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Ground flora and succession in commercial forests

M O HILL
Institute of Terrestrial Ecology, Bangor

1 Introduction

This paper describes the changes in ground flora induced by forestry in the uplands, emphasizing the long timescales and large spatial variations that are involved. Management options by means of which the forest manager may influence ground vegetation are outlined, considering both planted blocks and marginal habitats. Gaps in our knowledge are identified, and topics for further research are suggested.

Commercial forestry in Scotland generally starts with unplanted moorland, bog, heathland or heathy grassland. There are interesting exceptions to this generalization, such as afforestation of sand dunes and under-planting of uneconomic broadleaved woodlands; but the exceptions are almost all in the lowlands, and need not concern us here.

We are all aware that afforestation of unplanted ground is opposed, though not always simultaneously, by nature conservationists, landscape enthusiasts, hill walkers, grouse shooters and fishermen. Many of the arguments put forward by these people are based on a relatively narrow view of forestry, narrow both in time and in space. It is the business of the scientist to broaden the scope of the argument by putting the matter into a proper perspective.

2 Sources of data

In order to predict how vegetation will respond to various management options, the best source of information is direct experience based on long-term observation. For vegetation of planted forests in Britain, we are lacking in sources of such data from before 1940. From then on, there are a small number of long-term series of data, eg from Caeo Forest, south Wales, where observations date from 1944 (Hill & Jones 1978), J D Ovington's plots in southern England, where observations started in 1952 (Anderson 1979), and the Gisburn block of the Bowland Forest, a joint species trial started by the Forestry Commission (FC) and the Institute of Terrestrial Ecology (ITE), in 1955. A particularly notable series of observations is that started by ITE at Stonechest, just south of the Scottish border, in 1972 (Sykes *et al.* 1985).

In spite of these studies, we are seriously short of data based on long-term observation of particular sites. An alternative that can yield useful results is that of the chronosequence. When applied to Scottish forest vegetation, a chronosequence consists of a series of observations from supposedly similar sites that were planted at different dates. By comparing these sites and noting differences, patterns of vegetation change may be inferred. The method of the chronosequence is the classic one for documenting changes resulting from catastrophic events (fire, hurricane, landslip, etc) in natural vegetation. In the British context, the method has been applied with some success to succession in Sitka spruce (*Picea sitchensis*) plantations (Hill 1979) and to regeneration of birch (*Betula* spp.) scrub on moorland (Miles 1981).

The main difficulty with chronosequences is that they demand that the investigator has sound judgement as to what are, indeed, similar sites. Fortunately, various checks can be made. Detailed observations can be made on critical phases of vegetation change, for example on the phase immediately after clearfelling (Hill *et al.* 1984). It is also possible to check some of the theories that are derived by observation. Hill and Stevens (1981) had observed that many seeds germinating in forests after clearfelling are of species that seem unlikely to immigrate after the trees are cut down. This idea was confirmed by the observation that wind-borne seeds are largely confined to the superficial layer of conifer litter on the soil, whereas seeds of most other species are found in layers of the soil that were present before conifer litter started to accumulate (Figure 1).

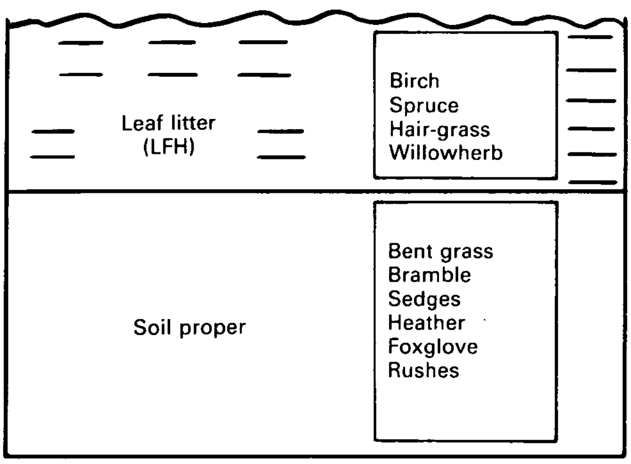

Figure 1. Position of buried viable seed in relation to the soil surface

Another kind of check that can be made is to see whether the pieces of information can be fitted together to make a coherent story. Such a story is sometimes called a word model, and it can be backed up by more quantitative models of particular aspects of the vegetation process. In particular, given a knowledge of certain species' power of spread and of their longevity as seed, it should be possible to predict the effects of various management practices on their abundance.

3 Vegetation changes in planted blocks

The vegetation changes that follow upland afforestation have been described at length elsewhere (Hill 1979, 1982). Some knowledge of these changes is necessary in order to evaluate the possible effects of differing management options. The long-term effect varies markedly from species to species (Table 1).

the west of Scotland in this habitat, and is very scarce or absent from other habitats in the west.

Fertilizer produces almost no qualitative effect on ground vegetation at this stage. It promotes the growth of plants that are already established, but does not lead to short-term changes, except in the presence of liming and heavy grazing (Milton 1940). Young forests are normally neither limed nor heavily grazed, so that fertilizer only helps to promote the growth of tussock grasses and dwarf shrubs that would increase anyway.

Table 1. Persistence of selected plant species in planted blocks of commercial forests (source: Hill 1978b)

	Scientific name	English name	Persistence in forest
	Agrostis capillaris	Common bent	Often abundant in clearcuts
	A. vinealis	Brown bent	Often abundant in clearcuts
D	*Anthoxanthum odoratum*	Sweet vernal-grass	Vanishes
I	*Betula* spp.	Birch	Generally increasing
D	*Calluna vulgaris*	Heather	Copious germination in clearcuts
	Carex binervis, C. pipulifera	Sedges	Locally abundant in clearcuts
I	*Deschampsia flexuosa*	Wavy-hair-grass	Often abundant in clearcuts
I	*Digitalis purpurea*	Foxglove	Locally abundant in clearcuts
I	*Dryopteris dilatata*	Broad buckler-fern	Abundant colonist after thinning
I	*Epilobium angustifolium*	Rosebay willowherb	Clearcuts on better soils
D	*Erica tetralix*	Cross-leaved heath	Scattered seedlings in clearcuts
D	*Eriophorum angustifolium*	Common cottongrass	Vanishes
D	*E. vaginatum*	Hare's-tail cottongrass	Scattered seedlings in clearcuts
D	*Festuca ovina*	Sheep's-fescue	Vanishes
	Galium saxatile	Heath bedstraw	Often abundant in clearcuts
	Juncus effusus	Soft rush	Copious regeneration in clearcuts
D	*J. squarrosus*	Heath rush	Scattered seelings in clearcuts
D	*Molinia caerulea*	Purple moor-grass	Dying out in planted blocks
D	*Nardus stricta*	Mat-grass	Vanishes
	Pteridium aquilinum	Bracken	Vanishes under Sitka spruce
I	*Rubus fruticosus*	Bramble	Rapid increase on better soils
I	*Sorbus aucuparia*	Rowan	Seedlings germinate in clearcuts
D	*Scirpus cespitosus*	Deergrass	Vanishes
	Vacinium myrtillus	Bilberry	Frequent to abundant

I increasing
D decreasing

3.1 Establishment to canopy closure (0–14 years)

The first major effects of afforestation are site preparation and cessation of sheep grazing. In Galloway, the usual result is a large increase of heather (*Calluna vulgaris*) and purple moor-grass (*Molinia caerulea*). Indeed, by the time that the trees are 5 years old, these species are normally dominant throughout the young forest. The same response is doubtless found elsewhere, though with a tendency for heather to be relatively more important in the east. Several common species of plant, such as deergrass (*Scirpus cespitosus*), heath rush (*Juncus squarrosus*) and mat-grass (*Nardus stricta*), rapidly decline.

Drainage and cessation of grazing are the main causes of the early increase in tussocky and shrubby species. Ploughing produces much less effect. Indeed, ground that is exposed by deep ploughing often remains bare for 5 years, becoming colonized by lichens and mosses. One species of moss, the rather attractive *Polytrichum longisetum*, has become widespread in

3.2 Canopy closure to clearfelling (14–55 years)

The effect of canopy closure depends strongly on the species that has been planted. Under Sitka spruce, all ground vegetation except mosses normally disappears; even mosses persist only in small amounts. A similar elimination can normally be observed under all species of conifer that cast a heavy shade, notably Norway spruce (*Picea abies*), Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Under pines (*Pinus* spp.) and larches (*Larix* spp.), the effect of canopy closure is harder to predict. There can sometimes be quite appreciable survival of ground vegetation, but, equally, there can often be almost no survival. Bracken (*Pteridium aquilinum*) is an interesting plant to observe at this stage. If it can survive the thicket stage under larch, it then becomes abundant in mature plantations, but it is quite often eliminated by larch thickets. On the other hand, small amounts of bracken almost always survive under pines, to increase again after thinning when more light reaches the forest floor.

The differences between the ground vegetation found under differing crop species are greatest shortly after canopy closure. For example, Ovington (1955) found very large differences between the vegetation under broadleaves and shade-casting conifers at 22 years. However, when the same plots were re-observed by Anderson (1979), 44 years after planting, the vegetation under all crop species resembled that which might be found in a native oakwood, and included bramble (*Rubus fruticosus*), bracken, creeping soft-grass (*Holcus mollis*) and bluebell (*Endymion non-scriptus*).

There were still marked effects of differing crop species. Bluebell was most plentiful under deciduous crops; wood-sorrel (*Oxalis acetosella*) was most plentiful under crops with thin litter; bracken and bramble were particularly abundant under Corsican pine (*Pinus nigra* var. *maritima*). Nevertheless, it was the similarity of the ground flora under differing crop species at this stage that was most impressive, not the differences.

Ovington's plots were on mineral soils in the English lowlands. The vegetation response to differing crop species on moors and in the uplands is more distinctive. Under densely shading crops such as Sitka spruce, there is often no appreciable ground vegetation at the time of clearfelling. In the lowlands, on the other hand, mature and fully thinned stands of Sitka spruce can support quite a rich ground vegetation. Upland plantations of pine and larch normally admit sufficient light to the forest floor to permit appreciable development of ground vegetation, with grasses (*Agrostis* spp., *Deschampsia* spp.), heather, broad buckler-fern (*Dryopteris dilatata*), bramble and bilberry (*Vaccinium myrtillus*) prominent, especially on extraction racks.

3.3 Clearfelling and replanting

Events following clearfelling depend rather precisely on the condition of the crop. If the stand was of good Sitka spruce, with no ground vegetation and little windthrow, then early regrowth of vegetation may be dominated by species that have lain dormant for a long time in the soil, notably heather, foxglove (*Digitalis purpurea*), rushes (*Juncus* spp.), sedges (*Carex* spp.) and gorse (*Ulex* spp.). Seeds of all these species can survive as buried seed throughout the dark phase of the rotation. Evidence from experiments (Kivilaan & Bandurski 1973; Toole & Brown 1946) and chronosequences (Peter 1893, 1894) suggests that buried seeds do not survive much beyond 80 years, so that, although they may persist through one rotation, they will not survive for 2 (Figure 2).

For other species which lack the potential to survive as buried seed, the presence or absence of a few vegetative individuals may be critical. Bracken, for example, commonly survives only along roads and rides, and may spread some way back into planted blocks from there. Wavy hair-grass (*Deschampsia flexuosa*), often notably abundant in areas that have been clearcut, has seeds which do not survive beyond one year. Unless a small population is already established at the time of clearfelling, the grass will be unlikely to spread extensively before canopy closure.

Seeds of conifers and birch are commonly present in large numbers in conifer litter at the time of clearfelling. They then germinate in the spring and early summer after clearance. Sitka spruce seed is shed irregularly between October and March (Brown & Neustein 1972), so that some seed is likely to be present on the forest floor if the stand is felled at any time except late summer. Neither birch seed nor spruce seed survives for more than a year once shed.

Intermediate between the types of seed with long and short longevity are those that appear not to survive through a rotation, but which can survive for about 20 years. The 2 common species of bent, *Agrostis capillaris* and *A. vinealis*, are in this category, having large persistent seed banks (Thompson & Grime 1979) but not apparently surviving through to the end of a full forest rotation (Hill & Stevens 1981). Probably also belonging to this intermediate category are bird-dispersed species such as bilberry, bramble, raspberry (*Rubus idaeus*) and rowan (*Sorbus aucuparia*). These seeds are gradually introduced to the forest floor by defecation of birds roosting in the tree tops. Inference of their longevity is therefore difficult. Analogy with the bird-dispersed pin cherry (*Prunus pensylvanica*), which was studied in North America by Marks (1974), suggests that potential survival for about 40 years is likely.

Events following clearfelling depend, therefore, on a complex interplay of factors, of which one of the most important is whether populations can establish in the short window of time, say 15 years, before the canopy closes again. Also of great importance is the type of soil. On poorer upland soils, coarse weedy species such as bramble and rosebay willowherb (*Epilobium angustifolium*) make relatively poor growth. Grasses, heather, sedges and rushes then predominate, even when seed sources for the coarse weeds are present. The level of grazing also has a large effect. In Beddgelert Forest, north Wales, exclusion of sheep resulted in a much more rapid spread of wavy hair-grass than in places where sheep could nibble off the inflorescences.

4 Vegetation changes outside planted blocks

Although planted blocks occupy most of the land area in forests, other types of habitat are more important for survival of interesting species. Hill (1978a) examined the occurrence of plant species throughout the area of 2 completely forested 1 km squares in north Wales, and came to the conclusion that roadsides were the most important habitat for survival of plant species. Bogs, streamsides and unplanted blocks made a significant additional contribution, but rides contributed little because they were occupied by heather and tussocky coarse grasses.

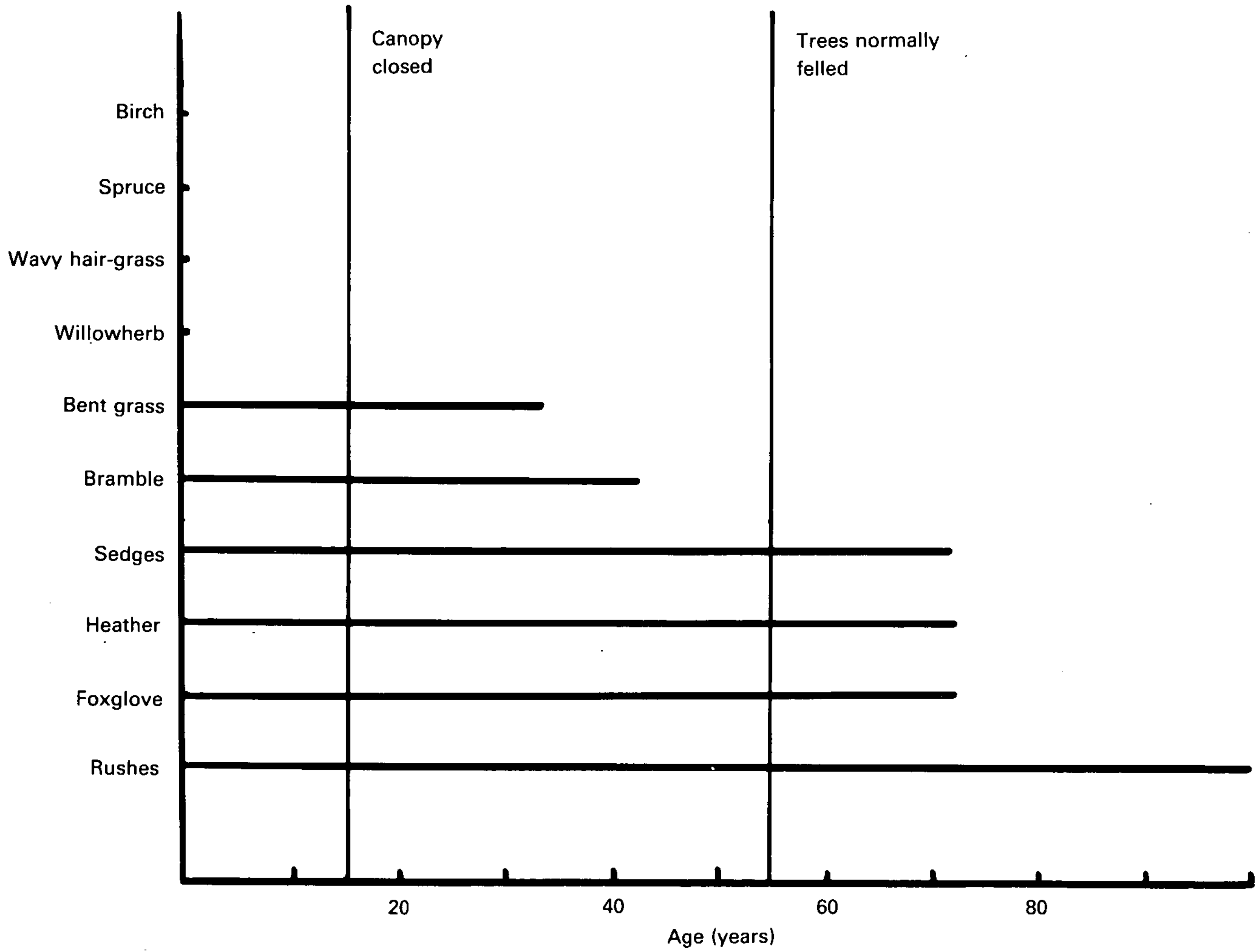

Figure 2. Seed longevity of selected species in relation to the length of a typical forest rotation

Roads do not, in fact, occupy a particularly large proportion of the total area in forests. Evans (1978) studied 5 Forestry Commission forests and estimated that 5% of their area was occupied by roads. Most of the interesting plant species grew on the verges, which accounted for only 1.6% of the forest area. The remaining 3.4% was occupied by banks, ditches and the road surface itself.

Streams and lakes can also contribute to the floristic diversity of forested areas, and the value of leaving unplanted margins is now generally appreciated. Goldsmith (1981) studied streams and lakes in a forested part of Galloway, and showed that, if the unplanted zone beside a stream is less than 3 m wide, very few species survived. Full floristic diversity was achieved with a 6 m margin, and marginal zones greater than 10 m wide could provide useful grazing for deer and other animals.

Unplanted areas within large forested blocks arise from various causes. Some are hilltops too high to plant, others are bogs where drainage would be costly, scree slopes where trees would grow too poorly, or smallholdings with a few fields. These areas often provide habitats for interesting plants or a supply of berries for birds. They are, however, unlikely to have much influence on the forest proper, unless they contain invasive and readily dispersed species such as birch, bramble and rowan.

5 Management options in relation to vegetation

5.1 Management of areas planted with trees

The vegetation of planted blocks generally has little intrinsic interest, even during the light phase between clearfelling and canopy closure. In this respect, it resembles the vegetation of the moors and grassland that had occupied the ground before afforestation. It follows that forest management of planted blocks should be directed not towards influencing vegetation as such, but towards primary objectives whose achievement may be affected by vegetation. The most notable of these objectives are crop establishment in the presence of weeds, maintenance of site fertility, creation of suitable habitats for ruminants and birds, and improvement of the visual impact of felling coupes and restocked areas.

The weed problem varies enormously from site to site. On poorer soils, heather is likely to be the only serious

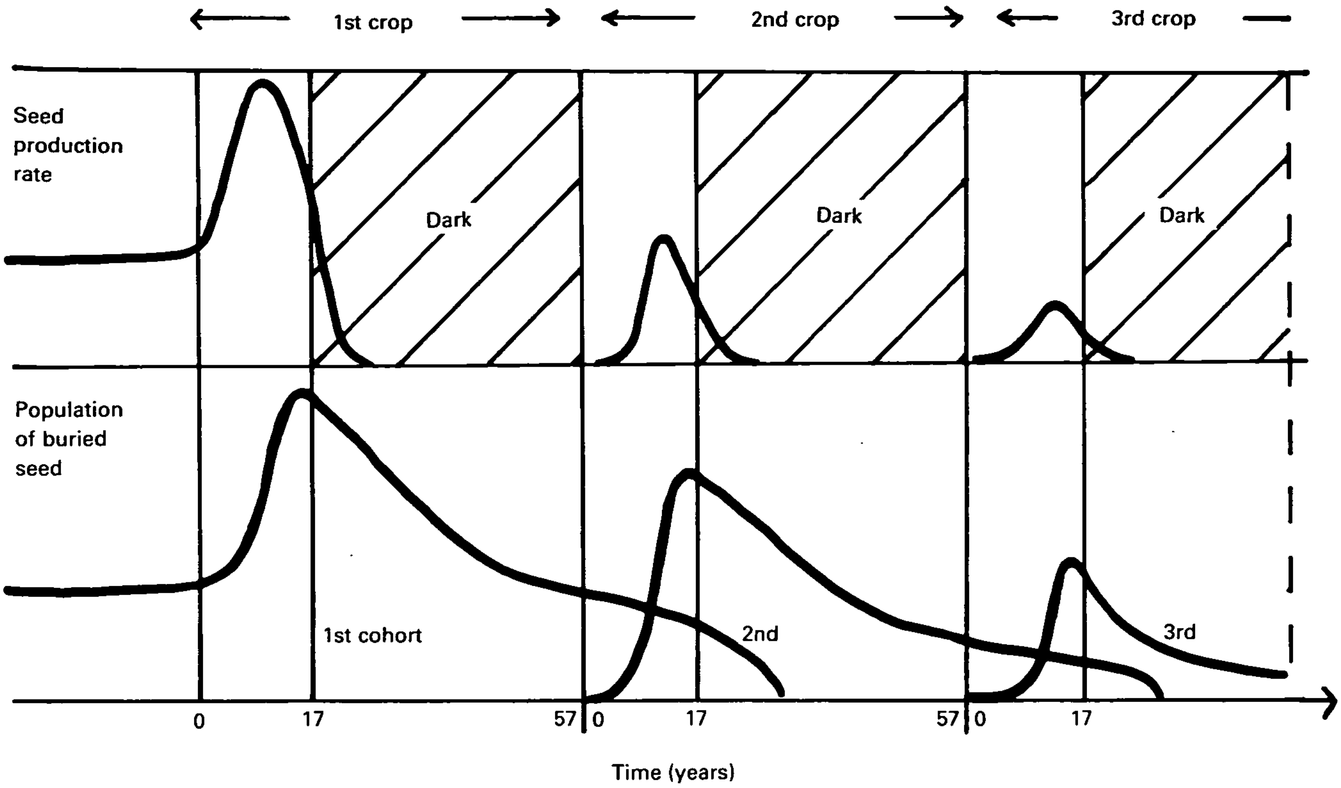

Figure 3. Hypothetical pattern of decline in heather population over 3 crop rotations

weed. In the first rotation, it is generally controlled by herbicide. The effect on the appearance of the site is dismal, but the trees fairly quickly close their canopy thereafter. It is interesting to speculate as to whether there will be an appreciable heather problem in later rotations (Figure 3). At the beginning of a first rotation on heathland, the soil contains buried viable seed from several decades of heather growth. Depending on the longevity of heather seed (currently unknown but probably more than 50 years), much more heather may germinate when the first crop is clearfelled than when the second crop is cleared. Indeed, with a timely herbicide application, very little heather seed may be shed between the end of the first rotation and closure of the canopy of the successor crop.

On fertile lowland sites, it is necessary to replant as quickly as possible after clearfelling, if weeds are not to make tree establishment difficult. On upland sites, there is much more flexibility, and there is a possibility that delayed replanting could serve some purpose in wildlife management. Some years ago, I was told by a forest manager working for Buccleuch Estates that delayed replanting could help in reducing damage to young trees by roe deer.

On the question of whether ground vegetation can have a significant effect in maintaining site fertility, there is little information. In some contexts, it could serve a useful purpose in retaining nitrogen in the ecosystem, as suggested by Marks (1974). For phosphorus retention, it is probably irrelevant, because mineralized phosphorus is adsorbed in the top layers of the soil. If so, then ground vegetation is of little advantage to the forester in upland Britain, where nutrient limitation of crop growth is generally due to shortage of phosphorus, not nitrogen.

One of the major management options that can affect vegetation is the choice between whole-tree harvesting, with lop and top removed from the site, and conventional methods of felling, in which lop and top, often called 'brash', is left on the site to decompose. Brash is certainly ugly, and it delays regrowth of ground vegetation. Furthermore, it hinders replanting. If visual amenity is considered to be of high priority at a site, then whole-tree harvesting is to be preferred. At present, there is no market for chipped branches, so that even with whole-tree harvesting, the brash must be disposed of at the roadside. This creates a further blot on the landscape, and one which is all too apparent to visitors, because it is beside the roads along which they will walk. The best policy would be to burn this superfluous material. In many other countries it is burnt; why not in Britain?

The smothering effect of brash is less with species other than Sitka spruce, so that 'greening up' of clearfelled sites is quicker. Hardwood twigs decompose much faster than conifer brash. Anecdotal evidence suggests that Sitka spruce brash is not only the most copious but also the least readily decomposed of all the conifer residues that one normally encounters in Britain. If the greening-up of the site after a short rotation is deemed to be desirable, Sitka spruce should be either avoided or harvested as whole trees.

5.2 Management of whole forests

We are still remarkably ignorant about the survival and spread of plant species at the landscape scale. Many animals, by contrast, are well known to range over the landscape, so that this is the natural scale at which to consider them, but the landscape scale is undoubtedly relevant also to some plant species. Birch seeds can be carried over several hundred metres by strong winds. However, in a cleared Sitka spruce plantation with a row of standing birches along the road, birch regeneration may be much reduced at a distance of only 100 m from the road.

Afforested areas are necessarily different from the rangelands that they have replaced. Fire is eliminated, grazing reduced and water supplies to marshes diverted. These influences are inimical to small and specialized wild plants of open ground. In lowland forests on sandy ground, vegetation along forest edges is commonly kept open by harrowing. Such semi-open communities are of great floristic interest. Similar effects can be achieved in the uplands by mowing verges and by occasional, but not too frequent, regrading of roads.

Nevertheless, the forest environment is generally one that favours development of scrub, ericoid shrubs and tall grasses. Interesting small plants will survive chiefly where there are either special topographic features, such as rivers or rocky bluffs, or where there is active management.

Is scrub development desirable? Steele and Balfour (1979) have suggested planting 10–20 ha nature conservation blocks along watercourses, using birch, hazel (*Corylus avellana*) and alder (*Alnus glutinosa*). These blocks would be left as permanent features, and would occupy 5% of the forest area. Such a policy, although interesting, would be costly. Broadleaved plantations would get some of the best ground. On the other hand, the worst ground often has greatest topographic variation, so that the best gains in natural history interest may result from leaving the worst ground unplanted.

Miles and Kinnaird (1979a, b) have described methods of promoting scrub regeneration on moorland, but there is no necessity to confine this activity to the first rotation. In most cleared forest plantations, regeneration of trees occurs naturally. It would ordinarily be sufficient not to replant selected areas for their second rotation and to leave nature to take its course.

Unfortunately, there is one important respect in which naturally regenerating vegetation can no longer be trusted. This is because of the spread of rhododendron (*Rhododendron ponticum*). In western Britain, rhododendron can be expected soon to occupy large areas of woodland, moorland and poor grassland (Shaw 1984). Traditional land use is incapable of excluding it, and it threatens to reduce large areas to an impenetrable thicket.

The rhododendron problem is potentially most serious in woodlands and wooded ravines in the west. Western ravines are notable as a habitat for bryophytes, especially for the rare Atlantic hepatics that are a unique feature of the British and Irish flora (Ratcliffe 1968). There can be no doubt that dense rhododendron along ravine-sides would shade out many of the best bryophyte habitats. Forestry could serve as a valuable adjunct to management for conservation in such places. Provided that the forest manager maintains a policy of rhododendron exclusion, interesting broadleaved woodlands and ravines can be conserved within a matrix of commercial plantations. However, if the matrix is moorland or open hill, and if rhododendron is starting to invade, then exclusion of rhododendron from woodlands and ravines will be almost impossible.

6 Conclusions and recommendations for research

Most of the management recommendations that are made above are non-controversial, and agree with the Forestry Commission's recent recommendations on wildlife conservation in restocked areas (Low 1985). At the present time, these ideas are beginning to be put into practice in upland north Wales, and doubtless also in parts of Scotland. For example, in Beddgelert Forest, north Wales, the Commission have drawn up a restocking plan which assigns 6% of the land area to 'long-term forest structure'. This long-term structure includes natural scrub, planted hardwoods, mature conifers and open water.

While it is gratifying to see the results of conservation-orientated research from the past decade being put into practice so rapidly, some important questions remain unanswered. Particularly interesting is the question of the overall survival and spread of plant populations in forested areas. Forests are far more dynamic than the grasslands and shrublands that they have replaced. In grasslands, individual clones may persist for centuries or millenia. In forest plantations, plant populations must constantly be on the move. So we need an understanding of the dynamics of plant populations at the landscape scale. How far do plants spread from refuges by roads, by streams and in hardwood clumps? How significant are such landscape features in the maintenance of plant populations in the longer term? To answer these questions, we require a combination of observations on permanently marked and repeated surveys of a few selected forests.

At a more practical level, we still need better documentation of the response of vegetation to differing crop species and site types, especially in the period after clearfelling. Events after clearfelling depend not only on the vegetation present under the crop when it was felled, but also on the rate of litter breakdown and nutrient release from the forest floor, and on the rate of disappearance of woody harvesting residues. All of these factors depend on the preceding species of crop.

Finally, it is worth giving serious consideration to the question of whether conifer plantations might be used by nature conservationists to provide *cordon sanitaire* against invasion by rhododendron. Does the spread of rhododendron adversely affect Atlantic bryophtes? If it does, can rhododendron be excluded from sensitive areas by suitably managed conifer forests?

7 Summary

Commercial forest plantations are large in area and take about a century to attain a pattern of age classes approximating to a normal forest. Effects of forest management on the non-crop vegetation need to be considered over commensurate areas and timescales. Within planted blocks, all vascular plants are eliminated during the thicket stage by Sitka spruce, and also by other spruces, firs and western hemlock. Survival of some vascular plants under larch and pine is normal. In mature upland plantations, there is often quite appreciable vegetation cover under larch and pine, but almost none under the crop species that cast heavier shade. After clearfelling, vegetation regrowth can be rapid, especially if the amount of brash is not excessive. Depending on the state of the ground vegetation at the time of clearfelling, the source of propagules may be existing vegetation or buried viable seed.

Vegetation within planted blocks is of little intrinsic value and its management should be considered in relation to crop establishment, wildlife and visual amenity. Most of the more interesting vegetation in forests is found along roads and streams. The value of leaving good unplanted margins has now been widely appreciated. There is a general tendency for scrub to develop in afforested areas. Such scrub should be encouraged. Parts of the forest that will not yield a commercial return of timber should be allowed to develop naturally.

Spread of rhododendron is a serious threat to good botanical habitats in western Scotland. The possibility of using forestry as a means of excluding rhododendron from threatened areas deserves consideration from nature conservationists.

8 Acknowledgements

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