition by fungi (Lindeberg 1944), and there is some evidence that pine leaf litter forms stable complexes with protein material *in vitro* (Handley 1954). In a pinewood on a podsolized sandy soil in Delamere Forest, when the leaf litter fell in the autumn it remained in the L layer for 6 months during which it was invaded by fungi (e.g. *Desmazierella acicola*). The following 2 years it was in the F₁ layer and fungal activity increased, the outsides of the leaves being attacked by *D. acicola* Lib. and the inside by the hyphomycetes *Sympodiella acicola* Kendrick and *Helicoma monospora* Corda. At the end of the 2 years the leaves were fragmented and became the F₂ layer; they were then broken down by the soil meiofauna (mites, collembola, etc.) and basidiomycete mycelia for 7 years before entering the H layer (Kendrick & Burges 1962). In the same forest microbial activity (assessed by the oxygen uptake of the soil) was highest in the L layer (2406.0 µl of oxygen/5 h/g of organic matter) and the F₁ layer (274.6 µl); activity in the F₂, H and mineral soil horizons was considerably lower (56.6–274.6 µl). The order of activity in the soil horizons was L > F₁ > F₂ > A₂ > H > C > B₁ (Parkinson & Coup 1962). Changes in the external features, chemical (carbon, nitrogen and polyphenol) composition and fungal populations of decomposing Scots pine litter have been described in detail by Hayes (1962, 1965). Gremmen (1957) discusses the many species of fungi which decompose the branch and leaf litter of *Pinus sylvestris*. The importance of the litter to the nutrition of the trees on relatively infertile soils was demonstrated by Goor & Tiemens (1963) who found that removing 1 year's litter significantly reduced the growth of Scots pine, with a danger of mortality on the poorer sites.

Pozdnyakov (1956) found that the stem flow waters from Scots pine were relatively acid (pH 3.7) compared with *Larix* sp. (pH 4.2–5.3) and *Betula* sp. (pH 4.7–4.8), had an ash content of 0.04–0.05 g/l, and influenced the soil properties at the bases of the trees. The throughfall waters transport nutrients from the canopy to the soil, and Tamm (1951) found that these waters contained considerably more calcium, potassium and sodium than the incident rainfall.

III. *Communities.* Scots pine is a component of many semi-natural and planted woodlands in Britain, and the ground flora associated with it is very varied. It would serve no useful purpose to describe these communities in detail, and the following discussion will be confined to the indigenous pinewoods in Scotland. In the latter woodlands Scots pine occurs in pure stands or mixed with birch (*Betula* spp.) and less commonly with oak (*Quercus* spp.). Other tree and shrub species often present are *Populus tremula*, *Alnus glutinosa*, *Sorbus aucuparia*, *Prunus padus*, *Juniperus communis*, *Ilex aquifolia*, *Salix atrocinerea*, *S. aurita*, *S. caprea* and *S. pentandra*. The relationship between pine, birch and oak is complex, and depends on both habitat factors and site history. The pinewoods, with or without some birch, are principally on north-facing aspects (see IIa); oak and birch frequently dominate the sides of the glens with southern aspects (Steven & Carlisle 1959). McVean (1964) suggests that this segregation may be primarily edaphic, but this needs confirmation. The most extensive stands of pure pine occur on Deeside and Speyside, where the climate is less oceanic than in the north and west of Scotland, where the birch component is more prominent. Pine and birch occur naturally at higher altitudes than oak (for both edaphic and climatic reasons), but the altitudinal zonation of pine and birch is less clear. There are examples of pine above birch, and *vice versa*, which may be due to past selective feelings or to edaphic factors.

The ground flora of the indigenous Scots pine and Scots pine/birch woodlands has been

Table 3. *The pinewood Vaccinium—moss association (Pinetum Hylocomieto-Vaccinetum) with myrtillosum and triquetrosus facies (after McVean & Ratcliffe 1962)*

Locality (see footnote)	Myrtillosum facies										Triquetrosus facies				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
	274	274	274	274	274	518	518	15	152	213	229	183	-	-	
Altitude (m)	16	16	16	16	16	16	16	16	16	16	4	16	4	4	
Plot area (m ²)	Domin ratings														
<i>Betula pubescens</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Calluna vulgaris</i>	4	3	2	3	1	+	+	3	3	1	1	-	1	2	
<i>Empetrum nigrum</i>	5	3	+	+	+	5	4	-	+	2	-	-	-	-	
<i>Erica cinerea</i>	-	-	-	+	-	-	-	3	3	2	-	-	-	-	
<i>E. tetralix</i>	3	3	2	-	-	-	-	-	-	2	-	-	-	-	
<i>Juniperus communis</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Pinus sylvestris</i>	-	-	-	-	-	-	-	-	1	-	-	+	-	-	
<i>Sorbus aucuparia</i>	-	-	-	-	-	-	-	2	3	-	2	2	-	-	
<i>Vaccinium myrtillus</i>	6	8	6	4	6	7	8	7	7	8	-	2	+	-	
<i>V. vitis-idaea</i>	5	4	5	8	5	7	4	3	4	4	-	-	1	+	
<i>Blechnum spicant</i>	+	-	-	-	-	-	+	+	-	-	+	-	-	-	
<i>Pteridium aquilinum</i>	-	-	-	-	+	-	-	-	2	-	-	-	-	+	
<i>Agrostis tenuis</i>	-	-	-	1	-	-	-	-	-	-	-	2	-	-	
<i>Deschampsia flexuosa</i>	-	-	3	-	6	2	3	3	4	+	3	5	-	3	
<i>Molinia caerulea</i>	-	+	-	-	-	2	-	-	-	-	-	-	-	-	
<i>Goodyera repens</i>	2	-	-	3	2	-	-	-	-	-	2	-	1	1	
<i>Listera cordata</i>	1	-	-	-	-	-	-	+	-	-	+	-	-	-	
<i>Luzula multiflora</i>	-	-	2	1	-	-	-	-	-	-	-	3	-	-	
<i>L. pilosa</i>	-	-	-	-	3	-	-	-	-	-	-	3	-	-	
<i>Galium hercynicum</i>	-	-	-	-	3	-	-	-	-	-	-	1	-	-	
<i>Lathyrus montanus</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	
<i>Melampyrum pratense</i>	+	1	1	-	3	2	-	+	3	3	2	-	-	1	
<i>Oxalis acetosella</i>	-	-	-	-	+	-	-	-	+	-	-	4	-	-	
<i>Potentilla erecta</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	
<i>Trientalis europaea</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	
<i>Viola riviniana</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	

<i>Campylopus flexuosus</i>	-	1	+	-	-	3	3	-	2	-	-	-	+	2
<i>Dicranum majus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. scoparium</i>	2	1	-	1	-	-	-	2	-	-	3	-	3	1
<i>Hylocomium splendens</i>	5	6	4	6	5	7	6	6	8	5	3	9	8	7
<i>Hypnum cupressiforme</i>	1	-	-	-	-	+	+	-	-	-	2	-	-	-
<i>Leucobryum glaucum</i>	-	+	-	-	-	+	+	-	-	-	-	-	-	-
<i>Plagiothecium undulatum</i>	-	-	-	1	4	3	3	1	-	-	+	2	-	-
<i>Pleurozium schreberi</i>	-	2	2	2	1	3	-	1	4	+	4	2	2	-
<i>Pseudoscleropodium purum</i>	-	-	-	2	-	-	-	-	-	3	-	-	-	-
<i>Ptilium crista-castrensis</i>	+	-	-	2	-	-	4	6	+	-	-	-	-	-
<i>Rhytidadelphus loreus</i>	2	1	1	-	-	5	4	-	-	2	-	3	1	-
<i>R. triquetrus</i>	-	-	4	+	1	-	-	-	-	8	9	3	3	6
<i>Sphagnum acutifolium</i> agg.	1	2	-	+	-	+	+	3	2	-	-	-	-	-
<i>Thuidium tamariscinum</i>	-	-	-	-	-	-	-	+	+	-	-	-	-	-
<i>Lepidozia reptans</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Lophocolea bidentata</i>	2	-	-	2	+	-	-	-	-	-	1	1	-	-
<i>Lophozia longidens</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Scapania gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Cladonia deformis</i>	1	-	-	-	-	-	-	-	-	-	-	-	1	1
No. of species (45)	18	14	13	17	18	14	12	17	18	13	15	17	13	11

(Average 14)

Constancy class V (species in bold type), 4; constancy class IV, 3.

LOCALITIES: 1-5, 13, 14, Rothiemurchus, Inverness-shire; 6, 7, Glen Quoich, Aberdeenshire; 8, 9, Beinn Eighe, Ross-shire; 10, 11, Amat Wood, Bonar Bridge, Sutherland; 12, Curr Wood, Dulnain Bridge, Inverness-shire.

Table 4. *The pinewood Vaccinium–Calluna association (Pinetum Vaccineto-Callunetum)*
(after McVean & Ratcliffe 1962)

Locality (see footnote)	1	2	3	4	5	6	7	8	9
Altitude (m)	46	46	46	183	213	259	396	305	396
Plot area (m ²)	16	16	4	8	16	4	4	4	4
Domin ratings									
<i>Betula pubescens</i>	+	+	–	–	–	–	–	–	–
Calluna vulgaris	6	7	8	7	7	4	5	7	8
<i>Empetrum nigrum</i>	–	3	–	1	2	–	–	+	3
<i>Erica cinerea</i>	–	–	–	+	–	–	–	–	–
<i>E. tetralix</i>	1	3	–	1	–	+	–	–	–
<i>Ilex aquifolium</i>	–	+	–	–	–	–	–	–	–
<i>Pinus sylvestris</i>	1	+	–	1	–	–	–	1	–
<i>Sorbus aucuparia</i>	2	1	–	–	1	–	–	–	–
Vaccinium myrtillus	6	5	4	4	6	7	7	5	6
V. vitis idaea	3	3	3	3	3	3	4	6	3
<i>Blechnum spicant</i>	–	–	–	2	1	–	1	–	1
<i>Pteridium aquilinum</i>	1	2	1	2	–	–	2	–	–
Deschampsia flexuosa	2	1	1	3	1	3	3	3	3
<i>Listera cordata</i>	+	–	–	2	–	–	–	1	1
<i>Luzula multiflora</i>	–	–	–	–	–	+	–	–	–
<i>Melampyrum pratense</i>	2	1	–	–	–	–	–	–	–
<i>Oxalis acetosella</i>	–	–	–	–	–	–	1	–	–
<i>Aulacomnium palustre</i>	–	–	–	1	3	–	–	–	2
<i>Dicranum majus</i>	3	3	1	3	2	–	1	–	+
<i>D. scoparium</i>	–	1	1	–	–	2	–	3	–
Hylocomium splendens	3	5	7	4	3	4	8	9	5
<i>H. umbratum</i>	–	–	2	–	–	–	–	–	–
<i>Hypnum cupressiforme</i>	–	–	2	1	–	–	2	1	–
Plagiothecium undulatum	2	2	2	3	2	3	2	+	2
<i>Pleurozium schreberi</i>	–	–	3	2	–	3	2	4	2
<i>Polytrichum commune</i>	–	–	–	–	–	–	+	–	–
<i>P. formosum</i>	–	–	–	–	–	–	–	–	3
Ptilium crista-castrensis	1	2	3	4	+	9	3	4	4
<i>Rhytidiadelphus loreus</i>	3	1	3	–	2	–	4	2	2
<i>Sphagnum girgensohnii</i>	–	+	–	–	5	+	–	–	+
<i>S. nemoreum</i>	7	8	7	–	8	–	2	–	2
<i>S. palustre</i>	+	–	–	–	–	–	–	–	–
<i>S. quinquefarium</i>	7	–	7	–	–	–	2	+	7
<i>S. russowii</i>	–	–	–	8	–	–	–	–	–
<i>Thuidium tamariscinum</i>	3	+	2	–	2	–	–	–	–
<i>Anastrepta orcadensis</i>	–	–	–	3	–	–	–	–	–
<i>Calypogeia trichomanis</i>	–	–	–	3	3	–	2	–	3
<i>Cephalozia bicuspidata</i>	–	–	–	–	3	–	–	–	–
<i>Cephaloziella</i> sp.	–	–	–	3	–	–	–	–	–
<i>Frullania tamarisci</i>	+	–	2	–	–	–	–	–	–
<i>Herberta hutchinsiae</i>	–	+	–	–	–	–	–	–	–
<i>Leptoscyphus taylori</i>	1	–	–	4	–	–	–	–	–
<i>Lophocolea bidentata</i>	–	–	–	1	–	2	–	–	–
<i>Lophozia floerkii</i>	–	–	–	2	3	–	–	–	–
<i>L. obtusa</i>	–	–	–	–	–	–	3	–	–
<i>L. ventricosa</i>	–	–	–	2	–	–	–	3	2
<i>Mastigophora woodsii</i>	+	–	–	–	–	–	–	–	–
<i>Plagiochila asplenoides</i>	–	–	–	–	–	–	2	–	–
<i>Scapania gracilis</i>	–	–	2	–	–	–	–	–	–
<i>Cladonia carneola</i>	–	–	–	–	–	–	1	–	–
<i>C. coccifera</i>	–	–	–	–	–	–	–	2	–
<i>C. cornuta</i>	–	–	–	–	–	–	1	2	–
<i>C. floerkeana</i>	–	–	–	–	–	–	–	1	–

<i>C. furcata</i>	-	-	-	1	-	-	-	-	-
<i>C. gracilis</i>	-	-	-	1	-	-	-	-	-
<i>C. impexa</i>	-	-	-	1	-	-	-	1	-
<i>C. pyxidata</i>	-	+	-	-	-	1	1	-	-
<i>C. rangiferina</i> agg.	-	-	-	-	-	-	-	1	-
<i>C. squamosa</i>	-	-	-	-	-	1	-	2	-
<i>Peltigera horizontalis</i>	-	-	-	-	1	-	-	-	-
No. of species (60)	23	23	19	29	20	15	23	22	20
(Average 22)									

Constancy class V (species in bold type), 7; constancy class IV, 4.

LOCALITIES: 1-3, Coille na Glas Leitire, Loch Maree, Ross-shire; 4, Mullardoch, Glen Cannich, Inverness-shire; 5, Amat Wood, Bonar Bridge, Ross-shire; 6, Loch an Eilein, Rothiemurchus, Inverness-shire; 7, Glenmore, Inverness-shire; 8, Iron Bridge, Rothiemurchus, Inverness-shire; 9, Invereshie, Inverness-shire.

described in detail by Steven & Carlisle (1959), McVean & Ratcliffe (1962) and McVean (1964). The first authors recognized fourteen communities beneath the tree canopy; McVean & Ratcliffe (1962) recognized two well-defined associations, the pinewood *Vaccinium*-moss association (Table 3) and pinewood *Vaccinium*-*Calluna* association (Table 4). The former is characteristic of moderately dense (light transmission one-sixth full daylight) pine forest in the central and northern Highlands up to 500 m; it is only local in the west and frequently occurs in pine plantations. The soils are well-drained sands and gravels with raw humus and a well-developed podsol profile. In addition to *Pinus sylvestris* the constant species are *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea* and *Hylocomium splendens* or *Rhytidiadelphus triquetrus*. *Deschampsia flexuosa* and *Ptilium crista-castrensis* occasionally attain co-dominance. Tall shrubs are completely absent. Two facies have been recognized, one dominated by *Vaccinium* spp., the other by the mosses *Hylocomium splendens* or *Rhytidiadelphus triquetrus*. The second association, the pinewood *Vaccinium*-*Calluna* association, is characteristic of more open (light transmission $\frac{1}{3}$ - $\frac{1}{2}$ full daylight) forest of pine and pine/birch. It occurs throughout the range of the native pine forest in Britain up to 300 m above sea level in the west and from c. 300-600 m in the eastern Highlands, where it tends to replace the pinewood *Vaccinium*-moss association at higher elevations. The soils are podsoles with considerable accumulation of raw humus. It can occur indefinitely without a tree cover after fellings, particularly on slopes with a northern aspect. There are eight constant species; *Pinus sylvestris*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Deschampsia flexuosa*, *Hylocomium splendens*, *Plagiothecium undulatum*, *Ptilium crista-castrensis*, *Sphagnum* spp. No separate facies have been distinguished (McVean & Ratcliffe 1962). Some species occur in the indigenous pine-woods which are uncommon elsewhere in Britain; *Linnaea borealis*, *Corallorhiza trifida*, *Goodyera repens*, *Trientalis europaea*, *Listera cordata*, *Moneses uniflora*, *Pyrola media*, *P. minor* and *Ramischia secunda*. Plants such as *Salix herbacea*, *Arctous alpina*, *Saxifraga aizoides*, *S. stellaria*, *S. oppositifolia* and *Lycopodium alpinum* which are more typical of mountain than woodland habitats occur within the upper limits of the indigenous pine-woods, particularly in the west (Steven & Carlisle 1959).

IV. *Response to biotic factors.* (a) *Fire.* Scots pine is susceptible to fire, and considerable areas of indigenous pinewoods as well as many plantations have been destroyed. The trees with thick, ridge-like bark appear able to withstand ground fires better than trees (usually the older ones) with thin plated bark. The burning of heather for agricultural purposes at the margins of pinewoods destroys a great deal of natural regeneration, and is

one reason for the failure of these woodlands to regenerate successfully. See also VIII(d).

(b) *Grazing*. Damage by sheep and deer causes serious increment losses when the trees get above the ground vegetation but are not high enough for their leaders to be out of reach. Trees can rapidly replace damaged leaders (Golubinskiĭ 1951) but this response varies with provenance and locality; the indigenous pine of Scotland, even if held in check for 10 years by grazing, soon grow new leaders when grazing pressure is reduced. The grazing of the terminal buds, or disbudding by birds, is followed by the production of abnormal foliage; the scale leaves become thick, leathery, green and straplike with anatomy homologous to that of the primordial leaves on the first year plant, i.e. with one vascular bundle, a well-developed endodermis and only two resin canals. The resting buds in the leaf sheaths grow to form shoots with up to eight leaves per leaf sheath instead of two (Carlisle 1954).

(c) *Competition*. Scots pine forest is the climax vegetation on many nutrient-deficient sites, indicating its high competitive ability on these sites. It grows well on humus iron podsols or thin peats dominated by *Calluna vulgaris*, where *Picea abies* and *P. sitchensis* generally fail or go into check. It is not clear whether this is due to the pine being able to compete successfully with the *Calluna* for nutrients, or a tolerance of the species to exudates or leachates from the *Calluna*. On sites with thick litter in Russia, Scots pine seedlings do not compete successfully with *Picea abies* (Hiljmi 1954). On sandy soils in the same country, Scots pine grows best in pure closed stands, and is a complete or partial failure when mixed with various hardwoods (*Quercus* sp., *Ulmus* sp., *Salix* sp.), although it grew well for a few years (Matyuk 1949). Scots pine and birch have similar site tolerance, but on soils favourable to both species the birch gives way to pine in direct competition; the birch competes more successfully under generally adverse conditions of soil and climate (Tansley, *Br. Isl.*). Kolesničenko (1962) found that the assimilation of Scots pine (3 year) was adversely affected by the leaf and root exudates of *Betula verrucosa*. The role of biotic factors in the apparent degradation of indigenous Scottish pinewoods has been studied by Malcolm (1957).

V. (a) *Gregariousness*. Although Scots pine will grow in isolation or thinly scattered among other tree species, it is essentially a gregarious species. In the natural woodlands, where it is mixed with birch and other tree species, the mixture is generally by groups.

(b) *Performance*. Height generally 15–30 m, sometimes 46 m (Dallimore & Jackson 1948). Girths of up to 3.3 m at 1.3 m above the ground recorded in native pinewoods in Scotland (Steven & Carlisle 1959). Net Assimilation Rate (N.A.R.) relatively low when grown in soil; in the summers of first, second, third, fourth and fifth year, the mean N.A.R.s were respectively 0.44, 0.25, 0.10–0.23, 0.09 and 0.07 g/g/week and 0.36, 0.42, 0.34, 0.18 and 0.11 g/dm²/week, the latter being based on projected leaf area (i.e. essentially the product of leaf length and breadth) (Rutter 1957). At 20° C, an 18 h photoperiod, and 2.6–3.8 × 10⁴ erg/cm²/sec visible light, the N.A.R. of 2-year plants was 0.227 g/dm²/week (Jarvis & Jarvis 1964). Rutter (1957) found that Scots pine (up to 5 year) grown in soil had average Relative Growth Rates (R.G.R.) of 1.0–0.4% per day in the May–September period in favourable conditions, and 0.21–0.15% per day from October–March, the older plants having the lower rates. In sand, root spray and solution culture the Relative Growth Rate is considerably more (Jarvis & Jarvis 1964). Ovington (1957) found that the total production of dry matter/m² leaf surface/annum was 0.18 kg between the third and seventh year, declining in the following period of canopy closure and intense competition until the first thinning at 20 years, after which the production values rose to 0.20 and

0.25 kg/m²/annum at an age of 23–35 years. These latter figures are based on actual surface area of the leaves and should be multiplied by 2.57 to make them comparable with Rutter's 'single side' leaf area figures. There is no evidence of any systematic fall of N.A.R. with age (Rutter 1957; Burger 1948). In 3–55-year-old Scots pine plantations on typical Breck soils in eastern England the dry weights of root + shoot increased with age from 40 kg/ha (3 years) to 150 720 kg/ha (55 years). At 55 years the living shoots weighed 116 650 kg/ha compared with 34 070 kg/ha for the roots; the mean shoot : root ratio was 2 : 7 for all ages, tending to increase with age. The maximum dry weight of cones (1730 kg/ha) and leaves (10 480 kg/ha) and the maximum leaf area (10.79 ha/ha measured as the surface area of a leaf pair cylinder) occurred at 20 years. In 55 years, allowing for thinnings and mortality, the plantations had produced 700 000 kg/ha, i.e. mean annual production 12 727 kg/ha/annum. The current annual increments of cones (800 kg/ha/annum) and leaves (4000 kg/ha/annum) became constant after 20 years; the current annual increment of branches, boles and roots reached maxima of 4500, 9300 and 3000 kg/ha/annum respectively at about 23–29 years and then declined. The current annual increment of dry matter for the whole tree reached a maximum (22 000 kg/ha/annum) at 28 years and then declined (Ovington 1957). Leaf area indices (L.A.I.s) (i.e. leaf area one side only: ground area) of Scots pine woodlands over 20 years old vary with season but are generally 2.5–4.5 (Rutter 1957, 1967; Burger 1948; Ovington 1957), i.e. low compared with other tree species such as oak (*Quercus petraea*) and beech (*Fagus sylvatica*) which have L.A.I.s of 4.7–5.5 and 3.2–7.5 respectively (Carlisle, Brown & White 1966; Möller 1945). Although the N.A.R. of *Pinus sylvestris* is probably lower (even in the summer) than any value recorded for plants growing in natural, unshaded conditions (Rutter 1957), the dry matter production was found to be considerably more than for nearby arable crops and hay (up to 9000 kg/ha/annum). This probably reflects the trees' evergreen habit and ability to assimilate in the winter months (Pearsall 1954; Ovington 1957; Rutter 1957).

The total energy content of a 47-year-old Scots pine plantation (less thinnings) in southern England was found to be 0.83×10^9 kcal/ha (trees 0.74, ground flora 0.03, litter L + F + H 0.05×10^9 kcal/ha); thinnings contained 1.01×10^9 kcal/ha. The mean annual increase in energy content was 0.39×10^8 kcal/ha, allowing for boles removed. These values exclude tree roots. This plantation utilized 1.1% of the total radiation falling upon the canopy and 2.4% of the light energy in the 4000–7000 Å wavelength range; the peak efficiency of utilization of radiant energy was 2.2–2.6%, i.e. lower than for *Fagus sylvatica* (1.5% of total energy, 3.5% of light energy) and for some agricultural crops such as *Beta maritima* (4.2%, 9.5%) and *Hordeum vulgare* (1.9%, 4.3%) (Möller & Nielsen 1954; Watson 1958; Hellmers & Bonner 1959; Blackman & Black 1959; Bourdeau 1959; Hellmers 1964.)

The maximum mean annual stem timber increment in hoppus ft/ac/annum (Yield Class) of Scots pine is less than for most conifers used in plantations in Britain (1 hoppus ft = $1.273 \text{ ft}^3 = 0.036 \text{ m}^3$). On some sites, however, it may be more productive than *Larix decidua* Mill. and the majority of hardwood species. The average Yield Class for Scots pine in British plantations is 90–100 hoppus ft/ac/annum (1 hoppus ft/ac = $0.089 \text{ m}^3/\text{ha}$) compared with 147, 157 and 171 hoppus ft/ac/annum for *Picea sitchensis*, *Pseudotsuga menziesii* (Mirb.) Franco and *Thuja plicata* Lamb. respectively. The volume production in individual fully-stocked stands of Scots pine varies from c. 60 to 160 hoppus ft/ac/annum; some introduced conifers, such as those mentioned above, produce up to 280 hoppus ft/ac/annum. In recent years (1961–65) there has been a tendency to plant the

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more productive introduced tree species in preference to Scots pine, but the latter is still planted where there is a well-established market (Forestry Commission).

(c) *Effects of frost, drought, etc.* Scots pine is resistant to both late and early frosts (Day & Peace 1946) but damage sometimes occurs (Venn 1962), susceptibility probably depending upon provenance. There are records of severe winter damage in Sweden, the northern and upland Scots pine provenances being relatively resistant to both drought and cold (Eiche 1966). Although Scots pine has a maximum cold tolerance (see II and VIe) as low as -26.7°C (Parker 1961), it is capable of growing in sub-tropical conditions (Kaminskey-Kröger, Wilhelmi & Bergemann 1959). Relatively tolerant of drought; most susceptible to drought damage in the thicket or pole stage (Ceuca 1957; Sokolov 1961). Summer drought may reduce height increment in the following year (Vinogradov 1962) and there is some evidence that after drought there is a fall in the leaf nitrogen, phosphorus, potassium and calcium concentrations (Wehrmann 1961). Sometimes severely damaged by hail, when the injuries render it liable to infection by pathogenic fungi (Frei 1961). Subject to snow break (Hanganu 1962). Strangulation by a crust of ice above or just below soil level has caused numerous deaths of 5–15 years trees in Sweden, particularly after a winter of deep snow followed by a long thaw, or with alternative thawing and freezing (Eiche 1962). Generally wind firm on the deeper soils, but may wind blow on shallow soils where plate-like root systems have developed. Wind break may occur in severe gales where the root system is firmly anchored in rock fissures, as in the gale (163 km/h) of 31 January 1953 in Scotland (Andersen 1954). In severe winters the leaves of young (1–10 year) trees sometimes turn brown particularly on exposed elevated sites, usually followed by a decrease in growth in the following year. Susceptible to injury by aerial pollution (SO_2) (Haut 1961; Lemke 1961; Podzorov 1961; Bossavy 1962; Nosyrev 1962; Rjabinia 1962; Kisser and Halbwachs 1965, and by sea salt spray (Edlin 1957; Evison 1957) although some provenances grow well on the sea shore.

VI. (a) *Morphology.* The root system form depends upon the soil, and the method of establishment. The root system is frequently shallow and plate-like with no distinct tap root. On adjacent sites on the Pennine peats, Scots pine grown on deep blanket peat (ash content 2.8–3.2% oven-dry weight) had a root system near the soil surface while those on disturbed peat mixed with a little mineral soil (ash content 10–30% oven-dry weight) had a deep root system (Brown *et al.* 1964). Vomperskij (1959) recognized five Scots pine root system types on peats in Russia; vertical tap root with horizontal roots spread out from its lower end (depth 30–55 cm); same but with an inclined tap root (30–55 cm); system becoming horizontal at 10–20 cm depth (20–35 cm); tap root dividing into several smaller roots which soon grow horizontally (20–35 cm); no tap root (15–20 cm). The first two are most frequent on well-drained soils and the last is associated with poor drainage. Root development is prevented where conditions are reducing (Eh at pH 5.0 < 350 mV (see IIb)). Root systems on peat sites exposed to the wind are sometimes of the I-girder form (Anon. 1964). The morphology of Scots pine roots is described fully by Laitkari (1929). On the aerial shoots a terminal bud surrounded by a number of lateral buds is produced at the end of each year's growth of main axis and branches. As the buds are in whorls with no internodal buds (see p. 269) such as are found in *Pinus contorta* Loud., no internodal shoots are produced apart from the dwarf shoots associated with the leaf fascicles. Short lammas growth is produced in some years (Sokolov & Artyushenko 1957). The winter leaf colour of Scots pine from northern localities and other regions with severe winter climate is yellow-brown or violet, but in milder and more southerly regions

it is dark green; the yellow-brown winter leaf colour has been associated with frost hardiness (Busgen, Münch & Thomson 1929; Engler 1913). Scots pine growing in northern latitudes and at high elevations generally have shorter leaves than trees in southern and low-lying localities (Sylvén 1916; Münch 1924); leaf length depends to some extent upon day length (Wareing 1950a, b). The leaves generally persist for 2–4 years, but shoots which are slow growing, shaded and bearing male flowers for several years in succession may keep their leaves for up to 9 years (Borthwick 1906; Sylvén 1916; Steven & Carlisle 1959). Trees in northern regions tend to keep their leaves longer than those in southern localities, the former keeping their leaves for the same period when transplanted in the south, suggesting that the character is at least partly genetically controlled (Holmerz & Ortenblad 1888; Sylvén 1916). Trees growing in adverse conditions tend to keep their leaves for a shorter period (1–2 years) than vigorous trees. Leaf retention is of importance as normal spring growth depends upon the presence of a full complement of old leaves (Newirth 1959), probably owing to the utilization of reserves in these leaves (Rutter 1957); the leaf area available for photosynthesis will obviously be greater on trees which retain their leaves longer, although the older leaves are less efficient in this respect (Freeland 1952).

(b) *Mycorrhiza*. Possesses both ectotrophic and endotrophic mycorrhizas (Laing 1923, 1932); mycorrhizas dichotomously branched as in other *Pinus* species in contrast to the racemose systems of other tree genera. Exhibits marked heterorhizy; sheath and Hartig net become fully formed ectotrophic mycorrhizas usually only in short roots. Long roots may become infected but do not develop a sheath (Harley 1959). Trappe (1962) lists 118 species of fungi observed to form mycorrhizal associations with *P. sylvestris*; twenty-seven of these (three spp. *Amanita*, one sp. *Coenococcum*, one sp. *Clitopilus*, two spp. *Cortinarius*, two spp. *Lactarius*, one spp. *Lyophyllum*, two spp. *Rhizopogon*, one sp. *Rhodophyllum*, one sp. *Russula*, one sp. *Scleroderma*, five spp. *Suillus*, seven spp. *Tricholoma*) form the mycorrhizas in pure culture. The classification, physiology and development of these mycorrhizas are discussed in the works of Melin (1923, 1962), Hatch & Doak (1933), Björkman (1940), Robertson (1954), Melin & Nilsson (1958), Slankis (1958) and Harley (1959). Dominik (1961) found that if Scots pine seed is germinated on an agricultural soil mycorrhizal fungi become parasitic on the pine seedling host reducing the latter's growth. Transplants raised in good forest nurseries developed a satisfactory symbiotic relationship with the fungi and were able to grow well on the agricultural soils, particularly if the planting hole was inoculated with pine forest soil from the A₁ horizon. Scots pine seed germination can be inhibited (Bokov 1956) by specific water soluble substances produced by the mycelia of mycorrhizas when these are abundant, for example in old closed Scots pine stands. Although there is evidence that nitrogen fixation occurs in the presence of *Rhizopogon roseolus* Dodge on the root systems of *Pinus radiata* (Richards & Voigt 1964), this has not been demonstrated for *P. sylvestris* (Bond & Scott 1955).

(c) *Perennation; longevity; reproduction*. An evergreen megaphanerophyte; sometimes a mesophanerophyte. Reproduces entirely by seed, but cuttings can be rooted (Runquist & Stefansson 1951). The oldest Scots pine recorded in Britain was 395 years old (Steven & Carlisle 1959); trees slightly older than this occur in Germany (Wohlfarth 1960). In the indigenous Scottish pinewoods most trees are less than 200 years old. Seed is set in most years; moderate or good seed years occur about every 4–6 years but this varies with locality. Seed may be set on trees as young as 6 years. Male inflorescences produced at about 10–15 years of age. In southern England cone production was found to reach a maximum of c. 0.6 kg/ha/annum at 20 years, thereafter remaining more or less constant up to 55 years (Ovington 1957). In 60–70-year-old Scots pine woodlands in Scotland, the

trees produced 229–315 mature cones/tree/annum in good seed years and only 11–23 cones/tree/annum in the intervening years (McNeill 1954).

(d) *Chromosomes*. The haploid (or gametic) chromosome number is twelve (Sax & Sax 1933; *Chr. Atl.* 1955). Langlet (1934) found that this number remained constant in different provenances throughout the north–south geographical range of the species. Karyotype analysis of Swedish Scots pine (Natarajan, Ohba & Simak 1961) has shown that all the chromosomes are median constricted, and consist of two short chromosomes (12–14 μ) without satellites, eight medium-sized chromosomes (16–19 μ) of which three pairs have satellites, and two long chromosomes (20–21 μ) with satellites. A karyotype variant with only three pairs of the chromosomes having satellites and more short chromosomes has been recorded in Russia (Pravdin 1964).

(e) *Physiology*. (i) *Photosynthesis*. The rate of photosynthesis in *P. sylvestris* is low compared with many broad leaved trees. Average rate (Polster 1950) is 9.2 mg of CO₂ absorbed per gram (fresh weight) of needle per day. The rate varies with needle age, reaching a maximum (1.4 mg CO₂/100 leaves/h) towards the end of the first year, falling to 1.0 mg CO₂/100 leaves/h in the third year (Freeland 1952; Stålfelt 1924). At low illumination intensities (30% of full light) however, the 3-year-old needles have the highest rate. Similarly, shade leaves have a lower compensation point than sun leaves (Stålfelt 1921, 1924). Monsi (1960) has calculated that seedlings can survive if the light intensity is equal to or greater than 12% of full daylight. Full light intensity (64 100 ft-candles) gives maximum photosynthetic rate per leaf (Decker 1954), unlike many deciduous trees which have a maximum rate at less than full light. Similarly, the often marked mid-day drop in rate seen in other trees is negligible in *P. sylvestris* (Polster 1950). It photosynthesizes for at least part of the winter. In southern England, young *P. sylvestris* trees (3–4 years) increased in dry weight during the winter months by amounts up to 50% of the weight at the beginning of the winter (Rutter 1957). Whilst various workers have demonstrated net photosynthesis at temperatures below freezing (e.g. Freeland 1944, down to –6° C), others found no photosynthesis through much of the winter (e.g. Bourdeau 1959). Parker (1961) concludes that the ability to photosynthesize during cold weather falls off to a minimum by about February, associated with changes in the chloroplasts. Eventually net photosynthesis becomes negative and such plants need a period of between a few hours and a few days to regain their ability to photosynthesize when moved to a warmer environment. However, those kept in a warm glasshouse continued net photosynthesis at a relatively high rate when placed outside during the winter. The internal changes brought about as a response to long exposure to cold preclude photosynthesis rather than low temperatures *per se*. Whether or not net assimilation continues in Scots pine during the winter will thus depend on the degree of exposure to prolonged cold. Apparently this is insufficient in southern England. Parker also found that the loss of photosynthetic ability is associated with reduction in transpiration and an increase in winter hardiness (this did not apply to other species he studied). Growth in the spring is initially dependent on stored materials in the rest of the tree, including the older needles (Rutter 1957). Newirth (1959) showed that at the beginning of shoot growth respiration exceeds photosynthesis, and that a full complement of old needles is necessary for normal flushing. Mean respiration rates (Polster 1950) are 7.9 mg of CO₂/g fresh weight/day; CO₂ evolution from the roots varies from 48.4 to 62.3 mg of CO₂/g dry weight/day according to the (European) provenance (Eidmann 1943). For a discussion of photosynthetic and respiratory activity and N.A.R.s see Rutter (1957) and section V(b).

(ii) *Photoperiodism*. In Scots pine the photoperiod affects the duration of growth,

internode length, leaf number, leaf length and cambial activity (Wareing 1950a, b, 1951). In general, short days curtailed growth and hastened the onset of dormancy whereas long days prolonged duration of activity or increased the rate of growth or both (Wareing 1951). Increased height growth in longer days is brought about by an increased extension of the existing internode initials in the bud (Wareing 1950b). However, further growth can be produced at day lengths of 16 h or more by a continuous re-flushing process in which new internodes extend soon after they are laid down (Downs & Borthwick 1956). Similarly, summer dormancy can be broken by application of long days of 18–20 h (Wareing 1951). The ease with which long-days can break dormancy decreases in the autumn, and in the winter unchilled plants can only break dormancy with difficulty. Under natural conditions following a period of winter chilling, day length appears to be of no importance in breaking dormancy in the spring (Wareing 1951). Downs & Borthwick (1956) and Jensen & Gatherum (1965) have shown complex interactions between temperature and day-length. At the longer day lengths of 16–20 h height growth was greater at 13.3° C than at 21.7° C, whereas at 12 h day length the higher temperature led to the greater height (Jensen and Gatherum 1965). Needle length is reduced by short days (Wareing 1950b). Cessation of cambial activity is directly controlled, at least to some extent, by the shortening days of autumn. However, onset of cambial activity in the spring occurs when day length is no greater than that associated with cessation of activity in the autumn, and appears to be dependent on the development of new shoots (Wareing 1951). The provenance affects the photoperiodic response of Scots pine (Vaartaja 1954; Wettstein-Westersheim & Grull 1954; Jensen & Gatherum 1965). An increase in numbers of both male and female flowers under long-day conditions is reported by Wareing & Longman (1960). The onset of shorter days in the autumn is a contributory cause of winter hardening (Parker 1961).

(iii) *Temperature*. For normal growth and development, *P. sylvestris* requires a period of winter chilling to break the autumn dormancy (Wareing 1951). Extension growth then starts when temperatures reach about 5° C. It is difficult to determine an optimum temperature as many other factors interact with it, and the difference between night and day temperatures may well be important as it is with other species of pine. However, Jensen & Gatherum (1965) give 18.5° C as an optimum, above which under their experimental conditions growth was reduced. Owing to the fact that extension growth depends on the extension of internodes already formed in the bud in the preceding season (Wight 1933), the temperature of the previous year is also relevant in determining extension growth. Mikola (1962) found that, for the northern parts of Scots pine's distribution at least, the closest relation was between height growth and temperatures in the preceding summer. Needle growth increases with increasing temperature (Jensen & Gatherum 1965) and thus can be related directly to current season's temperatures (Mikola 1962). Leibundgut & Dafis (1964) found root growth starts when mean soil temperature reaches 12° C, with shoot growth 16–18 days later. (Glasshouse data; results seem atypical.) Root growth throughout the season was closely related to maximum daily air temperatures. The optimum temperature for the growth of detached roots is 18–19° C (Slankis 1949). The maximum temperatures which seedlings can tolerate for 2–4 min is given by Kayll (1963) as 60° C. The lower limit of temperature varies throughout the year and appears to be dependent upon pre-conditioning (or hardening) by both temperature and day length. At its lowest, in January and February, seedlings can withstand temperatures down to –26.7° C (Parker 1961), but unhardened plants will be killed by considerably less cold (see II). Tumanov and Krasavčev (1955) also describe the relation

of temperature to hardening off and de-hardening in Scots pine. The effects of frost are given in section V(c).

(iv) *Nutrition*. Ingestad (1962) has given a comprehensive account of the nutrition of Scots pine, mainly based on nutrient solution culture experiments. He gives optimum foliar nutrient concentrations (% dry weight) for maximum growth as: N 2.4–3.0; P 0.15–0.40; K 0.9–1.6; Ca 0.04–0.30; Mg 0.12–0.18 and S 0.20–0.25. Although it has fairly high requirements of nutrients for maximum growth, especially for nitrogen, potassium and sulphur, Scots pine is very tolerant of a low level of nutrition, and growth is not markedly reduced over a fairly wide range of nutrient supply. This is particularly true for calcium, for which the supply concentration can be varied over a 40 000 fold range without reducing growth more than 50% of the maximum. Under field conditions of adequate growth, foliar nutrient concentrations, particularly for nitrogen, can be somewhat lower than these optima. However, nutrient deficiency symptoms become visually apparent and growth markedly reduced when the foliar concentrations (% dry weight) drop to or below the following levels; N 0.7–1.6; P 0.06–0.10; K 0.3–0.4; Ca 0.05; Mg 0.06–0.09 and S 0.07 (Nemec 1942; Tamm 1956; Wittich 1958; Goor 1961; Ingestad 1962). The visual symptoms of deficiency in the various elements are (Ingestad 1962; Goor 1961):

N, Needles paler and smaller, yellow-green.

P, Needles dull bronze-green, or darker green.

K, Yellow needle tip merging gradually into a yellow-green or green base.

Mg, Yellow needle tip with abrupt transition to green base.

Ca, Young needles chlorotic and faded at tips becoming brown tipped.

Colour pictures of these deficiency symptoms have been published (Brüning 1959; Goor 1963). The discoloration of Scots pine foliage, however, commonly occurs in certain provenances in the autumn in which shortening day length, lower light intensity and lower temperatures all influence the process (Gerhold 1959). Ingestad suggests that the ranges he has given for optimum foliar concentrations are of sufficiently general applicability to use needle analysis as a reliable diagnostic tool under field conditions. Using such an approach, various cases of nutrient deficiencies in Scots pine plantations have been reported, particularly on the poorer peats. Such deficiencies usually become marked in plantations which are reaching the age of maximum nutrient uptake, i.e. 20–30 years old. Under the severe climatic conditions associated with high elevations, however, marked potassium deficiency has been reported within a few years of planting (Brown *et al.* 1964). Under conditions of poor aeration, the trees' ability to take up most nutrients (particularly nitrogen) is impaired (Hotjanovič 1958; Brown *et al.* 1966). Under conditions of low nutrient availability, the presence of mycorrhizas can have a markedly beneficial effect on nutrient uptake (Harley 1959; Ingestad 1962). Scots pine makes its greatest demands on a site when between 20 and 35 years old (Morosow 1928 in Leyton 1958). The annual uptake of a managed plantation was found to fall off after about 20 years for N, P, Ca and Mg and a little later for Na and K (Ovington 1959a). Although much of this annual uptake was annually returned to the forest floor as litter, where the needles take up to 10 years to decompose (see IIb), there is a gradual accumulation of nutrients in the standing crop. A 55-year-old plantation in south-east England was estimated to contain the following total quantities of nutrients (kg/ha) in the trees: N 453; P 41; K 150; Mg 64; Ca 272 and Na 36 (Ovington 1959a).

(v) *Storage materials*. Scots pine, as with other pines, is said to store food predominantly as fats (oils) rather than as starch (Kramer & Kozlowski 1960). These authors show data

from Arrhenius (1942), giving the late winter fat content in Sweden as between 6–7%; with the onset of growth during early summer this falls to around 2%. However, the starch content of various parts of the trees has been shown to vary through the year in relation to the trees growth (Wight 1933; Rutter 1957) apparently also acting as a storage material. Ziegler (1964) concludes from measurements of respiratory quotients in Scots pine branches that starch is converted to fat in proportion to the lowering of the temperature in winter. Conversely fat is changed to starch as temperatures rise. Fat content of the bark was higher than that of the wood (bark 10.9%, wood 2.58%, for the spring sample).

(vi) *Turpentine*. Turpentine is the volatile part of the resins produced by pines as the end products of certain metabolic processes (Mirov 1958; Lvov 1954), and apparently serves no further essential functions. Commercial tapping of Scots pine for turpentine is practised, especially in Eastern Europe. Different physiological races of Scots pine may contain turpentines of somewhat different composition (Mirov 1958), but typically they contain mainly α -pinene, some β -pinene and small quantities of Δ^3 -carene, limonene, terpinolene and dipentene (Bukala & Kuczynski 1952; Bardyšev *et al.* 1950). The specific optical rotations of these substances vary considerably (Šjolaja 1951).

(vii) *Aeration of the substratum*. Reduced aeration of the rooting zone reduces root respiration and hence also amino-acid content, but causes a build up of carbohydrates. At the same time nutrient uptake is reduced, particularly of nitrogen (Hotjanovič 1958, 1959; Brown *et al.* 1966). Complete removal of oxygen causes root elongation to cease; young Scots pine seedlings are killed within 2 days, older plants withstanding anaerobic conditions somewhat longer (Leyton & Rousseau 1958) (see IIb).

(viii) *Water relations*. Scots pine canopies intercept 20–33% of the rainfall, but this varies with rainfall intensity, potential evaporation, age of stand and leaf area. Maximum interception occurs on average at about 35 years of age, decreasing in older stands. The water needed to saturate the canopy is equivalent to 0.14–0.18 cm of rainfall. In 64-year-old Scots pine stands in Russia the maximum stem flow was 2% of the total rainfall, but in a young (16 year) plantation in south-east England with 4600 stems/ha it was 15–30% of the throughfall (Krečmer & Fojt 1960; Molchanov 1960; Rutter 1963). According to Hartel & Eisenzopf (1953), absorption of water through the needles is greatest in younger needles, reaching a maximum at 2 years. It also increases with height of needle up the tree and the apical position on the branch. Absorption is lowest in winter. Leyton & Juniper (1963) showed that the water absorbing capacity per unit area of the needle bases below the sheath (on the adaxial surface) was more than three times that of the rest of the leaf. Although this may well be of importance under drought conditions, Rutter (1963) concluded that negligible quantities were absorbed through the needles compared with the large quantities of intercepted water which were re-evaporated. Various measurements of transpiration rate have been made. Ivanov *et al.* (1951) found a good linear relation between transpiration and temperature, with 103 mg water transpired/g (fresh weight) foliage/h at 12° C, and 183 mg at 20° C, under conditions of adequate soil moisture. On a daily basis, Polster's (1950) estimate was 1.88 g/g (fresh weight) foliage/day, calculated as equivalent to 0.235 cm of rain transpired/day. Total annual estimates of transpiration for stands (as equivalent depth of rain) vary from 5.0–30.5 cm (Raber 1937) to 36.1 for a 33 year stand and 20.3 cm for a stand of 150 years (Ivanov *et al.* 1951). See also Eidmann (1961) and Koščeev (1952). On deep soil with high storage capacity, the transpiration rate is only reduced below that which occurs when the soil is near field capacity when conditions are exceptionally dry. The critical soil water deficit appears to be 22 cm (Rutter 1967). Transpiration may be reduced more often on shallower soils. Rutter & Fourn (1965)

have shown that plantations of Scots pine (20–32 years old) have a potential evaporation rate in general about 1.2 times that of the calculated (Penman 1956) evaporation rate of open water, although this varies seasonally according to the pattern of rainfall. Transpiration through the cuticle of Scots pine needles is low, e.g. 1.53 mg per g fresh weight per hour, i.e. 1–2% of the total transpiration figures given above (Stålfelt 1956; Pisek & Berger 1938); it is lowest in winter (Hartel & Eisenzopf 1953).

The transpiration ratio (i.e. the weight (g) of water transpired while 1 g of dry matter is produced) varies from 213 to 306 (Eidmann 1961; Raber 1937). The significance of this ratio is doubtful as there is no causal relationship between water transpired and dry matter produced. The effects of drought are described in section V(c).

VII. *Phenology*. Roots and shoots begin to grow in late March to April in Britain, but this may be delayed to early May in northern Scotland and at high elevations. Root growth begins before shoot growth (just before bud break), reaches a maximum during the summer and decreases in August and September (Rutter 1957; Leibundgut & Dafis 1964; Wareing 1958); it usually ceases in the autumn but there is evidence that there is sometimes a slight increase in root growth just before winter, root growth continuing slowly throughout the winter if conditions are mild (Borthwick 1906). Rutter (1957) observed that the extension of young Scots pine (2–5 year) in southern England had virtually ceased by the second half of June. There is evidence (Wareing 1958) that when shoot growth begins, root growth ceases but is resumed later. On a peat site at 549 m in the Pennines, shoot growth began as late as early May (mean air temperature 9.9° C, mean soil temperature at 5 cm depth 6.9° C, day length 15 h) continued rapidly until the end of June (air temperature 6.8° C, soil temperature 10.1° C, day length 17 h) after which it declined until it ceased at the end of July (air temperature 11.50° C, soil temperature 10.7° C, day length 16 h) (E. J. White). The growing season was 80 days compared with 138 days for *Betula pubescens* on the same site; in southern England, however, the mean growing season of Scots pine is 61 days (Mitchell 1965) a difference which can be explained in terms of temperature and day length (see Vc). The ratio of shoot extension in the day to extension at night tends to be lower (0.9) than for many tree species (usually > 1) (Danilov 1954). After bud break there is a period when there is no gain in plant dry weight, even though the roots and shoots are growing; at this time the previous season's leaves' weight decreases. Later, in May and June, the main increase in the weight of the plant is in the new shoot, but in August and September the assimilates are more evenly divided between the new shoots and the old shoots and roots. Radial growth of the stem begins at bud break (April) and persists to October; there is some evidence of a small decrease in stem diameter in the winter. Leaf extension begins at the end of May, about 3–6 weeks after bud break and the initiation of shoot extension, and ceases in late July or early August (Rutter 1957). Growth in leaf length is completed in the first year, but increases in leaf thickness have been observed in 2- and 3-year-old leaves (Borthwick 1906). The concentrations of nutrients in the leaves vary with season; nitrogen, phosphorus and potassium are at a minimum in early summer and reach a maximum in late autumn and winter (Tamm 1955).

Female inflorescences develop in the mid May-early June period from the whorl of lateral buds at the apex of the current year's new shoot. The male flowers appear at the base of current year's shoots on the older branches when the buds open in early spring. Anthesis takes place about June and the female flowers are pollinated, but fertilization is delayed until the following spring (Borthwick 1906). Ripe seeds are released from the

mature cones 9–12 months after fertilization and, if the substratum and environment are favourable, germinate within 10 days. As the female cones take 2 years to mature, it is possible to forecast a good seed year 12 months in advance. Wareing (1957) describes the development of the male and female inflorescences in detail. Details of fertilization and embryo development are given by McLean & Ivimey-Cook (1951) and Bonner & Varner (1965).

VIII. (a) *Flora biology*. Although generally monoecious, mature trees occasionally bear only male or only female flowers, but how long this state persists is not known. Male inflorescences mostly arise on older shaded branches of relatively low vigour; female inflorescences tend to be most frequent on the more vigorous, well-illuminated shoots. Reproduction is amphimictic. Anemophilous, the pollen is caught by a drop of fluid on the ovule micropyle which draws the pollen grain towards the nucellus as the drop dries. Self pollinated cones usually have fewer developed seeds with a lower germination percentage than cross pollinated cones. There is some evidence of parthenocarpy, the cone scales and seed wings (but not the seeds) developing without fertilization (Forshell 1953). Sexual dimorphism has been recorded (Galpern 1949; Sylven 1916; Mušketik 1960). The authors have noted two cases of polyembryony, two seedlings developing from one seed.

(b) *Hybrids*. Scots pine crosses with some difficulty with *Pinus montana* Mill., *P. banksiana* Lamb., *P. contorta* Dougl., *P. murrayana* Balf., *P. patula* Schlecht. & Cham., *P. radiata* D. Don, *P. palustris* Mill., *P. pinaster* Ait. and *P. densiflora* Sieb. & Zucc. (Dengler 1939; Richens 1945; Schreiner 1949; Johnsson 1951; Schmidt 1956; Jamblinne 1957). There is no definite evidence of hybridization in natural conditions.

(c) *Seed production and dispersal*. Five to forty seeds per cone; number of seeds per cone, mean seed size and percentage of empty seeds is positively correlated with cone size and dry weight (Šimák 1953, 1960; Daškevič 1961). Mean seed weight for indigenous Scottish pinewoods 4.96 g per 10^3 seeds (Steven & Carlisle 1959); varies from 4.0 to 6.7 g per 10^3 seeds in Europe (Rafn 1915; Hickel 1911). Forty-five kg cones yield 0.9 kg seeds (Anon 1948). Seed yields of 2.6 and 10.0 kg/ha/annum have been recorded in Scots pine stands in Europe (Starčenko 1959; Heikinheimo 1932). Various methods (girdling, root pruning and glucose injection) have been used in attempts to improve seed production by promoting the accumulation of carbohydrates and minerals in the crown, but with little success. The most promising results have been obtained by thinning and fertilizer treatment (Hausser 1960; Girgidov 1960; Bergman 1955). There is some evidence that a high water deficit in the summer is favourable for the differentiation of female buds (Girgidov 1960). Hyde (1951) noted that there was a correlation between the production of pollen and the quantity of seed produced in the second autumn afterwards. If this is the case, it could be a useful means of forecasting good seed years. The winged seed is dispersed by wind and can travel as far as 810 m (Smith 1900) or further if blown over a hard snow or ice surface. The seeds (Denham 1921) fall at a rate of c. 0.72 m/sec and a 25 km/h wind would blow the seed 187 m. The seed can remain afloat on water for 1–4 weeks and be transported long distances on rivers (Ridley, *Disp. Plts.*). It is probably transported by animals and birds to a certain extent.

(d) *Viability of seeds; germination*. There are great variations in the germinative power of the seeds related to provenance, date of collection, cone size, tree age, position of cone in the crown and seed colour (Stone 1958). Germination may be as high as 99% (Hickel 1911; Anon. 1948); seed from eleven indigenous pinewoods in Scotland had 65–95

(mean 85) % germination. Seeds from large or medium sized cones germinate better than those from small cones (Kočkarj 1950). Dark-coloured seeds generally have better germination than those of light colour (Baldwin 1942). Rehackova (1954) reports a rhythm of germinative capacity throughout the year, with spring and autumn peaks. The numbers germinated in a given time varied little with season. Vaartaja (1950, 1956) found better germination from covered than uncovered seed, but several workers have demonstrated the beneficial effects of light on germination (Sarvas 1950; Jones 1961; Huss 1961; Nordström 1953). Nyman (1963) observed that under conditions of dry, dark storage, Scots pine seed had an irradiation requirement to ensure rapid germination. Six h imbibition of water together with 24 h irradiation, or continuous irradiation through germination gives the best results, though a marked increase in both germination capacity and speed follow 24 h irradiation of the dry seeds. Red light is the most effective and the effect lasts (decreasingly) for about 2 years. Complete or partial removal of the seed coat eliminates the requirement for light, as also does moist storage for a few weeks. These dormancy breaking requirements are satisfied by normal handling and sowing methods. Under British conditions other pre-treatments such as soaking in water or dilute acids are unnecessary (Holmes 1950, 1952). The European and American literature however, suggests that under their conditions a variety of pre-treatments is beneficial (Bergman 1960; Šimák & Gustafsson 1957; Miegroet 1952; Kapost 1964) although Zentsch (1958) found no significant increase in germination per cent following three methods of stratification. Some extreme northern continental provenances are said to benefit from stratification (Anon. 1948). Ğorĝeva (1959) found that Scots pine seed germinates best at a temperature of 20–25° C. If the seeds are soaked they can withstand subsequent drying so long as the radicle tip has not emerged (Rohmeder 1951). Scots pine seed can be stored for many years if kept at a constant moisture content (below 5–8%) in sealed containers under cool conditions (c. 2° C). Such seed retains its germinative capacity of 97% for 4 years, and remains usable for at least 15 years. Seed of northern provenance keeps better than that of southern provenance (Holmes & Buszewicz 1958).

The conditions needed for natural establishment of seedlings have been discussed in detail in the literature (Macdonald 1952; Steven & Carlisle 1959; Henman 1961; McNeill 1954, 1955; Jones 1947; MacVean 1961a, b, 1963a, b). In general, successful natural regeneration arises on sites which are open or under a light tree canopy and which have a discontinuous layer of raw humus or shallow peat overlying well-drained mineral soils and have ground vegetation which is not luxuriant (usually *Calluna vulgaris*), an adequate seed supply within c. 90 m and the absence of heavy grazing. The nutrient requirements are discussed elsewhere (Ve). In the indigenous pinewoods regeneration generally arose when catastrophes such as ground fire (which burned off part of the humus mat, destroyed competing vegetation, and released nutrients), and wind blow (which disturbed the soil) coincided with good seed years.

(e) *Seedling morphology*. Germination epigeal. The radicle emerges from the micropyle and the hypocotyl extends bearing the emerging cotyledons (and generally the seed itself) above the soil's surface. The cotyledons are fully developed in 10–16 days, and vary in number from three to ten (usually five to six) (Steven & Carlisle 1959).

The question of whether or not *Pinus sylvestris* is truly polycotyledonous, or whether the several cotyledons are derived from the division of two original cotyledons or the inclusion of one or more foliage leaves has been debated for more than a century (W. S. Lacey). At present Scots pine is usually regarded as polycotyledonous. The different views are presented by Hill & Fraine (1909), Bucholz (1919) and Doak (1935). There is

some evidence that Scots pine, in common with some other *Pinus* species, forms a cotyledonary tube (Hill & Fraine 1909). The apical bud develops to form a shoot bearing juvenile or primordial leaves. Bifoliar fascicles with their bases enclosed in membranous sheaths develop in the axils of the primordial leaves to form the adult foliage 8–10 months after germination (Fig. 3). In subsequent years the primordial leaves are reduced to brown scales and all the foliage produced by the plant is in the form of the bifoliar shoots of limited growth produced in the scales' axils.

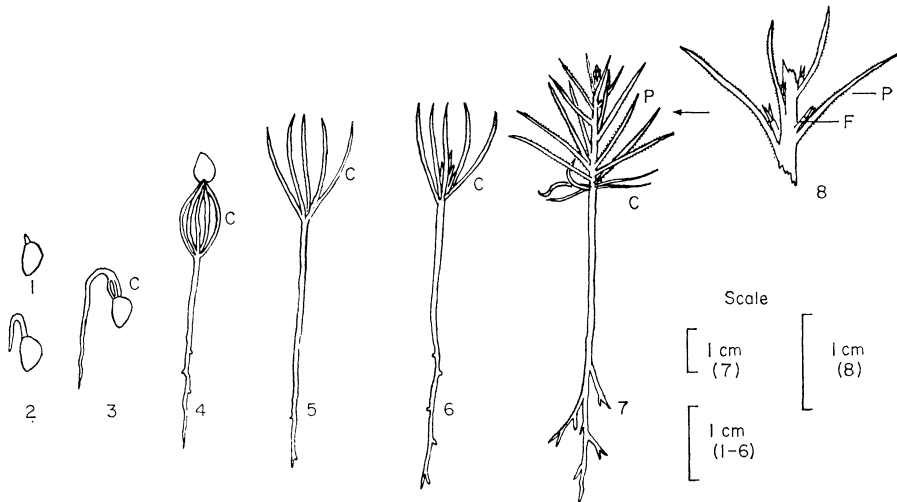


FIG. 3. The development of the *Pinus sylvestris* L. seedling in the 6–8 months following germination. C, cotyledons; P, primordial leaves; F, bifoliar fascicles. The numerals 1–8 represent the sequence in time.

IX. (a) *Animal feeders or parasites.* The leaves, shoots and bark of Scots pine are, in common with those of other tree species, eaten by sheep, deer, rabbits, hares and squirrels in Britain, the latter species also eating the seed. Small rodents such as *Microtus agrestis* (L.) will sometimes eat young pine stems and roots near the soil surface. Capercaillie (*Tetrao urogallus urogallus* L.) and black grouse (*Lyrurus tetrix* L.) eat the leaves, buds, and young cones of Scots pine and may cause appreciable damage locally; cross-bills (*Loxia curvirostra scotica* Hartert) feed on the seeds (Anon 1956a). The following list of invertebrate fauna associated with and feeding on Scots pine is not necessarily complete.

ACARINA

Oligonychus unguis (Jacobi) occurs in Britain and feeds on the leaf bases sometimes causing premature leaf abscission (D. Macfarlane). *Phytoptus pini* Nalepa produces branch galls and is widely distributed in Western Europe, and has been recorded in Britain (Swanton 1912; Connold 1909; Pritchard & Baker 1955; D. Macfarlane).

INSECTA (O. W. Richards)

HEMIPTERA

Many species occur on Scots pine, but it is not always clear if they feed upon the plant or upon associated insects. Most occur on many other hosts but some, such as *Gastrodes grossipes* (Degeer), *Phoenicocoris obscurellus* (Fallen), *Orthops rubricatus* (Fallen), *Bothynotus pilosus* (Boheman), *Pilophorus cinnamopterus* (Kirschbaum), *Pleisiodema*

pinetellum (Zetterstedt), *Phytocoris pini* (Kirschbaum), *Atractotomus magnicornis* (Fallen), *Matsucoccus pini* (Green) appear to prefer Scots pine as a host; *Orthotylus fuscescens* (Kirschbaum) appears to live exclusively on Scots pine, at least in Britain (Butler, Hem.-Het.; Kloet & Hincks 1945, 1964).

HOMOPTERA

Mindarus abietinus Koch, *Schizolachnus pineti* (Fabricius), *Cinara pinea* (Mordv.), *C. pini* (Linnaeus), *Neochmosis pinicola* Kaltenbach and *Pineus pini* (Gml. in Linnaeus) all feed on the foliage and young shoots of Scots pine and other conifers in Britain, the latter species sometimes being a serious pest on young trees. *Cinara pini* (Linnaeus), *Psylla hartigi* Flor and *Protolachnus agilis* Kalt also occur on Scots pine, but whether or not they feed on it is not known (Theobald, Aphid. 3; Chrystal 1944; Edwards, Hem.-Hom.; Schwerdtfeger 1957; Kloet & Hincks 1964).

LEPIDOPTERA

Feeding on Scots pine leaves. *Bupalus piniarius* (Linnaeus), *Cedestis gysselinella* (Duponchel), *C. farinatella* (Zeller), *Hyloicus pinastri* (Linnaeus), *Batrachedra pinicolella* (Zeller), *Epinotia rubiginosana* (Herrich-Schaeffer), *Ocnerostoma piniariella* (Zeller), *Panolis flammea* (Hübner), *Lymantria monacha* (Linnaeus), *Petrova resinella* (Linnaeus) and *Zeiraphera diniana* (Guenée). Only *Bupalus piniarius* sometimes causes serious damage in Britain; *Panolis flammea* and *Lymantria monacha* are serious pests on the continent of Europe, but cause little damage in Britain.

Feeding on shoots and/or buds. *Exoteleia dodecella* (Linnaeus), *Pseudococcyx posticana* (Zetterstedt), *P. turionella* (Linnaeus), *Rhyacionia pinivorana* (Zeller), *R. buoliana* (Schifferrueller), *R. pinicolana* (Doubleday) and *Eulia ministrana* (Linnaeus). Only *Rhyacionia buoliana* causes serious damage in Britain by distorting stems; *Pseudococcyx turionella* does a certain amount of damage by causing stem forking.

Feeding on Scots pine cones. *Laspeyresia conicolana* Heylaerts, *Olethreutes decrepitana* (Herrich-Schaeffer), *Dioryctria abietella* (Schifferrueller), and *D. mutata* Fuchs; not serious pests.

Feeding on Scots pine bark. *D. splendidella* Herrich-Schaeffer, *Laspeyresia cognatana* Barrett, *L. coniferana* (Saxesen) and *L. cosmophorana* (Treitschke); not serious pests. (Chrystal 1944; Ford 1949, 1958; Croke 1951; Anon. 1962, 1956b; Heslop 1964; Bevan 1966; J. Heath).

COLEOPTERA

The bark beetles (Scolytidae) *Anisandrus saxeseni* (Ratzeburg), *Cryphalus abietis* (Ratzeburg), *Hylastes angustatus* (Herbst), *Hylurgops palliatus* (Gyllenhal), *Ips sexdentatus* (Boerner), *I. typographus* (Linnaeus), *Dryocoetes autographus* (Ratzeburg), *Pityogenes bidentatus* (Herbst), *P. chalcographus* (Linnaeus) and *P. quadridens* (Hartig) feed on stem bark and cambium and occur in Britain on Scots pine and other conifers. The weevil *Hylobius abietis* Linnaeus also feeds on the same materials. Of these only *H. abietis*, *Pityogenes bidentatus* and *Hylastes angustatus* cause appreciable damage. Bark beetles with an apparent preference for Scots pine in Britain are *Pityophthorus lichtensteini* (Ratzeburg), *Onthotomicus suturalis* (Gyllenhal), *O. laricis* (Fabricius), *Ips acuminatus* Gyllenhal, *Hylastes ater* (Paykull), *H. attenuatus* Erichson, *H. opacus* Erichson and *Pityophthorus pubescens* (Marsham); the first two of these are uncommon, but the latter four are quite serious pests locally. Beetles feeding on the stems of Scots pine and other conifers in Britain causing appreciable damage by shoot pruning and loss of foliage are

Myelophilus piniperda (Linnaeus), *M. minor* (Hartig), *Pissodes castaneus* (Degeer), *P. pini* (Linnaeus) and *P. validirostris* Gyllenhal. Scots pine is the principal host of the *Myelophilus* species; *Pissodes notatus* larvae also eat the young cones. The weevil *Brachonyx pineti* Payk. feeds on Scots pine leaves in Britain, but does not cause serious damage in this country; in Norway, however, it has caused extensive damage. Longhorn beetles which feed on the stem timber of Scots pine are *Rhagium mordax* (Degeer), *R. bifasciatum* Fabricius, *Hylotrupes bajulus* (Linnaeus), *Criocephalus rusticus* (Linnaeus), *Asemum striatum* (Linnaeus) and *Acanthocinus aedilis* (Linnaeus). None of these is a serious pest in Britain (Munro 1926; Chrystal 1944; Anon. 1946; Anon. 1952; Bakke 1958; Steven & Carlisle 1959; Anon. 1960a; Bevan 1962; Fowler, Coleopt. 4; D. Macfarlane).

HYMENOPTERA

The saw flies (*Acantholyda erythrocephala* (Linnaeus), *Diprion pini* (Linnaeus), *D. similis* (Hartig), *Neodiprion sertifer* (Geoffroy), *Gilpinia frutetorum* (Fabricius), *G. pallida* (Klug), *G. virens* (Klug) and *Microdiprion pallipes* (Fallen) all feed upon Scots pine leaves in Britain; *Xyela julii* Brébisson feeds upon the staminate flowers. *Xyelatana piliserra* Thoms. occurs on Scots pine in Scotland; habits probably similar to *Xyela julii*. *Diprion pini* and *Neodiprion sertifer* cause severe defoliation but rarely cause tree deaths in Britain; they are serious pests on the continent of Europe (Anon. 1955). The wood wasps *Sirex cyaneus* (Fabricius) and *Urocerus gigas* (Linnaeus) sometimes cause appreciable damage to Scots pine and other coniferous trees in Britain by boring in the stem timber (Chrystal 1944).

DIPTERA

There are many species of gall midges on pines in America but only *Cecidomyia pini* (Degeer) and *Thecodiplosis brachyntera* (Schwägrichen) have been recorded on Scots pine in Britain. The former produces resin masses on branches and leaves, and the latter causes unusually short leaves with swollen bases (Barnes 1951).

The indigenous pinewoods of Scotland are remarkably free from serious damage by fauna. There is appreciable damage by grazing of young trees by sheep and deer in unfenced areas, but the only insect pests of any importance in these woodlands are *Myelophilus piniperda* and *Hylobius abietis*, and damage by these is not serious (Steven & Carlisle 1959).

(b) *Plant parasites* (D. M. Henderson). *Butt rot*: *Armillaria mellea* (Vahl ex Fr.) Kummer (Basidiomycete, Agaricales); a serious parasite on young Scots pine in Britain, causing butt rot particularly on poor or badly-drained soils when the decaying stumps of recently felled trees are present. Literature on the species, which attacks a variety of trees, reviewed by Peace (1962). *Fomes annosus* (Fr.) Cke. (Basidiomycete, Aphyllophorales); the most serious pathogen on Scots pine and other trees in Britain; occurs elsewhere in the north temperate zone. Causes death of young trees and butt rot in older trees; decays heartwood and roots of living trees, particularly at the base of the stem. Scots pine relatively resistant, but can be killed by *Fomes* on alkaline soils and old plough land. Infection may lead to insect invasions, e.g. by *Myelophilus piniperda* (Rennerfelt 1946; Rishbeth 1950; Jorgensen & Petersen 1951; Anon. 1957; Peace 1962.) *Polyporus schweinitzii* Fr. (Basidiomycete, Aphyllophorales); causes butt rot on conifers. Occurs in Europe and America; common in Britain on pole stage and older trees; present in the indigenous pinewoods in Scotland. Not serious but a potentially dangerous parasite (Peace 1962; Steven & Carlisle 1959). *Sparassis crispa* (Wulf.) Fr. (Basidiomycete, Clavariaceae);

causes a yellow brown butt rot of Scots pine in Scotland and Germany (Cartwright & Findlay 1946).

Top rot: Trametes pini (Thor) Ft. (Basidiomycete, Polyporaceae); causes top rot in older trees. Widely distributed in Europe and North America; present in Britain; locally frequent in indigenous pinewoods in Scotland. Not sufficiently common to be serious (Peace 1962; Cartwright & Findlay 1946; Steven & Carlisle 1959).

Canker, distortion and dieback of stem and/or branch: Atropellis tingens Lohm. & Cash. (Ascomycetes, Helotiales); produces cankers on stem and branches of Scots pine and some other two-needled pines. Occasionally serious. Does not occur in Britain (Diller 1935, 1943; Peace 1962). *Cenangium ferruginosum* Fr. (Ascomycete, Helotiales); occurs as a pathogen on Scots pine and other conifers in Germany causing twig dieback (Laubert 1926; Schoenwald 1931); present in Britain. *Cronartium* spp. (Basidiomycete, Uredinales); cause swellings, cankers, distortion and dieback of pine stems and branches abroad, but few species occur in Britain. *C. flaccidum* (Alb. & Schw.) Wint. has aecial stages on Scots pine and the uredial and telial stages on *Tropaeolum* and *Paeonia* in Britain. On the continent of Europe the most important alternate host is *Vincetoxicum officinale* Moench. Not a dangerous pathogen in Britain (Peace 1962; Wilson & Bisby 1954). *Cronartium gentianeum* Thüm. has its aecial stage on Scots pine, and the telial stage on *Gentiana asclepiadea* L. Causes blister rust in Switzerland; not in Britain (Peace 1962). *Cronartium harknessii* (Moore) Meinicke. has the aecial stage on Scots pine and other pines; uredial and telial hosts are Scrophulariaceae. Confined to America but could be serious disease if imported to Europe; causes death of young plants and malformation of older trees (Peace 1962; York 1929). *Crumenula pinea* (Karst.) Ferd. (Ascomycete, Helotiales); produces cankers on Scots pine and other two-needled pines in Britain and on the continent of Europe (Vloten 1929; Guyot 1934). Not serious. *Cucurbitaria pithyophila* (Fr.) Ces. & de Not. (Ascomycete, Sphaeriales); causes canker and swelling and dieback of Scots pine and other pines; recorded in Scotland; not at present a serious disease (M'Intosh 1915; Peace 1962). *Dasyscypha* spp. (Ascomycetes, Helotiales); occur on cankers formed by other fungi on weakened Scots and other pines in Britain. Of slight importance. *Diplodia pinea* (Desm.) Kickx. (Fungi Imperfecti, Sphaeropsidales); browns needles, stunts growth and may cause dieback on young Scots and other pines in plantations and nurseries in Europe; common in Britain. Widespread damage reported in 1911, but since then not serious (Bancroft 1911; Prodan 1935; Martinez 1942; Peace 1962). *Fusarium lateritium* var. *pini* (Nees.) Hepting (Fungi Imperfecti, Moniliales); has been established on Scots pine by inoculation. Occurs in Britain but no evidence of pathogenicity. Causes girdling and dieback of branches and leaders, and sunken cankers and resin flow on larger stems of *Pinus* spp. in the United States (Peace 1962; Hepting & Roth 1953). *Melampsora populnea* (Pers.) Kerst. (*M. pinitorqua* Rostr.) (Basidiomycete, Uredinales); a rust causing the death or the bending of the shoots, with subsequent distortion and formation of multiple leaders. Attacks several two-needled pines, but mainly affects Scots pine. Alternate host *Populus tremula*. Locally serious pathogen in Britain (Murray 1955). *Leucopaxillus giganteus* (Sow. ex Fr.) Sing. (Basidiomycete, Agaricales); associated with progressive dieback of Scots pine in the past in Britain; damage not observed in recent years (Peace 1936, 1962; Dennis, Orton & Hora 1960). *Peridermium pini* (Pers.) Lev. (Basidiomycete, Uredinales); causes swellings on stem and branch of Scots pine but sometimes on *Pinus nigra*. Locally common and sometimes causes serious damage (Peace 1962; Pawsey 1964b). *Rhizina undulata* Fr. (Ascomycete, Pezizales); causes group dying of Scots pine

and other conifers in Europe (including Britain) and America. Invades and kills the roots of young trees, particularly on or near the sites of fires, eventually causing dieback of the stem. Not very serious but a potential danger (Peace 1962; Murray & Young 1961).

Leaf damage and defoliation: *Coleosporium* spp. (*C. campanulae* Lev., *C. euphrasiae* Wint., *C. melampyri* Karst, *C. petasitis* Lev., *C. senecionis* Fr., *C. sonchi* Lev., *C. tussilaginis* Pers. (Lev.). (Basidiomycete, Uredinales); needles of two- and three-needled pines (most often Scots pine) damaged. Not usually serious, but defoliation may occur. Widely distributed in Britain; only of importance in nurseries. Alternate hosts include *Senecio vulgaris*, *Tussilago farfara*, *Campanula* spp., *Euphrasia* spp., *Odontites verna*, *Parentucellia viscosa*, *Rhinanthus minor*, *Melampyrum* spp., *Petasites* spp., *Calendula* spp. and *Sonchus* spp. (Peace 1962; Moore 1959; Wilson & Bisby 1954). *Dothistroma pini* Hulb. (Fungi Imperfecti, Sphaeropsidales); browning of needles of Scots and other pines. Not serious on the former in Britain; more serious on *Pinus nigra* and *P. radiata* (J. S. Murray, D. H. Phillips). *Hendersonia acicola* Münch (Tub.) (Fungi Imperfecti, Sphaeropsidales); causes grey-white leaf discoloration in summer and subsequent defoliation. Generally distributed on Scots pine and other two-needled pines in Britain (Laing 1929). *Hypoderma desmazieri* Darter (Phacidiales); causes leaf cast on Scots pine and some other two-needled pines in America but has not been recorded on Scots pine in Britain. Not serious. (Darker 1932; Peace 1962). *Hypodermella conjuncta* Dark. and *H. sulcigena* (Rostr.) Tub. (Phacidiales); occur on Scots pine in Britain, causing leaf cast. Not serious in Britain (Darker 1932). *Lophodermium pinastri* (Schrad.) Chev. (Phacidiales). Imperfect form *Leptostroma pinastri* Desm. (Fungi Imperfecti, Sphaeropsidales); causes needle cast of Scots pine and may completely remove previous year's needles. Widely distributed in Europe and North America; occurs throughout Britain. Attacks a range of *Pinus* species but most common on Scots pine. Appears to be most severe following a damp summer. Provenances differ in their resistance to attack. Not normally serious in the forest but suppressed trees may die. Sometimes serious in nurseries, but more serious on the continent of Europe than in Britain. (Peace 1962; Pawsey 1964a). *Naemacylus niveus* Pers. ex Fr.; associated with defoliation of *Pinus* species in Europe and the United States (Přihoda 1950; Darter 1932). Occurs on fallen Scots pine needles in Britain, but so far no evidence of defoliation (Peace 1962). Not serious. *Phoma acicola* Sac. (Fungi Imperfecti, Sphaeropsidales); occurs widely on Scots and Corsican pines causing damage to needles. Present in Britain. Not particularly serious (Peace 1962; D. H. Phillips and J. S. Murray). *Sclerophoma pithyophyla* v. Höhn. (Fungi Imperfecti, Sphaeropsidales); damages current year's needles of young (1–5 m high) Scots pine in Britain. In Russia causes dieback and witches' broom on *Pinus*. Not of great importance at present but could be serious pathogen. (Peace 1962; Nazarova 1936).

Moulds: *Herpotrichia nigra* Hartig. (Sphaeriales); and *Phacidium infestans* Karst. (Phacidiales); attack young Scots pine in the nursery in Britain. Not serious. (D. H. Phillips, J. S. Murray; Peace 1962).

This list is not complete; Donaubaue (1964) lists the plant pathogens of Scots pine throughout its range. There are also many saprophytic and semi-parasitic fungi on Scots pine seeds; Urošević (1961) describes the effects of fifty-nine such species, some of which reduce germination success by 20% or more. There is evidence that some provenances of Scots pine are more resistant to fungal parasites than others (Donaubaue 1964).

In Britain the most serious diseases are the butt rots, *Armillaria mellea* and *Fomes annosus*, and these cause extensive damage in plantations. In the indigenous pinewoods of

Scotland, however, the trees are remarkably free from disease (Steven & Carlisle 1959); in the period 1950–56 the authors saw very little evidence of butt rot. The most common pathogens in these woods are *Trametes pini* and *Polyporus schweinitzii*, but these are nowhere serious; *Lophodermium pinastri* is present but causes very little damage. These woodlands appear to be in a state of pathological equilibrium, but, as Peace (1962) points out, this could easily be upset by the introduction of new pathogens.

(c) *Diseases*. The only reported virus disease on conifers is spruce virosis on *Picea excelsa* Link; there is some evidence that it also attacks the genus *Pinus*. Two virus-like diseases also occur in the genus *Pinus*; pine dwarf fascicle abnormality and leaf curl of pine seedlings. No definite bacterial or virus diseases, however, have been recorded on *P. sylvestris* (Seliskar 1964). Witches' broom and fasciation of shoots occur on Scots pine, but the causal agents are not known; some witches' brooms may be due to a fungal pathogen (Nazarova 1936).

X. *History*. Macroscopic remains of Scots pine have been found in the Cromer Forest Bed Series (c. 500 000 years ago in Interglacial deposits). Scots pine and other tree species were present in Britain near the beginning and ends of all the interglacial periods of the Quaternary (Campbell & Robertson 1934; Lacaille 1954; Simpson & West 1958). In Late-glacial times it may have been present on a few favourable sites in southern and eastern England (Zone II, c. 10 000–9000 B.C. and Zone III, c. 9000–8000 B.C. (Godw. *Hist.*)). In the Pre-Boreal period (Zone IV, c. 8000–6800 B.C.) the forests of middle Europe were predominantly pine (Firbas 1949) and, although birch was still the predominant tree species in the north, there is little doubt that by this time pine had reached southern and eastern England. Scots pine spread throughout the British Isles in Boreal times, attaining its greatest frequency c. 6000–5000 B.C. (Zone VI). At the end of the latter period it gave way to deciduous forest in southern Britain, the process being slower in the north and west (Godw. *Hist.*). In Boreal times Britain was connected to the continent and immigration of trees from the latter was possible. By the end of the period, however, Britain became an island as the ice melted and the sea level rose, and further natural immigration of tree flora became more difficult. In the Atlantic period (Zone VII a, c. 5000–3000 B.C.) the proportion of pine diminished in relation to alder and oak, and was comparatively scarce in the British Isles by the Sub-Boreal period (Zone VII b, c. 3000–500 B.C.). Pine had practically disappeared from Ireland by this time. The Sub-Atlantic period (Zone VIII, c. 500 B.C. and later) was a period of deforestation, partly due to man and partly to climatic changes, and only a few pine survived in England, Ireland and Wales (Godw. *Hist.*). Destruction of forests by man was probably appreciable in Neolithic time, increasing in the Bronze Age, and most widespread between the eighth and fifteenth centuries. Some of the indigenous pinewoods survived in Scotland, owing to their inaccessibility (Steven & Carlisle 1959). Some authorities claim that there are remnants of these pinewoods in England, but more evidence is needed (see I). Scots pine was planted in Britain at least as early as A.D. 1600 and in the last 250 years has been widely used in plantations. It fell into disfavour as a plantation tree in the period 1790–1810 owing to poor timber quality resulting from the use of unsuitable genotypes. In the early nineteenth century seed from indigenous Scottish pine was widely used, and the resulting high quality timber restored the species to favour with foresters (Steven & Carlisle 1959). In recent years more productive introduced species are frequently being used in preference to Scots pine (see Vb).

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