

Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations

J.W. HUMPHREY*

Forest Research, Northern Research Station, Roslin, Midlothian, EH25 9SY, UK

* E-mail: jon.humphrey@forestry.gsi.gov.uk

Summary

European forestry strategies place emphasis on developing alternative management practices to clearfelling within commercial forests as a means of increasing the non-market benefits of sustainable forestry. In the UK, many thousands of hectares of forest are being transformed to continuous cover forestry and a number of minimum intervention natural reserves are being created to encourage the development of old-growth conditions. This paper defines the term 'old growth' in the context of upland spruce-dominated plantations in Britain and evaluates different options for the location, design and management of old-growth areas to enhance biodiversity. Evidence outside of Britain from semi-natural analogues of upland spruce plantations suggests that old growth can develop 100–200 years after stand initiation in those parts of the landscape not subject to frequent catastrophic disturbance by wind and fire. Old-growth stands in these forests are characterized by a high proportion of large, old trees, multiple age classes and high volumes of fallen and standing deadwood. Studies of old spruce stands in the British uplands suggest that old-growth features can begin to develop after 80–100 years, conferring substantial benefits to species-groups such as hole-nesting birds, mammals (e.g. red squirrel), bryophytes, lichens and fungi. Based on the likelihood of wind damage it is suggested that ~50 per cent of the current land area in upland Britain could support large patches (50–100+ ha) of old growth. To enhance colonization by woodland species, these old-growth patches should be within 2 km of existing semi-natural woodland, managed ideally on a minimum intervention basis. If production of timber was also an objective, old-growth stands could be managed by single tree selection or small group-fell silviculture, provided that over-prolific regeneration of shade-tolerant conifers was controlled and some deadwood and veteran trees were maintained. In surrounding areas subject to normal patch-clearfelling, small enclaves of old-growth forest (0.25–2 ha) could be retained to provide temporary habitat for species and facilitate dispersal through the landscape. The planning and design of old-growth areas needs to be considered at the landscape scale to ensure an appropriate balance between old growth and other types of woodland and non-woodland habitats. An imaginative approach to incentives will be required to encourage positive management for old growth.

Introduction

Biodiversity is a key component of sustainable forest management and has become firmly enshrined in international forestry policy and practice over recent decades (MCPFE, 2002; Rollinson, 2003). In the 1990s, management for biodiversity in the UK was driven largely by statutory nature conservation requirements such as site protection, implementation of the UK Biodiversity Action Plan (UK Biodiversity Action Plan (BAP); Anon., 1995), and the adoption of the UK Forestry Standard with its associated guidelines (Anon., 2004). UK BAP initiatives such as the restoration of native woodland on planted ancient woodland sites, and the establishment of new native woodlands, will form a significant part of sustainable forest management for the foreseeable future (Thompson *et al.*, 2003). However, the positive role of plantations in the conservation of biodiversity is being increasingly recognized world-wide (Brockerhoff *et al.*, 2001; Hartley, 2002; Lindenmayer *et al.*, 2003). In Britain, there is raised awareness of the value of plantations comprising introduced conifer species as habitats for native flora and fauna including some endangered species (Petty *et al.*, 1995; Humphrey *et al.*, 2002b) and of the need for improved integration with native woodland (Mason *et al.*, 1999a) and other habitats at the landscape scale, e.g. through Forest Habitat Networks (Peterken, 2003).

Part of the value of plantations relates to the potential area available for habitat enhancement. In Britain, ~76 per cent of the 2.8 million ha of forested land in the UK is made up of plantations (Forestry Commission, 2002). These could play a significant role in ameliorating the effects of climate change on species by reducing the fragmentation of small isolated semi-natural woods (Peterken, 2003) and providing a resilient matrix that allows for species dispersal in response to anticipated geographical shifts in habitat availability (Hossell *et al.*, 2000).

Restructuring of plantations in 1980s and 1990s led to the creation of a multi-age class forest structure over large areas (Hibberd, 1985). This process went some way to reducing the large-scale visual impact of even-aged plantations and benefited species groups favouring the early successional stand stages such as songbirds associated with scrub

(Fuller and Browne, 2003). While many of these species of open ground and young woodland are of considerable conservation importance in upland Britain (Quine *et al.*, 2003) there have been repeated calls for retaining planted stands beyond normal economic felling rotations (over 40–60 years in the case of Sitka and Norway spruce) due to the perceived biodiversity benefits (Peterken *et al.*, 1992; Kerr, 1999; Quine *et al.*, 2003). The UK Forestry Standard (Anon., 2004) and the UK Woodland Assurance Scheme (Anon, 2000b) place emphasis on the creation of mature and old forest conditions using alternative silvicultural systems to clearfelling (continuous cover forestry – *sensu* Mason *et al.*, 1999b) and the designation of minimum intervention ‘natural reserves’. The intention of these measures is to create situations:

‘where trees can be retained for the long-term to provide an extended conifer woodland ecosystem, by the formation of the dead branches and large fallen wood characteristic of natural forests. Aim to retain 1% of the area where stands are reasonably stable’ (Anon., 2004)

Managers are actively engaged in implementing continuous cover forestry. For example, the Welsh woodland strategy (Anon., 2002) includes a commitment to transform 50 per cent of the state forest area to continuous cover within 20 years, although currently <10 per cent of state forests in Britain are managed in this way (Mason, 2002).

Given the current changes in policy and practice towards continuous cover forestry and natural reserves, there is ample incentive for increasing the amount of old-growth forest habitat in upland plantations in Britain. However, there are still many uncertainties inherent in this course of action. Firstly, given the oceanic and windy climate of upland Britain, and the lack of current research on existing stands retained beyond normal felling age (Mason and Quine, 1995), it is not known whether stands will survive being blown down long enough to develop mature habitat conditions over a sufficient area to deliver biodiversity benefits. Secondly, these potential biodiversity benefits have not been adequately quantified, and there may be more cost-effective ways of conserving biodiversity in plantation forests such as deforestation and creation of more

open ground (Peterken, 1996; Pywell *et al.*, 2002), management of edges and early successional habitats (Ferris and Carter, 2000) or conversion to native woodland (Thompson *et al.*, 2003). This paper reviews recent UK and international research with the objectives of:

- 1 Exploring the applicability of the old-growth concept to UK forests
- 2 Establishing the rationale for creating and maintaining old-growth stands in upland conifer forests
- 3 Determining the practical feasibility of creating and maintaining old growth and the biodiversity benefits that might accrue
- 4 Proposing management principles at stand and landscape scales for encouraging habitat development, including consideration of stand location and size, as well as silvicultural treatments

The focus is on the British uplands which include portions of Wales, northern England, southern Scotland and the Scottish Highlands (Figure 1). Climatically, the uplands comprise the Cool Wet, Warm Wet, Alpine, and Sub-Alpine climatic zones as defined by the Forestry Commission's Ecological Site Classification (Pyatt *et al.*, 2001). Moisture deficit (MD) is the primary climatic variable separating the uplands from the lowlands, with the latter occurring where MD values are greater than 90 mm (Pyatt *et al.*, 2001). The main commercial forest types within the uplands are dominated by Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with occasional stands of Douglas-fir (*Pseudotsuga menziesii*), larch (*Larix* spp.) and other minor conifers (Forestry Commission, 2002). Mason and Humphrey (1999) have reviewed the options for maintaining old-growth stands in pinewoods. This paper focuses on the prospect for creating and maintaining old growth within upland spruce-dominated plantations.

What is old growth in the UK context?

The term 'old growth' is widely used but difficult to define (Er and Innes, 2003). To some the concept of old growth is about stature, where aesthetic and spiritual values are attached to large trees such as the towering stands of Douglas-fir in

the Pacific Northwest (PNW) of North America (Carey, 2003b). In contrast, old growth is sometimes seen as being synonymous with the term virgin forest or forest untouched by man. Although the concept of old growth arose in the PNW (Franklin *et al.*, 1981), even in that region it has been difficult to ascribe quantitative discriminators of old-growth conditions which remain applicable across a range of different forest types (Er and Innes, 2003). When this is extended to consider boreal and temperate forest zones in Europe and Asia, quantification becomes even more problematic (Bengtsson *et al.*, 2000; Kuuluvainen, 2002).

Attempts have been made to discriminate old-growth stands from younger stands in terms of measures of species composition, function and stand structure. Certain species are thought to be dependent on old-growth conditions (Carey, 1998) such as epiphytic lichens (Storaunet *et al.*, 2000), saproxylic invertebrates (Alexander, 1998), fungi (Kruys *et al.*, 1999) and hole-nesting birds (Uliczka and Angelstam, 2000). Functional distinctiveness relates to the balance of processes such as mortality, growth and decay (Er and Innes, 2003). However, structural measures are thought to provide the most straightforward and reliable indicators of old growth (Carver *et al.*, 2002). Oliver and Larson (1996) describe old-growth stands as a structural endpoint coming after three process-based stages in forest succession following disturbance: stand initiation – colonization by young trees; stem exclusion – initial colonizing trees dominate the stand and there is death due to inter-tree competition; understorey reinitiation – canopy trees grow tall enough to let in side light and understorey of shrubs and advance regeneration begins to develop; old growth – overstorey trees die in an irregular fashion and some younger trees begin growing to the overstorey.

Old growth is considered to be more structurally heterogeneous than younger stands in relation to a range of features such as the occurrence of a multi-layered canopy of trees, large diameter live trees (some with broken tops), large volumes of standing and fallen deadwood and decaying ancient and veteran trees (Franklin *et al.*, 1986; Peterken *et al.*, 1992; Linder, 1997; Ohlson and Tryterud, 1999). Such characteristics are not usually found in the earlier stages of succession.

Structural indicators have been developed for old-growth Douglas-fir forests in the PNW (Spies and Franklin, 1991), but attempts to follow this approach comprehensively for other forest types are just beginning (Er and Innes, 2003; Gillis *et al.*, 2003). There is also increasing realization that stands can go through a number of profoundly different structural states whilst still being technically old growth (Franklin *et al.*, 2002). Alexander *et al.* (2003) reviewed the applicability of the old-growth concept to UK conditions and considered that:

‘Old-growth stands are stands in primary or secondary forests (including wood pastures and parkland) that have developed the structure and species normally associated with old primary woodland of that type that have sufficiently accumulated to act as a woodland ecosystem distinct from any younger class’.

This definition, based on the Convention of Biological Diversity (CBD) definition of old growth (<http://www.biodiv.org/programmes/areas/forest/definitions.asp>), allows for the development of ‘new’ old growth in secondary woodlands (when there is functional connectivity with existing old growth) and does not exclude woodland modified by management. Effectively, this separates the old-growth concept from that of virgin woodland. This is particularly important in the British context where, although sites may have been continuously wooded throughout history (i.e. site continuity as woodland), there may have been breaks in ‘habitat continuity’ of old trees and decaying wood. Such habitats can be re-introduced. There may also be instances where areas are structurally similar to old growth, but do not yet have the full complement of associated species for a variety of unknown reasons. Given the lack of old growth in the UK at the moment and the need to build up habitat linkages at the landscape scale to counter the effects of climate change (Hossell *et al.*, 2000), it would seem wise to include these stands within the umbrella of the old-growth concept.

Peterken (2000) has proposed that old-growth features can start developing in stands after 150 years of minimal intervention, but Butler *et al.* (2001) stresses the importance of taking the age of the dominant tree species into account. Thus old growth might develop in birch (*Betula* spp.) stands of 100 years, but not in oak (*Quercus* spp.) stands until over 250 years.

Development of old growth in upland spruce stands

Taking age and structure into consideration, it is proposed that old growth in upland spruce forests in the UK can be defined as areas of forest with:

- trees 80–100 years old or more
- a significant proportion of trees more than 80–100 cm diameter at 1.3 m height with some having deep crowns
- a mix of trees of different ages and sizes including broadleaves
- variability in vertical and horizontal structure
- occurrence of a shrub layer
- large volumes of standing and fallen deadwood

The relatively low age compared with that of, for example, oak is attributable to the rapid growth of spruce in upland Britain (Hibberd, 1991) and reflects evidence from analogous semi-natural spruce forests in Scandinavia and the PNW (Svensson and Jeglum, 2000, 2001; Deal and Tappeiner, 2002; Ott and Juday, 2002).

Upland spruce forests in the UK are, of course, far from natural in terms of their current structure and composition, but nevertheless are subject to natural processes of growth, disturbance, senescence and colonization by native species (Mason *et al.*, 1999a). A process of naturalization is taking place (Quine, 2001a) and many 80- to 100-year-old stands are beginning to develop the structural complexity and decaying wood habitats associated with old growth (Humphrey *et al.*, 2003e). For example, stands in Glenbranter and Inverliever forests (Figure 1) were found to have up to 10 trees ha⁻¹ over 80 cm in diameter (E.G. Poulson, unpublished data). Windthrow is also a common feature in some old stands creating considerable volumes of standing and fallen deadwood (Humphrey *et al.*, 2003c) (Figure 2).

Value of old conifer stands in the UK for biodiversity

Survey work reported by Humphrey *et al.* (2003e) suggests that old conifer stands in upland Britain can provide important habitat for species normally

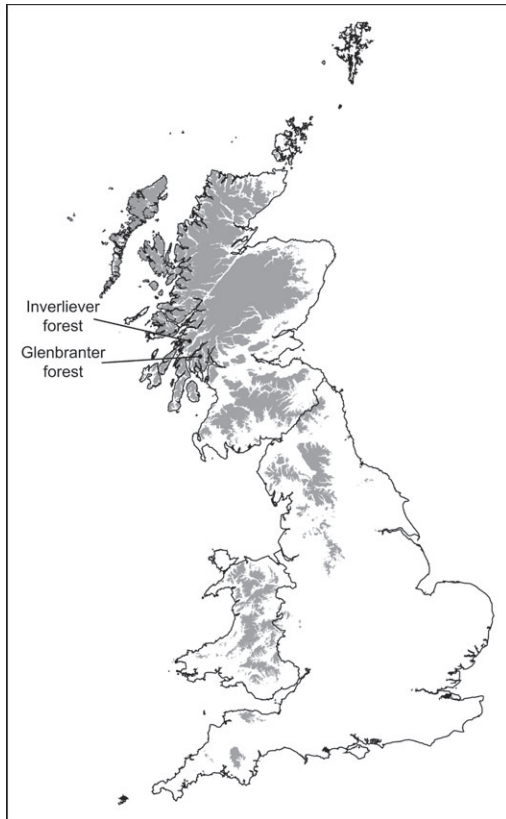


Figure 1. Map of Great Britain showing areas (shaded grey) regarded as uplands for forestry purposes (based on the Forestry Commission's Ecological Site Classification climate zones – Pyatt *et al.*, 2001). Locations of stands mentioned in the text are indicated.

associated with native woodland (both broad-leaved and Scots pine-dominated). Relationships between some of the key features which influence habitat value for dependent species groups are summarized in Table 1. For some groups (e.g. mycorrhizal fungi) planted stands appear to be as species-rich as semi-natural woodlands on similar site types (Humphrey *et al.*, 2000). Twenty-nine Red Data Book fungal species were recorded in upland Sitka spruce stands, a considerable number of these being species normally associated with native pinewood (Humphrey *et al.*, 2003b). The suggestion that some fungi, and other groups such as saproxylic diptera (Rotheray

et al., 2001) may be capable of 'host shifting' or expansion is substantiated, to some degree, through work by Fraser and Lawton (1994) who showed, as evidence of host expansion, that 5.5 per cent of British moth species are found on introduced conifers. The species were mostly polyphagous tree-based species.

Importance of deadwood

The most important structural feature defining old-growth stands is undoubtedly the occurrence of large, old trees and habitats associated with dead and decaying wood (Siitonen, 2001). There has been a wealth of research in temperate and boreal forests demonstrating the importance of decaying wood for biodiversity (Hunter, 1990; Samuelsson *et al.*, 1994; Esseen *et al.*, 1997). Managed stands invariably have much less deadwood than old growth (Kruys *et al.*, 1999; Fridman and Walheim, 2000; Similä *et al.*, 2002) and is one of the main reasons why many species associated with old growth are much less abundant in younger managed stands (Ross-Davis and Frego, 2002; Carey, 2003a).

For a considerable number of woodland species in Britain, decaying wood is vital for sustenance and shelter for all or part of their lifecycle (Alexander, 1998). It may be that some specialist saproxylic species will never colonize planted spruce stands, either because the substrates are

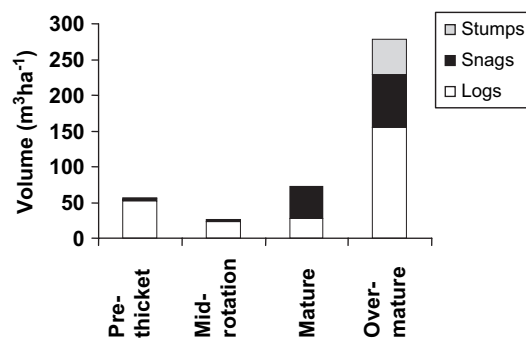


Figure 2. Volumes of deadwood in different stages of upland spruce stands. Pre-thicket stands were 8–10 years in age; mid-rotation 20–30 years, mature 40–50 years, and over-mature 60–80 years. From Humphrey *et al.* (2003c).

Table 1: Details of native species found in old stands in upland conifer plantations in relation to key features

Taxonomic group	Forest/stand type	Feature of importance	Response	Source
Ground vegetation community	Over-mature Sitka spruce stands in the Scottish Highlands	Heterogeneous light conditions including continuity of light shade	Increase in woodland herbs and ferns compared with younger stands; communities similar to those of semi-natural woodland on similar site types	Humphrey <i>et al.</i> (2003d)
Carabid (ground) beetles	Over-mature spruce and pine stands across Britain	Heterogeneous light conditions	Increase in proportion of forest specialist carabids in over-mature stands	Jukes <i>et al.</i> (2001)
Mycorrhizal and wood saprotroph fungi	Mature and over-mature stands of Scots pine and Sitka spruce in the Scottish Highlands	Dense canopy conditions with high fallen deadwood volumes; distance from stand to remnant native pinewood	High mycorrhizal and wood saprotroph diversity compared with younger stands; occurrence of threatened RDB* pinewood fungi in Sitka stands nearer to existing pinewoods	Humphrey <i>et al.</i> (2000) Humphrey <i>et al.</i> (2003b)
Stipitate hydroid fungi	Mature spruce and pine stands in the Scottish Highlands	Woodland canopy with trees of 20–40 cm in diameter; low intensity disturbance of ground layer	Species occurrence related to presence of trees, ability of fungi to host-shift from pine to other tree species	Newton <i>et al.</i> (2002)
Bryophytes	Over-mature stands of Sitka spruce in Scottish Highlands and Borders	Heterogeneous light conditions including continuity of shade and fallen deadwood	Richer bryophyte communities compared with younger stands – similar species complement to semi-natural broadleaved woodland. Species-richness related to size and decay status of fallen deadwood	Humphrey <i>et al.</i> (2002a); Humphrey <i>et al.</i> (2003a)
Lichens	Over-mature stands of Scots pine and Sitka spruce in the Scottish Highlands and Borders	Gaps in canopy; large volumes of standing deadwood	Lichen diversity increases with amount of light and well-decayed snags	Humphrey <i>et al.</i> (2002a); Humphrey <i>et al.</i> (2003a)
Red squirrel	Mature and over-mature stands of Norway spruce and Scots pine	Older trees produce larger and more reliable cone crops and better sites for drays	Conifer cone crops help maintain red squirrel populations in large planted forests	Cartmel (2001); Lurz <i>et al.</i> (2003)

Continued

Table 1: Continued

Taxonomic group	Forest/stand type	Feature of importance	Response	Source
Small mammals	Mature Scots pine and Corsican pine (<i>Pinus nigra</i> var. <i>maritima</i>) stands	Structural complexity of conifer canopy	Conifers had higher densities of wood mice than semi-natural woodland, due to better provision of aerial habitat and shelter in the conifer stands	Howes and Perrow (1993)
Song birds and hole-nesting birds	Over-mature conifer stands in general	Patches (min. 2 ha) of retained conifers with standing and fallen deadwood, gappy canopy, well-developed shrub layers	Cavity nesters benefit from standing deadwood (e.g. great spotted woodpecker, pied fly catcher); firecrests (<i>Regulus ignicapillus</i>) siskins (<i>Carduelis spinus</i>) and goldcrests (<i>R. regulus</i>) like open deep-crowned trees in Norway spruce/Douglas-fir mixes; patches of shrubs benefit willow warbler (<i>Phylloscopus trochilus</i>), chiff-chaff (<i>Sylvia hippolais</i>) and thrush (<i>Turdus philomelos</i>)	Currie and Bamford (1982); Currie and Elliot (1997)
Capercaillie (<i>Tetrao urogallus</i>)	Mature and over-mature stands of spruce and pine	Large areas (>50 ha) of old conifer woodland (pine or fir) with varied structure	Pine and fir provide winter food, ericaceous shrubs provide summer food; large trees provide perches on lek sites	Kortland (2003); Picozzi <i>et al.</i> (1992)
Raptors	Over-mature conifer stands in general	Large trees, open structure	13 out of 16 raptor species which breed in upland forest use old stands for breeding or foraging	Petty (1998); McGrady (1997)
Canopy invertebrates	Mature conifer forest	Dense canopy conditions	Structural complexity of the canopy promotes high diversity and abundance of spiders and other invertebrates	Hambler and Speight (1995); Ozanne (1996); Ozanne (1999)
Lepidoptera	Conifers in general	Bark, trunks and foliage	5.5% of angiosperm-feeding lepidoptera recorded feeding on conifers	Fraser and Lawton (1994)

Continued

Table 1: Continued

Taxonomic group	Forest/stand type	Feature of importance	Response	Source
Detritivores and other stream invertebrates	Mature and over-mature conifers in riparian zones	Fallen deadwood in streams facilitating retention of organic matter	Detritivore diversity and abundance increases in response to additional deadwood in streams (>10 cm diameter); logs provide habitat for larvae of crane flies (<i>Lipothrix</i> spp.)	Dobson and Cariss (1999); Linstead and Gurnell (1999); Humphrey <i>et al.</i> (2002c)
Saproxylic diptera	Spruce stands in north-east Scotland	Decaying sap under bark and decaying sapwood on fallen deadwood and stumps	25 diptera species of which three are notable feeding on sap and using stumps as nest sites	Rotheray <i>et al.</i> (2001)
Pinewood flora	Mature stands of Scots pine	Shaded conditions, light disturbance of the ground layer	Herbs such as twinflower (<i>Linnaea borealis</i>)	Pitkin <i>et al.</i> (1995); Mason and Humphrey (1999)

* RDB = Red Databook.

not suitable, or the species do not have adequate dispersal abilities and remain restricted to sites with long-term continuity of decaying wood habitats (Butler *et al.*, 2002). Spruce is unlikely to support species that are specific to particular trees such as the oak polypore fungus (*Piptoporus quercinus*) or the Rannoch sprawler (*Brachionycha nubeculosa* – a moth associated with veteran birch and willow *Salix* spp.). However, it is worth noting that there has been much less research into the ecology of deadwood and veteran tree-dependent species in the uplands than in the lowlands.

Data in Table 1 suggest that some species are capable of utilizing decaying wood in plantations and of dispersing considerable distances between patches of suitable habitat. Uncommon hole-nesting birds such as pied flycatcher (*Ficedula hypoleuca*), redstart (*Phoenicurus phoenicurus*) and great spotted woodpecker (*Dendrocopos major*) (Currie and Elliot, 1997) utilize standing deadwood in old planted stands, while raptors such as goshawk (*Accipiter gentilis*) use upturned root plates as prey plucking posts (Petty, 1998). Recently, Humphrey *et al.* (2000, 2002a) have demonstrated the value of fallen and standing deadwood in old spruce stands for supporting diverse populations of wood saprotroph fungi, lichens and bryophytes. Old conifer stands along parts of streamsides can provide input of large diameter deadwood into the riparian zone benefiting aquatic diversity (Dobson and Cariss, 1999).

Influence of structural complexity

The structural complexity of the dense conifer canopy appears to be an important feature for some invertebrates (Hamblen and Speight, 1995), but mature trees also provide higher levels of cone productivity than younger trees (Ratcliffe and Petty, 1986) providing a vital resource for birds such as crossbills (*Loxia* spp.; Summers and Proctor, 1995) and for red squirrels (*Sciurus vulgaris*; Lurz *et al.*, 2003). Similarly the abundance of epiphytic lichens and hole-nesting birds increases with tree age, size and depth of crown (Holimon *et al.*, 1998; Boudreault *et al.*, 2002). In the case of the red squirrel, retained stands of conifer provide crucially important habitat, as the red is out-competed by the non-native grey

squirrel (*S. carolinensis*) in broadleaved woodland (Lurz *et al.*, 2003). A number of species groups, such as the carabids, also benefit from the heterogeneous light environments found on the forest floor in old stands (Table 1).

Distribution of old growth at the landscape scale in relation to natural disturbance regimes

Natural disturbance has a profound effect on the structure, pattern and dynamics of forest landscapes and plays a key role in the maintenance of biodiversity in natural boreal and temperate forests (Linder *et al.*, 1997; Quine *et al.*, 1999; Kuuluvainen, 2002). Increasingly, forest design and management is being based on a consideration of the scale, pattern and legacy of natural disturbance in forest landscapes (Angelstam, 1998; Bell, 2003). Broadly speaking, fire is the key disturbance factor in boreal forests while wind dominates coastal temperate and nemoral forests (Quine *et al.*, 1999). Large herbivores, such as wild cattle and horses, are thought to have been the main disturbance agent in lowland European forests in pre-historic times (Vera, 2000), but the putative dynamics of this process have been obscured by hundreds of years of stock management in woodlands (Mitchell and Kirby, 1990). Also large herbivores are not thought to have had such a dominant effect on the dynamics of upland forest types in comparison to lowland forests (Svenning, 2002).

A distinction is usually drawn between forests that are subject to low frequency catastrophic disturbance, where whole stands are destroyed, and forests where high frequency chronic and less damaging disturbance is the dominant feature. Both types of disturbance result in sequences of forest development that end in structurally diverse forests (Franklin *et al.*, 2002). Most natural disturbances leave structural legacies which then in turn influence the structural development of the new stand (Fries *et al.*, 1997; Franklin *et al.*, 2002).

In simple terms, large areas of old-growth forests develop where the time interval between stand replacement events is longer than the time taken for the dominant trees to reach biological maturity (Quine *et al.*, 1999). The spatial distribution of old growth in the landscape can change over time in

response to disturbance, but there can also be continuity at the forest patch scale (Wimberly, 2002). For example, significant areas of old growth can survive in refugia in landscapes dominated by frequent fire disturbance (Zackrisson *et al.*, 1995; Jasinski and Angelstam, 2002) and also as open, spatially diverse stands with a scattering of over-mature trees at different densities (Franklin *et al.*, 2002).

No forests can be considered entirely natural and free from human influence, but significant areas of semi-natural wooded landscapes can still be found in some parts of Europe and North America which yield examples of old-growth conifer-dominated stands and their dynamics (Peterken, 1996; Fries *et al.*, 1997; Lähde *et al.*, 1999; Jasinski and Angelstam, 2002). Quine *et al.* (1999) suggest that the western hemlock–Sitka spruce forest zone in south-east Alaska and northern British Columbia may provide a relevant analogue for the development of old-growth stands in windy oceanic climates such as in northern and western Britain. The complex topography of this zone results in a mix of two disturbance regimes with large-scale infrequent blow-downs, and small-scale chronic canopy gap formation from death of one or several trees (Alaback, 1990; Ott and Juday, 2002). The latter is thought to predominate over much of the landscape (Alaback and Juday, 1989) possibly in the region of 70–80 per cent of total land area (Kramer *et al.*, 2001).

Although fire is an important disturbance agent of boreal and hemi-boreal forests in Fennoscandia and Russia (Jasinski and Angelstam, 2002), Fries *et al.* (1997) estimated that between 12 and 30 per cent of the area of Norway spruce forest in Scandinavia was dominated by gap phase dynamics driven by wind. Historical research has allowed the identification of areas of old growth and uneven-aged stands dominated by Norway spruce (Ohlson and Tryterud, 1999; Storaunet and Rolstad, 2002). These support many of the species of upland semi-natural woodland in Britain such as the lichens *Lobaria pulmonaria* and *L. scorbiculata* (Storaunet *et al.*, 2000). Unfortunately, due to the fragmented nature of old forest in Norway and the lack of relevant studies, it is difficult to determine the effects of disturbance at the landscape scale, and to estimate how much of the landscape would be suitable for the development of large areas of old growth.

Native pinewoods in the Scottish Highlands provide potential references for spruce forests as they have a longer site-history and also contain species with the ability to colonize spruce stands (Humphrey *et al.*, 2000). However, opportunities for comparison are limited by the small spatial extent of pine on similar site types and within comparable climate zones to spruce, and by the pervasive influence of management on the structure of native pinewoods. Natural disturbance regimes are thought to vary across the pinewood zone with those in the east more affected by fire (Worrell, 1996), and those in the west, sympatric with the main spruce areas, being dominated by wind disturbance (Hope, 2003). Recent models of western pinewood development in relation to wind disturbance suggest that over 50 per cent of the forest landscape would be in the old-growth stage, on average, over a period of 1000 years (Hope, 2003). Similarly, Quine *et al.* (1999) and Quine *et al.* (2002) estimate that between 24 and 55 per cent of the forest landscape in upland Scotland might be capable of supporting large patches of old growth in low wind risk areas, with smaller patches surviving in more exposed locations.

In response to the effect of disturbance, it is likely that the patch size distribution of old growth across the landscape would be right-skewed (see Wimberly, 2002) with a small number of large patches and many small patches. Landscape planning could therefore incorporate this principle with a few large non-intervention reserves balanced with the retention of small pockets of old growth in other stands. The question arises as to whether this landscape model is appropriate for maintaining populations of key species and, if so, where the patches of different sizes should be located in the landscape.

Spatial configuration and size-class distribution of old growth patches in relation to species ecology

Size of old-growth patches

There have been various attempts to define a minimum size of functional woodland, as there is recognition that interior habitat differs from edge

habitat and supports different species assemblages (Ozanne *et al.*, 2000). Edge effects are thought to occur up to 50 m into a stand (Ozanne, 1996), so it follows that, in order to have any interior habitat at all, a circular woodland needs to be at least 0.8 ha in size. Given that other factors such as tree height, shrubs and topography affect edge width, threshold sizes of 1–3 ha have been proposed, ideally 5 ha (Peterken *et al.*, 1992; Currie and Elliot, 1997).

The problem with the minimum size concept is that different species require different minimum patch sizes. In pinewoods and other boreal forests, intact forest areas of over 50 ha may be needed to sustain populations of capercaillie (*Tetrao urogallus*) (Kortland, 2003) and similar species (Niemela, 1999). Conversely, small fragments of old growth could provide temporary refugia for some species (e.g. woodland ground flora species) in highly managed landscapes (Franklin *et al.*, 2002). Given the same total area, collections of small stands may hold as many species as a single large stand (Magura *et al.*, 2001; Mason, 2001). Sætersdal *et al.* (1993) found that over 75 per cent of the cumulative area of 60 deciduous woods in Norway was required to ensure that all rare vascular plant species were represented in at least one patch. As most upland landscapes are managed for a variety of objectives, the option of a few large reserves (50–100+ ha to provide habitat for species requiring large areas) in some areas combined with a higher frequency of small patches in other areas would seem to be a pragmatic solution for retaining old-growth species, as it would allow zoning of management approaches. For example, clearfelling could continue in parts of the landscape where the retention of small patches was the dominant management approach.

Connectivity of old-growth patches to foster dispersal

Part of the strategic approach to locating large old-growth patches would take into account the degree of connectivity between the intended old-growth stand and other ancient and long-established woodland to allow colonization and dispersal of the desired species. This does not simply mean physical connectivity as Peterken

et al. (1992) emphasized; functional connectivity is the key to determining whether species can move between suitable habitat patches (Lindenmayer *et al.*, 2002). Certain upland landscapes appear to be more ‘permeable’ to woodland species than more intensively managed lowland landscapes, i.e. the matrix or area between suitable habitat patches is more conducive to species survival as they disperse (Peterken, 2003). This might be because of higher forest cover in general or due to the occurrence of other semi-natural habitats such as heathland, wet grassland, riparian zones, cliffs, rocky outcrops, etc., all of which can provide temporary refugia for woodland species (Peterken, 1996).

However, landscape permeability and hospitality to woodland species are only two of many factors which determine whether species can disperse between suitable patches. A key factor is the dispersal ability of the species themselves. Peterken and Game (1984) showed that ancient woodland plant species are very slow colonists of nearby secondary woods, with dispersal rates of 0.3–0.5 m a⁻¹ being typical. This has been supported by recent research by Vickers *et al.* (2000) and in other parts of lowland Europe (Verheyen and Hermy, 2001; Honnay *et al.*, 2002; Graae *et al.*, 2003). There are differences in dispersal abilities between plants which relate to dispersal mechanisms. For example, Grashof-Bokdam and Geertsema (1998) found that wind- and bird-dispersed seeds in secondary woods were dispersed further than ant-dispersed seeds. Dispersal distance for the more restricted species was ~100 m, but >500 m in some cases. It has been suggested that, in the past, propagules of woodland species may have been dispersed by large herbivores travelling over considerable distances (Gill and Beardall, 2001; Svenning, 2002). Recent experimental work with dogs has provided evidence that this could have occurred in the case of woodland herbs (Graae, 2002).

In oceanic temperate and boreal forests, there is evidence that the dispersal abilities of old-growth woodland species varies between different taxonomic groups (Esseen *et al.*, 1997; Nilsson *et al.*, 2001). Some species are dependent on long-term continuity of suitable habitat as they are unable to disperse between areas of suitable habitat (Ohlson and Tryterud, 1999;

Nilsson *et al.*, 2001). For example, the colonization of stands by old forest lichens and carabids is restricted by proximity of propagule sources and not habitat quality (Sillett *et al.*, 2000; Hilmø, 2001; Koivula *et al.*, 2002). In contrast, Martikainen *et al.* (1999) found that bark beetles in old-growth boreal stands are capable of travelling 10 km or more between areas of wind-blow. In spruce stands in south-east Norway, Økland (1996) found that mycetophilid diversity increased in old-growth stands in relation to the amount of old growth within a 100 km² area.

In Britain, many upland woodland species are capable of dispersal over considerable distances. In a study of invertebrates in upland birchwoods in the eastern Highlands, Woodcock *et al.* (2003) found no evidence that dispersal was limiting the development of coleoptera communities. Ratcliffe *et al.* (1998) reviewed the dispersal abilities of a range of key woodland species (both plants and animals) in the Scottish Highlands and found that maximum dispersal distances ranged from 100 m to over 20 km, with the vast majority of species able to disperse up to 2 km.

Also in upland oceanic areas there may be a larger 'pool' of inoculum available which would have a direct impact on the success of dispersal. For example, lichen and bryophytes occur in much richer and abundant assemblages in northern Britain where the climate is wetter and less polluted (Rose, 1993; Hodgetts, 1996; Humphrey *et al.*, 2002c). Humphrey *et al.* (2004) found that bryophyte species-richness in planted stands was positively correlated with the amount of semi-natural woodland within 1 km, with species such as woodland vascular plants, beetles and mycorrhizal fungi showing similar relationships with other measures of connectivity.

The implications of these findings are that old-growth natural reserves would be best placed in already well-wooded landscapes (Peterken, 2003), but there appears to be no ecological justification for focusing solely on creating physical linkage between old-growth stands and semi-natural woodland. Ideally the larger reserves would be no more than 1–2 km apart (Ratcliffe *et al.*, 1998), but the occurrence of small patches of old growth in windier areas could function as

'habitat stepping stone' linkages between the larger patches, or as temporary habitat (Niemela, 2001; Dolman and Fuller, 2003).

Prospects for survival of large old-growth reserves given minimal intervention

The most straightforward approach to creating old growth may simply be to designate areas as minimal intervention natural reserves (e.g. no stand management) and allow natural processes to generate variability in stand structure and higher volumes of dead and dying trees (Humphrey *et al.*, 2002c). Management would be restricted to the control of deer browsing (red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) to ensure tree regeneration, and removal of invasive species such as *Rhododendron ponticum*. The assumption in this approach is that old-growth structure can be maintained in perpetuity and is not replaced by other forest types or by open ground. Evidence from near-natural old-growth western hemlock–Sitka spruce stands in south-east Alaska (Taylor, 1990; Deal and Tappeiner, 2002; Ott and Juday, 2002) and from Norway spruce-dominated stands in Scandinavia (Ohlson and Tryterud, 1999) suggest that both species of spruce can self-perpetuate in stands subjected to small-scale 'gap-phase' disturbance.

In south-east Alaska, Sitka spruce actively regenerates in all-aged 300-year-old stands (Deal and Tappeiner, 2002). These stands typically have naturally created gaps (usually by wind) of <50 m² to 250 m² in size (Ott and Juday, 2002). Although there is a high degree of variability across the region, the shape of the gap-size distribution is invariably right skewed, with a high frequency of small gaps, and very few larger gaps (Taylor, 1990; Ott and Juday, 2002). Western hemlock is the dominant tree species on most sites, comprising 25–100 per cent of total stand basal area, with an average of 83 per cent (Deal and Tappeiner, 2002). Sitka spruce, although less shade tolerant than western hemlock, is capable of regeneration in the larger gaps. Norway spruce is more shade tolerant than Sitka (Nixon and Worrell, 1999) and, in Scandinavian old-growth stands, is capable of maintaining higher basal areas and canopy dominance than Sitka under gap-phase conditions (Linder *et al.*, 1997; Ohlson

and Tryterud, 1999; Storaunet *et al.*, 2000; Svensson and Jeglum, 2000). Studies of primary forest succession in Norway spruce forests suggest that old-growth conditions can develop after 100–170 years (Storaunet *et al.*, 2000; Svensson and Jeglum, 2001), although maximum tree ages in long-established old-growth stands in southern Norway range from 400 to 450 years (Ohlson and Tryterud, 1999).

Work in British upland spruce stands in Britain suggests that the ecological behaviour of Sitka spruce in this country is similar to that in south-east Alaska, with a minimum gap size of 150–200 m² needed to establish natural regeneration in stands of 30–40 m in height (Quine, 2001b). However, gaps of 1000–4000 m² may be necessary to allow development of good timber trees (Nixon and Worrell, 1999; Malcolm *et al.*, 2001). The general consensus is that Norway spruce, being more shade tolerant than Sitka, will grow successfully in gap sizes of 500–1000 m² (Nixon and Worrell, 1999; Malcolm *et al.*, 2001).

Given the evidence from overseas above, and the windy, oceanic climate of north-western Britain (Quine *et al.*, 1999) it seems safe to assume that both Sitka and Norway spruce are capable of self-perpetuation in upland conifer plantations given protection of regeneration from excessive browsing by red or roe deer (Nixon and Worrell, 1999; Quine, 2001a).

Silvicultural approaches to promoting and retaining old-growth structures

Within state forestry in Britain there is a move to create large (200+ ha) pilot areas of continuous cover in low-wind risk zones (Forest Enterprise, 2002). These areas could provide scope for developing mosaics of non-intervention old growth, and stands managed by low impact silviculture; the low impact stands acting as ‘buffer’ for the old-growth stands in terms of maintaining a constant micro-environment (Peterken *et al.*, 1992). This approach has also been advocated for retaining old-growth Norway spruce stands in south-east Norway (Ohlson and Tryterud, 1999).

However, some old-growth reserves could be subject to low intensity management if quality timber production were also an objective of these

continuous cover areas. Evidence from Alaska (Deal *et al.*, 2002) and from Norway (Storaunet *et al.*, 2000; Storaunet and Rolstad, 2002) suggests that selective logging is not detrimental to the maintenance of old-growth structures and associated species, provided that the stand is given time to ‘recover’ between interventions, i.e. to allow reinstatement of large diameter trees and deadwood.

Rolstad *et al.* (2001) found that, in Norway spruce stands in south-east Norway, a rich epiphytic flora survived on mature trees despite a history of selective logging. Also deadwood left after felling can develop the appropriate decay stages for rare fungi after 20–50 years (Groven *et al.*, 2002). Økland *et al.* (2003) found no strong effect of different cutting intensities on ground vegetation as long as humidity was kept high. Selective logging can also allow a greater proportion of broadleaves to be retained within Norway spruce stands (Jantunen *et al.*, 2002) and increase the abundance of understorey plants such as *Vaccinium myrtillus* (Bergstedt and Milberg, 2001) of value for woodland grouse (Atlegrim and Sjöberg, 1996).

In south-east Alaska, partial cutting of western hemlock–Sitka spruce stands stimulated the regeneration of Sitka spruce (Deal and Tappeiner, 2002). It was concluded that cutting no more than 40–60 per cent of basal area would ensure that old-growth structure was conserved, provided that some large and medium-sized trees, and logs were retained. Selective logging in these stands did not significantly affect understorey plant community diversity and composition unless >50 per cent of the basal area was cut (Deal, 2001). Ott and Juday (2002) suggest that patterns of basal area removal should mimic the size class distribution of natural gaps, with openings covering between 5 and 15 per cent of stand area, comprising a range of felling intensities from one to seven trees (with the largest number of gaps created by felling one or two trees). The aim would be to balance the creation of new gaps with the expansion of old gaps in equal proportion (Ott and Juday, 2002). Silvicultural interventions of this sort could be on a 20–80 year cycle to allow medium-aged trees to attain old-growth dimensions and for gaps to fill with regeneration. From this review of the management of old-growth spruce stands in Norway and Alaska four general

principles emerge which are applicable to upland spruce plantations in Britain.

1. In terms of biodiversity there is a need to view silviculture as a means of creating and perpetuating habitat quality rather than focusing solely on the objective of ensuring natural regeneration (Malcolm *et al.*, 2001). Of importance also is the need to work with natural processes, such as accepting decay and encouraging veteranization of mature trees (Read, 1999), as one of the key aspects of habitat quality to maintain are old trees and decaying wood (Humphrey *et al.*, 2002c).
2. Selective logging in Norway and Alaska appears to equate to single-tree selection systems or small group systems in upland Britain (Malcolm *et al.*, 2001), but there is no reason why irregular shelterwood systems could not be used, provided that some areas remained uncut (Kortland, 2003).
3. There is a risk that shade-tolerant species like western hemlock may invade stands managed on small gap silviculture system (Deal and Farr, 1993) creating excessively shaded conditions and loss of understorey diversity. Some thinning of shade-tolerants will be necessary to retain habitat quality.
4. If it is intended to manage reserves on a non-clearfell system, it may be necessary to identify potential stands at an early stage of development, so that preparatory management can be undertaken (Mason and Kerr, 2001). For example, variable density thinning (Carey, 2003a) could be used to transform regular structure stands into irregular structure, thus enhancing wind-firmness (Mason, 2002) and allowing large trees with deep crowns to develop to provide adequate seed for future regeneration.

In line with the landscape design principles outlined previously, small patches of old growth (0.25–2 ha; Mitchell and Beese, 2002) could be created and retained in areas surrounding the larger old-growth reserves to provide temporary habitat or stepping stones between the larger reserves.

Conclusions

The lack of over-mature woodland with veteran trees and decaying wood habitats is a major cause

for concern in the UK, since such a large part of the woodland biota is dependent on these habitats, including many rare and threatened species (Butler *et al.*, 2001, 2002; Humphrey *et al.*, 2002c). The creation of old-growth stands in upland spruce plantations could bring significant benefits for biodiversity, in particular for species associated with old trees and decaying wood habitats. Habitat values are likely to increase over time as stands become progressively more naturalized and are colonized by native broadleaved trees and shrubs (Mason *et al.*, 1999a; Thompson *et al.*, 2003).

Old-growth habitat values are distinct from those provided by open ground or younger woodland (either of native or introduced tree species). Whilst conversion of commercially unproductive plantations to young native woodland will derive some biodiversity benefits, these benefits will be restricted, for at least the first 100–300 years (depending on tree species), to creation of habitat for early and mid-successional species. The creation of new native woodland on currently unwooded ground presents a similar scenario. In contrast, mature plantations may develop old-growth structure within 20–70 years and thus could make a more rapid contribution to the creation of substantial areas of new habitat for late successional and deadwood species. The large-scale nature of many planted forests presents an opportunity to create an extensive matrix for species to move through which would help counteract the effects of climate change (Hossell *et al.*, 2000).

The issue of minimum proportions of old growth in the landscape is best determined by consideration of the impact of natural disturbance and species dispersal statistics. In terms of wind risk, ~50 per cent of the existing land area could contain large old-growth reserves. This is substantially more than the current recommendation of 1 per cent (Anon., 2000b). The approach suggested from this review, is the establishment of a small number of 50–100+ ha reserves located in sheltered parts of the landscape, no more than 2 km from semi-natural woodland fragments. The exact number and location of these reserves within individual catchments/landscapes would be determined by the need to balance provision of old growth with other kinds of habitats.

The key to reconciling different objectives for biodiversity is to plan at the landscape scale and develop strategies for integrating old-growth stands with other forest and non-forest habitats. The Forest Habitat Networks which are currently being developed for areas of upland Britain (Ratcliffe *et al.*, 1998; Anon., 2000a) will provide a framework for delivery of biodiversity objectives at wider spatial scales, and will guide the integration of different land-use options.

Alternative silvicultural systems to clearfelling could be used to both speed up the transformation of young stands to old growth, and to perpetuate old-growth structure once it has been established. The underlying principle would be to focus on providing outputs, i.e. large old trees, decaying wood habitats, and variable canopy conditions, rather than pursuing any particular system. Any approach which does not include specifications for the retention of old trees and deadwood will fail to conserve a substantial portion of biodiversity at the stand-scale.

However, stands of old trees are likely to be retained for other reasons as well as biodiversity enhancement. Many are located near recreation facilities to provide amenity benefits, or on sites with poor access where extraction would not have been cost effective. Groves of large trees have aesthetic value and provide excellent recreational experiences. Increasingly, there is an emphasis on retaining permanency of forest structure in areas with high visual sensitivity, such as within popular view sheds and in landscapes with high aesthetic value. There are health and safety issues associated with retention of old trees and deadwood but it should be possible to manage risks to the public by carrying out regular checks of trees near footpaths and rights of way and other areas with high recreational pressure (Humphrey *et al.*, 2002c).

Although the vast majority of retained conifer stands are still very young in biological terms and research into management techniques for enhancing their biodiversity is in its infancy, the opportunities for pursuing a strategy of old-growth development in upland conifer forests are considerably greater now than in previous years. However, financial incentives will be needed to encourage owners and managers to develop old-growth stands. High quality timber could be produced from some stands provided

that markets were available but the cost of operations to create veteran trees and deadwood will need to be reimbursed in some way. This will require an imaginative approach to developing incentives, linked possibly to the idea of financing improvements in woodland conditions (Kirby *et al.*, 2002).

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