Hill, M. O.. 1979 The development of a flora in even-aged plantations. In: Ford, E. D.; Malcolm, D. C.; Atterson, J., (eds.) *The ecology of even-aged forest plantations.* Cambridge, Institute of Terrestrial Ecology, 175-192.

THE DEVELOPMENT OF A FLORA IN EVEN-AGED PLANTATIONS

By M.O. HILL

Institute of Terrestrial Ecology, Bangor Research Station, Penrhos Road, Bangor, Gwynedd, Wales, U.K.

SUMMARY

When a conifer plantation is established there is a big change in the ground flora as the canopy closes. Under crops of *Abies* spp, *Picea* spp and *Tsuga** spp, which generate heavy shade, vascular plants are largely eliminated during the thicket stage, and at least with the short rotations that are necessary in most of upland Britain, do not reappear in quantity before clearfelling. Bryophytes often increase, though under very dense canopies even these may be absent. Under the lighter canopies of *Larix* spp and *Pinus* spp a larger flora persists and there may often be an almost complete cover of vascular plants in the later stages of the rotation. The flora in western European conifer plantations is intermediate in composition between that of boreal forest and that of deciduous woodland. The fern *Dryopteris dilatata** is a particularly characteristic feature. On clearfelling there is often a rapid increase of vascular plants. The composition of the reappearing flora and the speed of its re-establishment depend on the amounts of seed present in the soil and on the vegetation present on the site at the time of clearfelling. In many plantations there are large populations of viable seeds in the surface layers of the soil, densities of 1000-5000 seeds per sq.m being typical, though those in peat are much lower. Seeds of plants with wind dispersal seldom survive in the soil, and have to be replenished each year. Many plant species survive in marginal habitats in

*Nomenclature follows Clapham, Tutin & Warburg (1962), Dallimore & Jackson (1974), and Smith (1978).

forests, notably on roadsides and beside streams. A moderate to large number of lowland species immigrate on roadsides, thereby diversifying the flora of upland areas in Britain. However, many plants of marshes and bogs are eliminated in afforested areas, so that on balance there is little change in the number of species present.

RÉSUMÉ

L'établissement d'une plantation de conifères amène un changement important de la végétation (au niveau du sol) à mesure que la voûte des arbres se referme. Dans le cas des essences (tels que Picea, Tsuga* et Abies) qui produisent beaucoup d'ombre, les plantes vasculaires sont largement éliminées au stade de fourré, et à cause des courtes révolutions, souvent nécessaires dans les régions élevées de Grande Bretagne, elles ne réapparaissent pas en quantité avant la coupe à blanc. Le nombre des bryophytes augmente souvent mais si le couvert est très épais, ils peuvent même être absents. Sous le couvert plus léger des Larix et des Pinus, la végétation persiste d'une manière plus importante et on peut souvent trouver une couverture presque complète de plantes vasculaires vers la fin de la révolution.

La composition de la flore des peuplements de conifères d'Europe occidentale est comprise entre celle des forêts boréales et celle des forêts de feuillus: la fougère Dryopteris dilatata* y est très caractéristique. Les coupes à blanc sont suivies d'un accroissement rapide de plantes vasculaires. La composition de cette flore et la rapidité de sa réinstallation dépendent de la quantité de graines présentes dans le sol et de la végétation existante au moment des coupes à blanc. On peut trouver dans de nombreux peuplements un grand nombre de graines viables dans les couches superficielles du sol, des densités de 1000-5000 graines/m.carré étant typiques, mais elles sont plus faibles dans les sols tourbeux. Les graines des plantes qui sont disséminées par le vent ne survivent que rarement dans le sol et doivent être réapportées chaque année. Beaucoup d'espèces survivent dans des stations marginales en forêt, surtout au bord des routes et des cours

d'eau. Un grand nombre d'espèces provenant de la plaine émigrent vers le bord des routes, amenant ainsi une certaine diversification de la flore de montagne en Grande Bretagne. Cependant de nombreuses espèces provenant de stations marécageuses sont éliminées dans les reboisements, ce qui nous montre qu'en fait, il n'y a pas de grand changement dans le nombre des espèces présentes.

ZUSAMMENFASSUNG

Eine Nadelbaumpflanzung führt zu einem grossen Wandel in der Bodenflora, sobald sich das Kronendach schliesst. Abies spp, Picea spp und Tsuga* spp beschatten so stark, dass Gefässpflanzen während des Dickungsstadiums weitgehend eliminiert werden und, zumindest bei den kurzen Umtriebszeiten, die fast überall im britischen Hochland nötig sind, auch bis zum Kahlschlag nicht mehr in nennenswertem Umfang auftauchen. Bryophyten breiten sich oft stärker aus, aber unter sehr dichtem Kronendach können sogar sie fehlen. Unter dem lichteren Kronendach von Larix spp und Pinus spp hält sich eine umfangreichere Flora. In späteren Stadien der Umtriebszeit bildet sich oft eine fast geschlossene Decke von Gefässpflanzen aus. Die Flora westeuropäischer Nadelbaumpflanzungen liegt in ihrer Zusammensetzung zwischen der eines borealen Nadelwaldes und der von Laubwäldern. Ein besonders charakteristisches Merkmal ist der Farn Dryopteris dilatata*. Nach dem Kahlschlag kommt es oft zu einer raschen Vermehrung der Gefässpflanzen. Die Zusammensetzung der wieder auftauchenden Flora und die Geschwindigkeit ihrer Ausbreitung sind abhängig von der Menge noch im Boden lagernder Samen und der Vegetation, die zur Zeit des Kahlschlags am Standort wächst. In vielen Pflanzungen liegen grosse Mengen lebensfähiger Samen in den obersten Bodenschichten. Dabie sind 1000-5000 Samen pro Quadratmeter durchaus typisch. In Torfböden liegt die Zahl allerdings niedriger. Vom Wind verbreitete Samen überleben selten im Boden und müssen jedes Jahr neu anfliegen.

Viele Pflanzenarten überleben in den Randgebieten der Wälder, hauptsächlich an Strassenrändern und an Flüssen. Eine mittlere bis grosse Zahl von Tieflandarten wandert

> entlang der Strassenränder ein und bringt so Abwechslung in die Flora des britischen Hochlandes. Viele Marsch- und Moorpflanzen sind jedoch in Aufforstungsgebieten ausgestorben, so dass sich insgesamt die Artenzahl wenig ändert.

VASCULAR PLANTS AND BRYOPHYTES IN PLANTATIONS OF DIFFERENT TREE SPECIES.

In British plantations, the heaviest shade is cast by the canopy of Western hemlock (Tsuga heterophylla). There is virtually no ground flora, except perhaps in very old stands after heavy thinning; even bryophytes are excluded. Under hemlock, therefore, the development of the ground flora is restricted to the establishing phase before canopy closure.

Sitka spruce (Picea sitchensis) casts a shade that is less dark, and although vascular plants are normally scarce or absent, a bryophyte cover of perhaps 5-10 per cent is usual (Fig. 1). After planting, higher plants decline rapidly as the canopy closes (ten to fifteen years); there is little regrowth later. During establishment of the second rotation, higher plants are generally less abundant that they were at the same stage in the first rotation. The difference is due in part to ineffective recolonization of bare ground and in part to the presence of slash which suppresses the growth of most vegetation. Sprawling plants such as Rubus fruticosus and Corydalis claviculata can sometimes cover larger areas of slash effectively, but these plants are absent on the peatier soils where Sitka spruce is often planted.

The development of a bryophyte flora follows a totally different pattern. Bryophytes, mostly mosses, increase from the first, and may continue to increase after canopy closure. There is, however, much variation in the pattern of bryophyte development, depending on the condition of the crop and the dampness of the ground. Generally, the more successful the crop and the drier the ground, the fewer are the bryophytes. During establishment of the second rotation, perhaps because of reduced competition from higher plants, bryophytes are distinctly more numerous than at the same stage in the first rotation.

Norway spruce (Picea abies) casts a slightly less dense shade than Sitka spruce, with the result that there is a more abundant ground flora. Bråkenhielm (1977), working in Småland, South Sweden, followed the development of the ground flora in even-aged plantations of Norway spruce on abandoned arable land over a period of ten years. The general pattern was similar to that under Sitka spruce in Britain, with higher plants decreasing and bryophytes increasing during the first ten years, followed by a rapid decline of higher plants as the canopy closed, and somewhat inconsistent changes in the bryophytes. There were, however, marked differences later. In

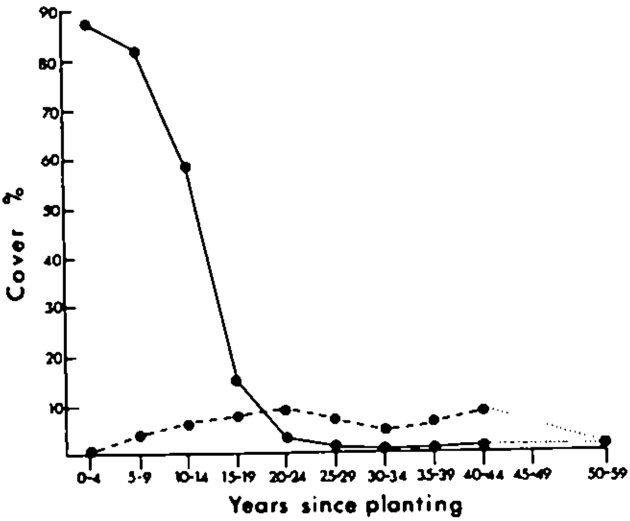

Fig. 1. Cover of vascular plants (solid line) and bryophytes (dotted line) in relation to age of crop in plantations of _Picea sitchensis_ in upland Britain.

particular, a woodland flora including some vascular plants began to establish itself when the crop was cleaned by felling of hardwoods and subordinate spruce at about twenty years. The vascular plants increased appreciably at the time of first thinning, about thirty years, but as the canopy reclosed they decreased again. Woodland bryophytes, on the other hand, also increased at this time, but did not die back as the canopy reclosed.

Pines (_Pinus_ spp) and larches (_Larix_ spp) cast a ligher shade than spruces, so that a larger ground flora is normally present through the rotation (Fig. 2). The cover of bryophytes is similar to that found under spruces. Unlike the pattern under spruces, there is a large increase in the cover of the ground flora towards the end of the rotation.

The flora of broad-leaved plantations will not be considered here, except to remark that although vernal species such as _Anemone nemorosa_ and _Endymion nonscriptus_ may become abundant on better soils in lowland areas, these plants do not generally increase under broad-leaved crops on the peatier soils of upland Britain. For example, the ground flora was examined in a Forestry Commission experiment at Clocaenog Forest, North Wales, where forty-three year-old stands of

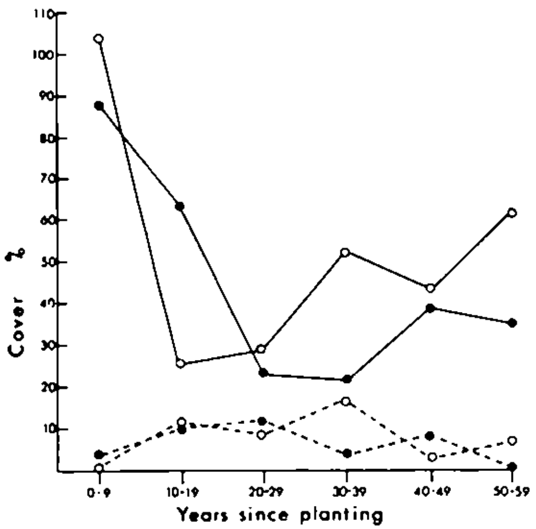

Fig. 2. Cover of vascular plants (solid lines) and bryophytes (dotted lines) in relation to age of crop in plantations of Pinus spp (closed circles) and Larix leptolepsis (open circles) in upland Britain. There is some irregularity in these curves due to random variation in a rather small sample of observations.

Pinus contorta and Betula spp could be compared. Both the ground flora species present and their cover were similar. The soil was a peaty gley intergrading with a brown earth.

COMPOSITION OF THE FLORA

On the geographical scale the composition of the flora under planted conifers depends both on climate and on the species available in the surrounding area to imigrate. On a local scale it depends on soil, species planted, stage of the rotation, and on the past history of the site.

The climate determines not only which plants can grow on the forest floor, but also which tree species are suitable for planting as crops in the first place. It is, however, worth noting some differences between northwest Europe and more continental regions further east. Heather (Calluna vulgaris) and ferns (especially Dryopteris dilatata) are perhaps the most characteristics species in many forest of northwest Europe. Heather is not shade-tolerant, but is common in plantation forests before closure of the canopy, reappearing from seed when the crop is clearfelled. The fern Dryopteris dilatata is often the only vascular plant to achieve appreciable cover in British conifer plantations, and it has been noted as a characteristic plant of Douglas fir (Pseudotsuga menziesii) plantations in Holland (Sissingh 1975).

Further to the east, as for example in Bråkenhielm's Swedish plantations, heather and ferns are less prominent or absent, but a wider variety of typical woodland plants occur. Bråkenhielm (1977) noted that Luzula pilosa, Melampyrum sylvaticum, Oxalis acetosella and Viola riviniana soon established themselves after the crop was cleaned or thinned. To some extent this difference reflects not only the climate, but also the availability of a suitable local flora to occupy the ground and a soil that was relatively good after years of agricultural use. The area of Sweden in which Bråkenhielm made his observations is very diverse, with fields, meadows, lakes and woodland forming an intimate and complex mosaic of habitats. Consequently there is a large available flora in the immediate vicinity of the plantations, and, in particular, a woodland flora that has not been eliminated by years of grazing as in so much of upland Britain.

In accordance with the greater cover of plants under pines and larches than under spruces, there is also a greater variety of species. Vascular plants that are particularly characetristics of pine and larch plantations on more fertile soils in Britain are bramble (Rubus fruticosus) and bracken (Pteridium aquilinum). These species are almost totally eliminated by Sitka spruce once it has closed its canopy. Bracken seldom reappears even after thinning. On heathier soils the grass Deschampsia flexuosa and bilberry (Vaccinium myrtillus) prevail and may survive in very small quantities even under Sitka spruce; though really successful thickets will eliminate them.

Both the overall cover of bryophytes and the diversity of species are similar under spruces and pines. There are, however, a few bryophytes that do not normally survive under Sitka spruce in Britain though they are frequent under those crop species with lighter canopies. Of these the most notable are Hylocomium splendens and Pleurozium schreberi, large pleurocarpous mosses that are often abundant in the boreal forest, and which are common before afforestation in the British uplands (Hill & Jones 1978). This is in contrast to Bråkenhielm's Norway spruce plantations in Sweden, where Pleurozium schreberi was one of the woodland plants that invaded after the crop was thinned.

The soil is one of the biggest influences on the composition of the flora. Where it is initially acid and infertile, few species of vascular plants occur. In Britain, the almost ubiquitous Deschampsia flexuosa, Dryopteris dilatata and Vaccinium myrtillus would often be the only vascular plant species present. On more fertile soils there is a much richer flora, and a greater variety of woodland plants may invade, including Oxalis acetosella, Rubus fructicosus and Sorbus aucuparia. Bryophytes, however, which grow mainly on the litter and stumps, are less affected by soil quality than by available moisture. They are not notably more plentiful on damp soils and on northfacing slopes than on dry soils and on south-facing slopes.

INFLUENCE OF THE DEVELOPING PLANTATION ON GROUND VEGETATION

The strongest influence of all on the composition of the ground flora is the crop. Before the canopy closes, light-demanding plants including weeds and pasture species can thrive. After the canopy has closed, only the most shade-tolerant species can survive under spruces. Even under pines and larches many formerly abundant plants such as Calluna vulgaris and most grasses othen than Deschampsia flexuosa vanish.

While light intensity is clearly the strongest single influence on the ground flora, its effects are difficult to separate from other influences correlated with the density of the canopy. In particular where the canopy is denser, less rain can penetrate, and there is a greater fall of litter. Root competition can also be expected to be greater. In a series of experiments to assess the effects of tree-root competition and of litter in a Pinus strobus forest in New Hampshire, Toumey (1929) severed the roots round some experimental plots, and removed the litter from a part of them. Removal of litter led to a large increase of vascular plants. Severing the roots led to a large increase of soil moisture during the summer, and to an appreciable increase of vascular plants.

Toumey concluded that light was not the factor controlling the entrance of natural vegetation under his experimental conditions. This conclusion, somewhat polemical at the time, is of course unjustified. No factor can be said to be ineffective unless it has been varied under controlled conditions. Nevertheless, his experiments aptly illustrate the combination of adverse influences that the ground vegetation in a conifer forest has to contend with. The full combination of adverse influences is often necessary for suppression of the ground vegetation. If any one of them is relaxed, the vegetation can develop. Bryophytes often show this clearly, growing vigorously on stumps that are left after thinning of the crop, but being almost totally absent on the forest floor where they are smothered by accumulating litter. The effect of root competition is probably less in wet regions such as the British uplands than in Toumey's experimental plots. Drought can be appreciable even in the west of Britain, but is certainly not as severe as in more continental regions.

Competition for mineral nutrients is presumably the main influence of root competition in wetter climates.

Because of the other influences of the crop it is unrealistic to speak of a unique critical value for the intensity of light below which vegetation will not grow. In addition various authors' thresholds for the cover of vegetation below which plants may be considered to be 'absent' have rarely been stated precisely. Measurements of relative illumination have varied, some authors making their observations on sunny days, and others on days when the sky is overcast. In general, the grey-day relative illumination is to be recommended as a measure of shade, as it depends little on the angle of the sun; for a comparison of the relative illumination under spruce with and without an overcast sky; see Eber (1972).

Even if authors had been consistent, and even if other environmental condition were comparable, the relation between relative illumination and the cover of the ground flora would not be exact, as the flora is seldom in equilibrium with the canopy. In Bråkenhielm's (1977) observation of Norway spruce plantations in South Sweden there was an increase in the ground flora after thinning, and a subsequent decrease as the canopy reclosed. Both during the expansion and during the subsequent die-back there would be a lag, so that the cover of the ground flora would depend on the previous few years of illumination as well as on current illumination.

In spite of these sources of variation, and in spite of possible differences in thresholds below which species are considered to be absent, the observation of various European authors are broadly consistent (Table 1). Vascular plants do not occur below about 10-20 per cent relative illumination. On a proportional basis the lower limit of illumination for bryophytes varies more widely, between 2 per cent and 9 per cent. The reason for the greater variability of the bryophyte threshold is the greater sensitivity of bryophytes to local influences, notably the accumulation of litter and the effects of desiccation. The most discordant value in Table 1 is due to Eber (1972). Here, the anomaly may be due to a difference of soil and slope, as Eber was working on steeply sloping, calcareous ground, whereas the other observations relate to acid or neutral soils on more level ground where litter would accumulate more thickly.

At all events, whether the main limiting factor is light, moisture or smothering by litter, the broad empirical relation between relative illumination and the ground flora can explain the differences found between spruces on the one hand, with Abies spp and Pseudotsuga menziesii resembling spruces in this respect, and pines and larches on the other. In spruce plantations the relative illumination is normally between 1 per cent and 10 per cent until they are over sixty years of

Table 1. Minimum relative illumination (grey-day) for growth of vascular plants and bryophytes under conifers. (Values are drawn from observations in the literature. Values for Clocaenog Forest in North Wales are based on my own observations).

Author	Crop	Minimum relative illumination for vascular plants	Minimum relative illumination for bryophytes
Cousens (1974)	Pinus sylvestris	17%	9%
Eber (1972)	Picea abies	6%	?
Koie (1938)	Pinus spp	10%	2%
Rheinheimer (1957)	Picea abies	20%	5-7%
Rheinheimer (1959)	Picea abies	?	7%
Schluter (1966)	Picea abies	12-15%	?
(Clocaenog Forest)	Picea and Pinus	12-13%	2-8%

age; whereas in pine and larch plantations after thinning, values between 10 per cent and 40 per cent are typical.

DIFFERENCES BETWEEN CONIFER PLANTATIONS AND NATURAL WOODLAND

Most conifer plantations in western Europe are in the climatic zone that would naturally support broad-leaved forest. As a result, their ground vegetation consists largely of species that also occur in nearby broad-leaved woodland. For example, in a detailed study of changes resulting from afforestation of some rough grazings in South Wales, Hill & Jones (1978) found only two species occuring in plantations that were not present in nearby oak (Quercus petraea) woods. Both were bryophytes that produce abundant spores, Plagiothecium curvifolium and Polytrichum longisetum, and presumably could have reached the area from considerable distances. Otherwise the origin of the flora was clearly local.

From the point of view of the wild flora, plantation forests differ from natural woodland in two major respects: the uniformity of the thicket stage and shortness of the rotation. When a crop reaches the thicket stage simultaneously over a wide area, species may be eliminated completely that would otherwise re-occupy the ground during later stages of the rotation. This means that opportunities for true woodland species in plantations are much reduced, as they lack suitable refuges during the establishment and thicket stages. There is perhaps more resemblance to a fire-succession. But in regions such as western North America where fire-successions have been extensively studied, the trees often reach ages of eighty to

Table 2. Commonest plants of coniferous plantations in upland Britain.

Data for this Table are derived from an unpublished report submitted by the Institute of Terrestrial Ecology to the Nature Conservancy Council. The two categories do not correspond to precise levels of frequency, but the plants in Category A have frequency approximately 40-100% in 200 sq.m, and plants in Category B have frequency approximately 20-40%. The establishment stage (0-20 years) of the first rotation has been excluded, but the establishment stage of the second rotation is included, this being regarded as a closer approximation to what will be present in a normal forest. Equal representation has been given to each of the age-classes 0-20 years, 20-40 years and 40-60 years.

A. Almost ubiquitous	
Deschampsia flexuosa	Hypnum jutlandicum
Dryopteris dilatata	Plagiothecium undulatum
Vaccinium myrtillus	Lophocolea cuspidata
Dicranum scoparium	
B. Other very common plants	
Calluna vulgaris	Campylopus paradoxus
Chamaenerion angustifolium	Dicranella heteromalla
Galium saxatile	Eurhynchium praelongum
Molinia caerulea	Mnium hornum
Rubus fruticosus	Pleurozium schreberi
Sorbus aucuparia	Hypogymnia physodes

V. vitis-idaea and Deschampsia flexuosa constant and sometimes co-dominant. Otherwise the commonest flowering plants are Linnaea borealis, Luzula pilosa, Melampyrum pratense and Trientalis europaea. On clearfelling, Deschampsia flexuosa becomes dominant, with abundant Epilobium angustifolium, Luzula pilosa and Rubus idaeus.

100 years or more. By that age most spruce plantations in the British uplands would have been windblown. The crop cannot be harvested at much more than fifty years of age and this short rotation is highly inimical to the establishment of a true woodland flora.

In spite of these differences there are marked resemblances between the flora of conifer plantations in the northern deciduous zone of Europe and that found in the boreal forest. The commoner species in British upland forests (Table 2) include two, Dryopteris dilatata and Hypnum jutlandicum, that are largely absent from the North European boreal forest; but the other species are all frequent or common there.

According to Sjörs (1965) Vaccinium myrtillus is dominant in the field layer under Norway spruce in the boreal forest of Sweden, with

REGENERATION OF THE GROUND FLORA FOLLOWING CLEARFELLING

Because of poor development of the ground flora in many plantation forests, the revegetation of sites that have been clearfelled is particularly dependent on seed surviving in the soil, and on the few vascular plants that may have survived the rotation. Woodland plants normally die back. In Britain this usually means Dryopteris dilatata, which often does not actually die but merely survives unhealthily without increasing, and several species of woodland bryophytes. The moss Plagiothecium undulatum is not very tolerant of desiccation, but Hypnum jutlandicum, which is also very common in mature plantations, can grow equally happily on dry heathland and is not adversly affected by removal of the tree canopy.

After clearfelling there are four main sources of the regenerating flora: viable seed surviving buried in the soil; seed entering the area after clearance; seed distributed by plants surviving on the site, and vegetative spread of the surviving green plants. Where there has been a succesful crop of a dense-canopied species such as Sitka spruce, seed surviving in the soil is generally the main source of propagules for the regenerating flora, at least away from the edges of felled compartments. Near the edges, many relatively light-demanding plants such as bracken (Pteridium aquilinum) may survive, so that in the season after clearance the centre of the compartment can be almost bare, while there is a dense growth of vegetation round the edge. Pteridium is almost totally dependent on vegetative spread, and does not reappear in areas from which it has been eliminated.

Some of the viable seed present in the soil at the time of clearfellings is of recent origin; some, often the majority, has survived for many years in the soil. These two categories can usually be told apart by the fact that the recently arrived seeds are mainly in the litter, while the seeds that have been present for longer are mainly in lower horizons. Peter (1893, 1894) working in the vicinity of Gottingen, was the first to demonstrate the remarkable longevity of seeds in forest soils although there had been several earlier, anecdotal reports. Using a simple technique of germinating seeds from boxes of soil in the greenhouse, he found that where plantations had been established on old arable or pasture land, the seeds of arable or pasture weeds remained abundant in the soil for up to fifty years. In plantations established for more than 100 years the flora of the previous land-use was largely eliminated though there was sometimes a small population of weed species in the surface layers of the soil. These he attributed to the use of the woodland by local farmers for sheltering livestock. Some small-seeded plants, chiefly of the genera Hypericum and Juncus, were present in the deeper layers of the soil, and these had perhaps survived for much longer. The seeds of true woodland species were very poorly represented in the soils, with the result that densities of viable seeds were much less in old plantations and ancient woodlands than in plantations established within the previous fifty years.

Peter's experiments were conducted with a care and thoroughness that have not been surpassed, and his conclusions have been amply confirmed by subsequent observers. My colleague P.A. Stevens, using essentially the same technique, has examined soil seed populations in British upland forests on several types of soil. He found seed densities typically in the range 1000-5000 seeds/sq.m on brown earths and peaty gleys, but much lower, typically 40-100 seeds per sq.m, on deep peat (P.A. Stevens, personal communication). Seeds of many species survived readily through the dark stage of the rotation, i.e. for about thirty-five years; but tree seeds (Betula, Picea and Pseudotsuga) appeared always to be of recent origin. In general the larger seeds survived less well than smaller seeds, and many grasses were scarcely represented in samples taken from older plantings. In particular, Deschampsia flexuosa did not appear to survive for long as soil seed, so that when it invades a clearfelled area, it has to do so from plants surviving on the site. Under larch and pine it is usually present before clearfelling, but it may be largely eliminated by well-grown Sitka spruce.

Among the small-seeded plants that showed good survival as soil seed, the most notable were Calluna vulgaris, generally in large numbers, Carex spp, Digitalis purpurea, Erica tetralix, Galium saxatile, Juncus spp, Luzula spp and Potentilla erecta. The reappearance of these species on clearfelled areas, is therefore often to be expected. Also, the grasses Agrostis canina, A. tenuis and Deschampsia cespitosa often reappear after clearfelling, and their seeds probably survive considerable periods of burial.

In addition to plants whose seeds survive on the site, certain plants with airborne seeds are capable of colonizing the area from outside. In Britain these are mainly Epilobium spp and Compositae; in many parts of North America and the Soviet Union, grasses of the genus Calamagrostis are often abundant. Chamaenerion angustifolium is generally the most plentiful windborne colonist of clearcut areas in Britain, though it often grows poorly and fails to become abundant on the poorer peaty soils. Plants with windborne seeds are particlarly characteristic of fire-successions elsewhere, as some individuals are able to disperse over long distances, and are, therefore, at an advantage where seeds buried in the surface soil have been destroyed.

Dispersal of berries by birds is undoubtedly responsible for some regeneration of Rubus spp, Sorbus aucuparia and Vaccinium myrtillus. However, the seeds of these plants are often buried in the mineral soil, and clearly have considerable longevity. Where seeds are introduced from outside this is most probably by roosting birds while the crop is still standing. It is quite possible that birds serve mainly to introduce these species in the first place, but that the bulk of their regeneration is from plants already present in the soil before the crop closed its canopy.

Depending on the species of crop and on its management there may be an appreciable flora already present on the site to serve as a source of seedlings after clearfelling. Deschampsia flexuosa is markedly affected in this way, frequently being the most abundant plant of clearcut areas which had supported a final crop with a canopy broken by endemic windthrow, disease, etc. Grasses such as Agrostis spp and Molinia caerulea may spread vigorously from a few existing plants and brambles (Rubus fruticosus) and bracken (Pteridium aquilinum) may spread vegetatively.

OUTLOOK FOR THE GROUND FLORA IN FUTURE ROTATIONS

In Britain, most plantation forests are still in their first rotation; large areas still remain to be planted in Scotland. Moreover, methods of silviculture and the choice of crop species have changed so much in the past fifty years that it is not possible to be sure what will happen in future rotations from a knowledge of what has happened to-date. Least known are the changes that may take place in populations of buried viable seeds. Existing populations of buried seeds were mostly derived from the flora that preceeded afforestation. At the end of the next rotation the original seeds will almost all be dead, and numbers may not be replenished during the open phase before closure of the canopy of the second crop. If so, then the seed population may gradually drop, so that successive crops may be progressively more free of weeds.

This, however, is certainly not the outlook for the more fertile soils. One of the sites where the buried seed population was examined by P.A. Stevens, was on a brown earth in Gwydyr Forest, North Wales, on a site that had always been woodland. The buried seed population was here exceptionally large, about 5000 seeds/sq.m, of which 4000 seeds/sq.m were of Digitalis purpurea. After clearfelling, Digitalis germinated abundantly, and will evidently leave a vast population of buried seeds to appear when the next crop is clearfelled. Digitalis is a species that can be expected to increase in future rotations, extending to areas that were formerly grassland as well as occurring in old woodland sites.

On peats, however, few seeds survive in the soil.

Deschampsia flexuosa is normally the principal colonist after clearfelling though if it has been largely eliminated by the previous crop, and has not already colonized windthrown areas, it may perhaps fail to establish a large population before the next crop closes its canopy. If so, then the ground flora on peats may eventually be very sparse.

There is much uncertainty in this prediction. Windthrow is proving to be more of a problem in Britain than had been anticipated. Patches of windthrow allow populations of mature plants to develop in planted blocks towards the end of the rotation and may eventually result in a more fine-grained pattern of age-classes than we have at present. If so, then a large ground flora may survive even on peats.

REGENERATION OF TREES FROM SEED

An important category of windborne seeds not mentioned above is tree seeds. In British forests this usually means the seeds of birches (Betula pendula and B. pubescens) and conifers. As with windborne seeds of herbaceous species, tree seeds do not survive for long in the soil, and are mostly replenished each year. They regenerate more readily in mineral soils than on peats, especially if there has been some disturbance.

Available data on the regeneration of conifers in Britain are rather scattered, and there are still many gaps in our knowledge. The subject has been ably reviewed by Brown & Neustein (1972), who draw attention to the role of small mammals in destroying the seeds. However, much of our knowledge is still anecdotal, and the effect of other vegetation on regenerating trees is little understood. Grasses and heather are considered to have an adverse effect on regeneration, whilst Polytrichum and Vaccinium are reputed to make a good seed bed (Robertson 1976). The factors controlling natural regeneration require further study.

FLORA OF MARGINAL HABITATS IN PLANTED FORESTS

There has been a widespread fear among nature conservationists in Britain that the extensive new plantations would impoverish the flora of the uplands, and it is true of course that much of the existing vegetation is destroyed when a forest is established. Although many species survive in the soil as seed, and although a small number immigrate, nevertheless if only the planted blocks themselves were considered, there would be an appreciable loss of species diversity in planted forests.

But, in addition to destroying existing habitats, afforestation also creates new ones, notably the rides and roads. Rides in my experience are rather a poor habitat for plants, as they are not disturbed enough to keep the vegetation open, with the result that they are normally dominated by a thick mat of coarse-growing plants such as Agrostis canina, Calluna vulgaris, Holcus mollis or Molinia caerulea. The coarse-growing dominant plant then excludes smaller plants, preventing establishment of a diverse flora. It is possible that rides have not yet had enough time for a characteristic flora to develop. In particular, until clearfelling of the first rotation, they may experience very little disturbance. After disturbance a characteristic flora may begin to immigrate, though completion of the proccess could take several rotations.

Roadsides, on the other hand, are disturbed from the first, and are normally kept open by various management practices such as mowing. They are colonized by a wide variety of plants, including many that are scarce or absent in upland areas before afforestation (D.F.Evans, personal communication) but mainly those characteristic of roadsides and hayfields in the lowlands. In Dalby Forest, North Yorkshire, where the roads are surfaced with limestone, the flora of the verges is particularly rich and includes a wide variety of immigrating species.

The flora of streamsides in forests varies greatly, depending on the size of the stream and the closeness of planting. At one end of the scale, small streams are commonly canalized and trees planted right up to their edge. Their flora is largely obliterated. Large streams and rivers often have roads running alongside them and have a flora effectively unmodified by afforestation.

The habitats that are worst affected by afforestation are marshes and bogs. Not only are they commonly drained for planting but many species of base-rich marshes are low-growing and dependent on heavy grazing for their survival. When the grazing animal is excluded many small plants such as Drosera rotundifolia, Pinguicula spp, Valeriana dioica and numerous bryophytes are more or less eliminated. Some may survive here and there on damp verges beside forest roads, but in general they die out.

The result of these various influences, some leading to an increase of the flora, others to a decrease, is that the overall effect of afforestation on the number of species present in an area is small. However, marshes and bogs are interesting habitats; and in areas where extensive afforestation is taking place it would be advisable to excercise restraint in planting them up. In that way, it should be possible to maintain the diversity of flora and habitat that many of us value.

ACKNOWLEDGEMENTS

The work on which this paper is based, was done for the Nature Conservancy Council and financed under NERC/NCC contract F3/03/78. I am grateful to my colleagues D.F. Evans and P.A. Stevens, of the Institute of Terrestrial Ecology, Bangor, for permission to quote some of their unpublished results.

REFERENCES

Bråkenhielm,S.(1977). Vegetation dynamics of afforested farmland in a district of southeastern Sweden. Acta Phytogeographica Suecica, 63, 1-106.

Brown,J.M.B. & Neustein,S.A.(1972). Natural regeneration of conifers in the British Isles. "Conifers in the British Isles". Proceedings Royal Horticultural Society 3rd Conifer Conference, London, 1970. pp.29-39. Royal Horticultural Society, London.

Clapham,A.R., Tutin,T.G. & Warburg,E.F.(1962). Flora of the British Isles. 2nd edition. Cambridge University Press, London.

Cousens,J.(1974). An introduction to woodland ecology. Oliver & Boyd, Edinburgh.

Dallimore,W. & Jackson,A.B.(1974). A handbook of Coniferae and Ginkgoaceae. Revised by S.G. Harrison. Edward Arnold, London.

Eber,W.(1972). Ueber das Lichtklima von Waldern bei Göttingen und seinen Einfluss auf die Bodenvegetation. Scripta Geobotanica, 3, 1-150.

Hill,M.O. & Jones,E.W.(1978). Vegetation changes resulting from afforestation of rough grazings in Caeo Forest, south Wales. Journal of Ecology, 66, 433-456.

Køie,M.(1938). The soil vegetation of the Danish conifer plantation and its ecology. Danske Videnskabaernes Selskabsskrifter, Series 9, 7, 1-85.

Peter,A.(1893). Kulturversuche mit 'ruhenden' Samen. Nachrichten von der königlichen Gesellschaft der Wissenschaften zu Göttingen, 17, 673-691.

Peter,A.(1894). Kulturversuche mit 'ruhenden' Samen. II. Mittheilung. Nachrichten der königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematische-Physische Klasse, 4, 373-393.

Rheinheimer,G.(1957). Ueber die Standorte der Moosvegetation in Nadelholzforsten bei Hamburg. Mitteilungen der Staatsinstitut für allgemeine Botanik, 11, 89-136.

Rheinheimer,G.(1959). Veränderungen der relativen Beleuchtungsstärke und der Bodenvegetation in einem Fichtenforst. Bericht der Deutschen botanischen Gesellschaft, 72, 246-250.

Robertson,S.U.(1976). The possible role of natural regeneration in Scottish forestry. Scottish Forestry, 30, 134-142.

Schlüter,H.(1966). Licht- und Temperaturmesungen an den Vegetationszonen einer Lichtung im Fichtenforst. Flora, Abteilung B, 156, 133-154.

Sissingh,G.(1975). Niederländische Nadelforsten und ihr Humus als Substrat für ihre Vegetation. "Vegetation und Substrat". (Ed. by H. Dierschke), pp. 317-41. J. Cramer, Vaduz.

Sjörs,H.(1965). Forest regions. Acta Phytogeographica Suecica, 50, 48-63.

Smith,A.J.E.(1978). The moss flora of Britain and Ireland. Cambridge University Press, London.

Toumey,J.T.(1929). The vegetation of the forest floor; light versus soil moisture. Proceedings 4th International congress of plant sciences, Ithaca, 1926. (Ed. by B.M. Duggar), Vol. 1, pp.575-590. George Banta, Menasha, Wisconsin, U.S.A.