

INFORMATION NOTE

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SUMMARY

To predict how successful natural colonisation is likely to be, consideration should be given to the quantity and quality of seed, vegetation structure, vegetation type and browsing pressure. In the northwest Highlands, the majority (typically 90%) of Scots pine and birch seed normally falls to the ground within the first 60 m from the canopy edge. Greater dispersal distances can be achieved in the northeast of Scotland due to the different climatic conditions. The presence of advanced regeneration should be interpreted with caution and not taken as a positive indication of prospects for further colonisation. A combination of very low soil nutrient availability and high soil moisture provides very unfavourable conditions for colonisation of birch, rowan and Scots pine. Grassland sites are often too competitive for colonisation by these species although there may be opportunities for birch on drier, more nutrient poor sites and where diverse ground flora indicates an old woodland site.

Natural colonisation can be very successful, particularly on infertile sites with low soil moisture, recently disturbed vegetation and a good seed supply. Lack of success is likely to be due to insufficient germinable seed, rank or competitive vegetation, a wet site type with very low soil nutrient status or excessive browsing.

INTRODUCTION

Natural colonisation (the natural regeneration of trees on land adjacent to existing woodland) is the preferred means of achieving native woodland expansion (Forestry Commission, 1994). However, it is often difficult to predict how successful this process is likely to be. A range of factors need to be considered when assessing the potential of new schemes and planning remedial action on unsuccessful sites.

This Note develops the principles outlined by Harmer (1999). While it is particularly relevant to northern Scotland, many aspects are also applicable to upland colonisation schemes elsewhere in Great Britain. Tree species discussed are restricted to the ones most likely to colonise these site types: birch (both *Betula pubescens* and *B. pendula* unless one is specified), rowan (*Sorbus aucuparia*) and Scots pine (*Pinus silvestris*).

The recommendations in this note should achieve colonisation within a time frame compatible with an owner's objectives and meet the requirements of grant aid. Longer time scales may be acceptable where the objective is to re-establish specialist habitats such as treeline or bog woodland. This guidance is based on existing literature and results from a survey of colonisation schemes. The survey was carried out over 11 sites in the northwest

Highlands, central Highlands and Grampian. Schemes were between 5–10 years old with areas ranging from 9–1 100 hectares. The majority of vegetation types on these sites were heath, mire and bracken communities although some grass communities were also surveyed (Thompson and Milner, unpublished data).

SEED PRODUCTION AND DISPERSAL

The availability of sufficient seed should be a primary consideration when deciding whether to use natural or artificial regeneration. The number of trees likely to bear seed, their distribution in relation to the colonisation site and their potential to produce viable seed should be assessed.

Is the size of the seed source adequate?

The area of woodland adjacent to the colonisation site does not need to be extensive to provide sufficient seed: survey results recorded successful colonisation where the seed source was only 30–50 m wide. The length of woodland edge adjoining the colonisation site and the seed bearing potential of trees, particularly on the woodland edge, are more important. However, woodland remnants comprising a very limited number of trees (e.g. fragments



surviving on steep banks within gullies) are only likely to provide sufficient seed to regenerate areas equivalent to approximately one tree height in width. Isolated trees within the site can provide additional seed although, again, the majority of seedlings are likely to regenerate within 1–2 tree lengths of source trees. It should also be noted that very small populations of trees may be genetically restricted (i.e. composed of a small number of genotypes). This may result in limited adaptability, affecting their capacity to reproduce, to survive critical early stages of regeneration or to adapt to changing climatic conditions.

What scale of scheme is envisaged?

This will be influenced by the distance of seed dispersal. In three sites surveyed in the northwest Highlands, the majority of birch seedlings were within 60 m of the canopy edge (Figure 1). A similar pattern of dispersal occurs with Scots pine (Nixon and Worrell, 1999, Figure 2.4). The small percentage of seed dispersed beyond this can lead to gradual colonisation of areas remote from seed sources although this process is very unpredictable and often protracted. The survey showed greater dispersal distances in Grampian (high densities of seedlings were often encountered beyond 100 m and in some cases, up to 500 m see Figure 2 for an example – note the use of different axis scales in Figure 1). One explanation is that seed can be blown considerable distances across snow fields which are more likely to occur in this region during the period of seed dispersal.

Most rowan seeds are distributed by birds and it is difficult to predict the eventual location of seedlings from the position of parent trees. Large numbers of rowan seedlings may be widely distributed over open land given appropriate site conditions and sufficient seed sources.

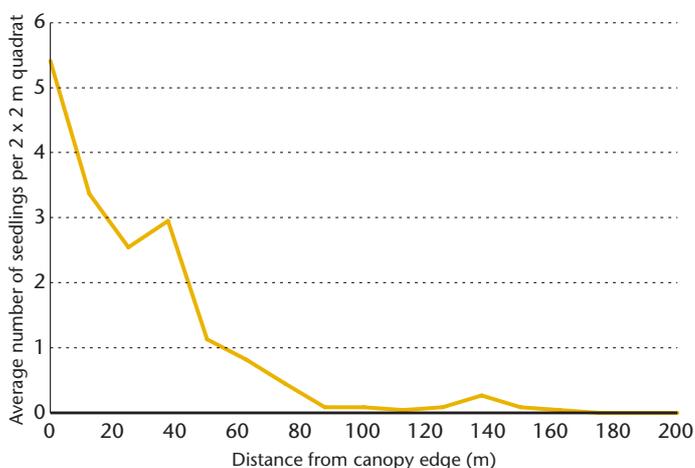
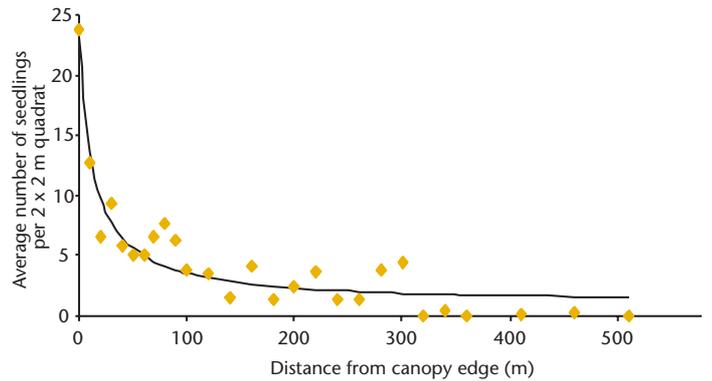


Figure 1
Number of birch seedlings over three north-west Highland sites against distance from canopy edge.

Figure 2

Number of birch seedlings against distance from canopy edge – example of a site in Grampian.



Where does the site lie in relation to the seed source?

The likely dispersal direction of Scots pine and birch seed should be considered in relation to the location of the colonisation site and the seed source assessed accordingly. Scots pine seed is dispersed between April and July by drying (easterly) winds. Birch seed may also be dispersed by drying winds although south westerlies are more typical during seed fall (between late August and December). Observations of large colonisation schemes with scattered seed sources show various directions of dispersal for birch: topography appears to be a key factor influencing local wind direction.

Is the quality of seed adequate?

Where few germinable seeds are produced, the period of colonisation may be protracted. Low seed viability is likely on sites with harsh climates: for example, the viability of birch seed within Inverpolly National Nature Reserve was between 2.5 and 15% (Emberlin and Baillie, 1980). Similarly, viability of Scots pine was as low as 2% at 270 m on Beinn Eighe (Miles and Kinnaird, 1979). Seed viability should not be a limiting factor for birch on less extreme sites with more favourable climates, since average values of between 25–40% have been recorded (Gordon, 1992 and Worrell, 1999 respectively). Decreasing viability of Scots pine seed has been observed with increasing altitude (Nixon and Cameron, 1994). Similarly, rowan was reported to have lower seed weight and viability with increasing altitude (Barclay and Crawford, 1984). Scots pine trees from isolated woodland fragments may produce fewer seeds of lower viability than trees from larger areas of woodland (Nixon and Edwards, 1997).

Is it possible to start the scheme in a good seed year?

In the absence of sufficient advanced regeneration (see below), success is more likely where the removal/reduction of grazing pressure is timed to coincide with a good seed year (ideally this should be immediately prior to seed fall). This should ensure minimal vegetation competition for newly germinated seedlings (see Vegetation structure). Typically, birch produces good quantities of seed every 3–4 years although frequency is reduced in areas with a more severe climate. An assessment of female catkins can be made in April/May to predict potential seeding, and it should be possible to confirm this in June. In a good year, 10–20% of trees will have abundant catkins (Worrell, 1999). Scots pine is also thought to produce seed frequently, although wide variation has been found between trees within a stand and between stands within any one year. In a 7 year study of native pinewoods at Mar Lodge by Edwards (in prep), only one good seed year was recorded. Scots pine typically produces around 800 cones per tree in a good seed year. Some estimate can be made the year before cones are mature (Gordon, 1992) although this cannot be confirmed until the August/ September prior to seed shedding the following spring. Care should be taken to distinguish between mature cones and spent cones from previous years (Nixon and Worrell, 1999).

SUITABILITY OF THE SITE FOR NATURAL COLONISATION

Once the seed source has been considered, a survey of the site should be undertaken to assess its suitability for natural colonisation. The frequency, abundance and distribution of advanced regeneration (see below) should be recorded together with a description of vegetation types, their distribution in relation to the seed source and their structure.

General observations on factors associated with present boundaries may help to determine whether the site is suitable, e.g. is there a sudden change in topography and/or soil type (altering levels of exposure or soil moisture), or has the woodland boundary been created by management (either of the woodland itself or of the adjacent land)?

Is there advanced regeneration?

The term advanced regeneration (AR) covers all seedlings present prior to any actions taken to initiate colonisation (e.g. reductions in grazing pressure). While this may

include recently established seedlings, in many cases the sward contains old seedlings which have been continually browsed-back to the height of surrounding vegetation. Where small seedlings appear to be newly recruited through rank vegetation, closer inspection will often reveal a large, browsed-back root stock deep within a carpet of bryophytes. The age of AR usually dates back to a disturbance event (e.g. fire or cessation of heavy grazing). This old advanced regeneration may account for the majority of seedlings in some colonisation schemes. Where high densities of AR exist, they are likely to respond rapidly to the removal or reduction of grazing animals and could be said to be ‘a woodland in waiting’.

The presence of AR needs to be interpreted with some caution:

- AR may occur remotely from existing seed sources where it has gradually colonised as chance events of suitable niche creation and widely dispersed seed coincided. Under these conditions, the length of time required to achieve satisfactory stocking rates may be very prolonged.
- Frequent AR at a low abundance should not be used as an indication of site suitability for further regeneration: these seedlings may have established many years ago under more suitable conditions for regeneration than those of the present day (e.g. after the vegetation had been disturbed by fire or heavy grazing compared with the well developed sward and deep litter layers present).
- AR within specific site types does not necessarily indicate that the whole site is suitable. For example, it is often abundant along roadsides where there is less deer pressure, soil disturbance from road construction and less competitive vegetation – particularly where land the other side of the fence has been grazed by sheep.

Complete absence of advanced regeneration is likely to indicate that either the site type is unsuitable (e.g. too fertile and competitive), that grazing or burning levels have been too high to allow seedlings to remain in the sward, or that there is insufficient germinable seed.

What is the vegetation structure?

This is a critical factor, particularly for birch, due to its inability to cope with competition from other vegetation. Food reserves within birch seed only allow seedlings to grow to 2 cm in height (the equivalent height for Scots pine is 8 cm) (Miles and Kinnaid, 1979). At this stage, seedlings need to emerge above, or into a gap in the

ground flora canopy to photosynthesise at a sufficient rate to provide all of the plant's food requirements. At the same time, seedling roots need to be in contact with a moist substrate. Some apparently suitable niches such as sphagnum mounds and mole hills can become too dry and lead to seedling death through drought. Rowan seedlings are shade tolerant and can cope with greater levels of competition. However, observations show a high abundance of seedlings only where competition is low.

Vegetation structure is largely determined by previous management and vegetation type. Successful regeneration of birch and Scots pine was observed:

- on heaths where heavy grazing preceded enclosure of grazing animals in a good seed year.
- where recently burnt or flailed heather provided areas of minimal competition.
- where very low levels of continued grazing by cattle or deer prevented the development of deep litter layers and reduced the abundance of species such as bracken. Regeneration can occur when red deer densities are <4–7 per 100 ha (Gill, 2000) and when cattle stocking rates are between 2.5 to 10 cattle months/ha/year (where cattle month is the product of stocking rate and length of time that cattle have access to the site – H. Armstrong, personal communication). Observations suggested that cattle can maintain suitable conditions for birch regeneration in purple moor grass.

Unsuccessful regeneration is often associated with:

- dense areas of bracken;
- heather in the *building* and *mature* phases where there are also deep layers of pleurocarpous (branched) mosses – typically *Hylocomium splendens* (see Box 1);
- competitive swards of grass, particularly 'improved' pasture.

It is often assumed that open niches will develop as vegetation structures decline beyond their optimum growth phase (e.g. the degenerate phase in heather >25 years old – see Box 1). However unvegetated patches rarely occur as shade tolerant species existing under the declining canopy quickly expand to fill available niches. Colonisation of mature, undisturbed vegetation is an unpredictable process and may take many decades, particularly on the more fertile site types considered here.

Box 1

Growth phases to describe heather (Gimingham, 1960).

- **Pioneer** – normally up to 3–6 years after disturbance. Period of establishment and early growth.
- **Building** – up to between 15–20 years old. Normal duration of about 10 years. This is the stage of maximum cover where bryophyte and lichen cover can be reduced to a minimum (short heather shoots bright green).
- **Mature** – up to about 25 years old. Normal duration of about 10 years. Central branches spread apart permitting sufficient light for establishment of mosses. (short heather shoots becoming duller).
- **Degenerate** – 25 years and older. Central frame branches die, leaving a gap. Peripheral branches may continue to grow horizontally and root adventitiously.

What vegetation types does the site contain?

Variations in soil fertility and wetness will be reflected by the variety and distribution of vegetation types across the site. An assessment of soil fertility and wetness should be made within the area of each main vegetation type to determine its suitability for colonisation. A useful way of doing this is to use the Ecological Site Classification (Pyatt *et al.*, 2001; Ray, 2001) (see Box 2) decision support system which uses climate data and field information from soil pits and vegetation quadrats. The interaction between soil moisture and soil nutrient status are considered under each vegetation type described below.

Box 2

Ecological Site Classification terminology.

SMR – Soil Moisture Regime: indicates availability or excess of soil moisture and availability of soil oxygen. The site types described in this Note fall within the Wet to Slightly Dry SMR classes. SMR is determined from soil type, rooting depth, texture and stoniness.

SNR – Soil Nutrient Regime: indicates the availability of soil nutrients for plant growth and the acidity of the soil. The site types described in this Note fall within the Very Poor to Medium SNR classes. The most accurate way to determine the SNR is to assess abundance of plant indicators within the site type.

Table 1 shows the suitability of site types and effect of vegetation structure for colonisation of birch and pine in the uplands. The distribution of vegetation types should be assessed in relation to areas which are likely to receive most seed.

Table 1

Broad indication of suitable site types, vegetation structure and prospects for successful colonisation.

Vegetation type	Prospects		
	Poor	Moderate	Good
Grasslands	Cocks foot, creeping soft grass	Herb rich (e.g. wood anemone, pignut) – old woodland sites or acid grassland with wavy-hair grass and tormentil	
Bracken	Dense bracken	Light bracken cover on nutrient poor sites	Sparse bracken in heather
Dry heath	Mature heather with deep layer of mosses		Recently burnt or heavily grazed
Wet heath	High abundance of deer grass	High abundance of heather and purple moor grass	
Mire	Cotton grass and deer grass – wet with low nutrient status	Cattle grazed purple moor grass	

- Scots pine/both birch species
- Scots pine and downy birch
- Both birch species
- Downy birch only

Poor

Low abundance (occurs in less than 10% of sampled quadrats) and low frequency (less than 500 stems ha⁻¹).

Moderate

Either clumped patches of regeneration (at densities of greater than 3000 stems ha⁻¹ within patches which may cover up to 30% of an area of this vegetation type) or well distributed seedlings at a low density (800–1000 stems ha⁻¹ widely distributed over this vegetation type).

Good

High abundance and high frequency (greater than 2000 stems ha⁻¹, widely distributed over this vegetation type).

Grasslands

- Regeneration of pine, birch and rowan is normally limited in grass swards due to high levels of competition for nutrients, water and light (see Vegetation structure).
- Where SNR is Poor to Very Poor and SMR is Slightly Dry, less competitive swards containing species such as wavy hair-grass (*Deschampsia flexuosa*) and tormentil (*Potentilla erecta*) may offer opportunities for the regeneration of birch and rowan.
- It is difficult to predict the threshold for site suitability on grasslands. Some birch regeneration was observed on richer sites (i.e. where the SNR is Medium), the flora of which is usually diverse (containing species such as wood anemone (*Anemone nemorosa*) and pignut (*Conopodium majus*) and often associated with old woodland sites. Successful regeneration was only observed on these sites where there was limited soil moisture (i.e. where the SMR is Fresh to Slightly Dry).

Bracken

- Bracken (*Pteridium aquilinum*) can occur on a range of site types. The SNR is usually poor and SMR usually Fresh to Moist but this can range from Slightly Dry to Very Moist.
- Light densities of bracken fronds are often encountered at the lower end of the Poor SNR, as a component of heather (*Calluna vulgaris*) dominated dry heath. This can provide suitable conditions for regeneration, in some cases, by limiting browsing pressure and possibly improving the microclimate.
- Where bracken is dominant, regeneration is only likely to establish on the edge of stands where side light is able to penetrate beneath the bracken canopy.
- If bracken control has been carried out, the developing sward should be re-assessed for its suitability. Moist sites at the richer end of the Poor SNR often have a competitive sward of species such as creeping soft grass (*Holcus mollis*) while drier, less fertile sites (composed of species such as wavy hair grass (*Deschampsia flexuosa*) or tormentil (*Potentilla erecta*) may be more suitable for colonisation (see Grasslands). Scarification may be beneficial on less fertile, drier sites (e.g. SNR: Poor to Very Poor, SMR: Slightly Dry to Fresh) if deep litter layers exist. Vegetation on moist, richer sites may be too competitive for successful colonisation by any species considered here.

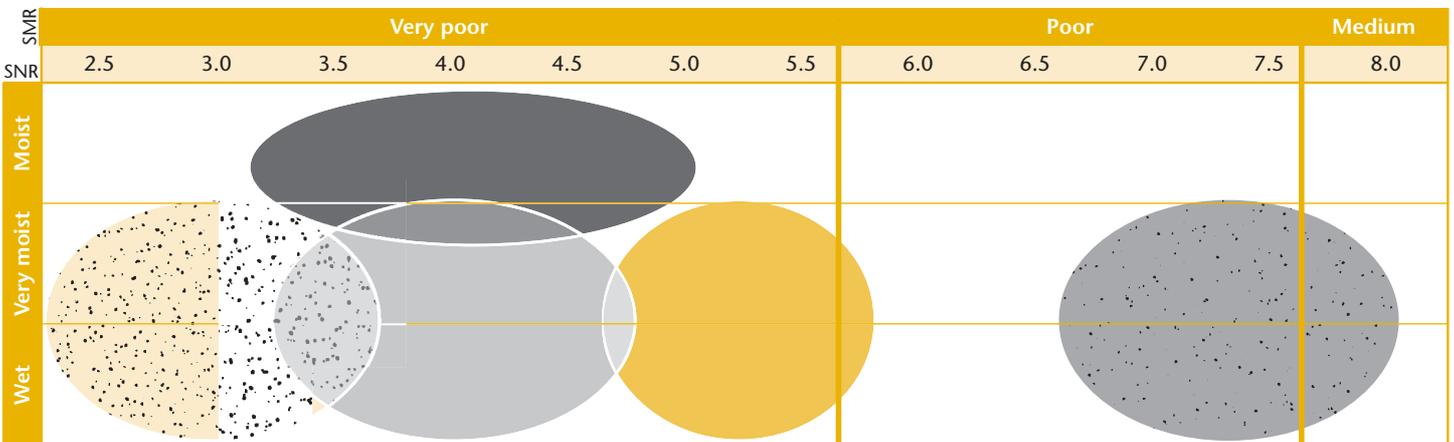
Dry heath

- Heather dominated dry heath occurs over a relatively small range of site types (i.e. they have Slightly Dry, occasionally Fresh SMR's and Very Poor, occasionally Poor SNR's).
- Climate influences both structure and species composition: higher rainfall increases the depth of pleurocarpus mosses and long periods of snow cover produce less competitive vegetation (characterised by species such as bearberry – *Arctostaphylos uva-ursi*).
- Although previous management usually has a larger influence over the structure of this vegetation type than composition of species, differences between dry heath communities affect their suitability for colonisation. In general terms, those in the drier northeast (e.g. Grampian) maintain less competitive (and therefore more suitable) conditions for colonisation over a longer period than the more oceanic dry heath communities (see Box 1).
- Scots pine regeneration is most frequently encountered on this vegetation type, typically on podsolc soils overlying glacial deposits.

Wet heaths and mires

- For downy birch the most important factor influencing the suitability of these vegetation types is the availability of nutrients in relation to water logging. Sites become unsuitable where there is a very low soil nutrient status and restricted rooting depth due to soil wetness. The colonisation survey recorded a lower threshold of site suitability for downy birch regeneration where the SMR is Wet to Very Moist and the SNR is at the lower end of the Very Poor class (i.e. where Hill-Ellenburg soil nutrient values fell below 4.5. See Ray, 2001 and Figure 3).
- Very young Scots pine seedlings are killed in water-logged conditions, restricting their distribution to drier microsites on wetter vegetation types. Where they survive, older seedlings are restricted by nutrient availability in a similar way to downy birch.
- Where Scots pine and downy birch seedlings are encountered on blanket mires, they will usually be at very low densities, with very slow growth rates. In the majority of cases, seedlings are unlikely to develop into established trees, although examples of bog woodland

Figure 3 Suitability of wet heaths and mires for colonisation, using Ecological Site Classification (with reference to Pyatt, in prep).



Vegetation type	Typical plant indicators	Prospects for tree regeneration	Typical NVC community
	Cotton grass, deer grass/cotton grass, heather blanket mire.	Very poor prospects – only for bog woodland.	M17/M19
	Cross-leaved heath, deer grass.	Downy birch more likely to colonise than Scots pine although prospects are normally poor.	M15
	Heather and purple moor-grass wet heath.	Potential for frequent downy birch although often at a low density.	M15
	Heather dominant wet heath.	Potential for frequent downy birch and rowan although often at a low density. Some limited prospects for Scots pine.	M15
	Purple moor-grass mire.	Potential for moderate regeneration of downy birch (usually clumped patches).	M25

do occur (e.g. Scots pine regenerated onto previously cut-over bog in Abernethy).

- On wet heaths dominated by cross-leaved heath (*Erica tetralix*) and deer-grass (*Trichophorum cespitosum*) downy birch is more likely to colonise than Scots pine, although prospects are normally poor.
- On wet heaths where heather is dominant, seedlings of downy birch are often encountered, though usually at low densities. Rowan is only found on these drier examples of wet heath, at similar densities to downy birch (e.g. at Craig Meagaidh).
- On more nutrient rich wet heaths, purple moor grass (*Molinia caerulea*) and heather are abundant and conditions can become suitable for downy birch regeneration (given appropriate vegetation structure) albeit usually at a low density.
- On nutrient flushed mires, purple moor-grass becomes dominant and birch regeneration can occur in clumped patches, particularly where vegetation structure is undeveloped due to recent or continued grazing by cattle.

How easily can browsing animals be controlled?

The condition of the sward prior to the start of a regeneration scheme is a critical factor, with a greater level of success being observed where heavy grazing and browsing has preceded deer control or fencing. Where the continued presence of deer is planned (i.e. control by culling without fencing), general recommendations are that the density of animals should be in the region of 4–7 per 100 ha. However, the density of herbivores generally varies across landscapes and some sites will be more susceptible to heavy browsing than others (e.g. low altitude sites, in otherwise exposed areas, where large numbers of deer shelter in the winter). Some areas have very high rabbit populations. These can only be reduced sufficiently through the co-operation of neighbours and use of techniques such as box trapping (Pepper, 1998).

CONCLUSIONS

There are many opportunities for the expansion of upland birchwoods and native pinewoods through natural colonisation, particularly where adjacent ground within the dispersal distance of seed sources is composed of suitable vegetation types, where vegetation structure is not

rank or competitive and where browsing animals can be reduced to an appropriate level.

Seed dispersal distances are usually greater in the northeast than the northwest of Scotland. While this may be due to climatic differences, the processes involved are not fully understood.

Where there is abundant advanced regeneration, simply reducing grazing pressure may be adequate to achieve established natural colonisation. However, where AR occurs at low densities or is restricted to certain vegetation types, consideration should be given to the conditions which allowed these seedlings to establish and the current structure of vegetation or distribution of suitable vegetation types.

The Ecological Site Classification decision support system is a useful tool to identify thresholds of site suitability, particularly where soils are wet and infertile. Further work is necessary to identify thresholds for Scots pine, birch and rowan where vegetation becomes too competitive on moist fertile soils.

Checklist for proposed colonisations schemes

Is there sufficient seed?

Is the extent of the proposed scheme realistic given the distribution of seed trees and location of suitable vegetation types?

Is the orientation of the scheme suitable for seed dispersal?

Is there any advanced regeneration? If so:

- Is there enough for the desired stocking?
- How old is it?
- If very old and only a few 'seedlings' exist, has vegetation structure become unsuitable or is AR restricted to more suitable site types?

If there is no advanced regeneration:

- What is the limiting factor and can it be controlled?

Is vegetation structure rank? Would the introduction of grazing animals such as cattle be realistic or is mechanical treatment such as flailing an option?

Are you confident about the characteristics of the site types within the scheme? If marginal site types exist (e.g. grasslands, mires or wet heaths) have you used ESC to help determine their suitability?

If bracken control has taken place, is the remaining sward suitable for colonisation?

Is it possible to reduce browsing pressure (i.e. start the scheme) in a good seed year?

How easily can browsing animals be controlled?

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