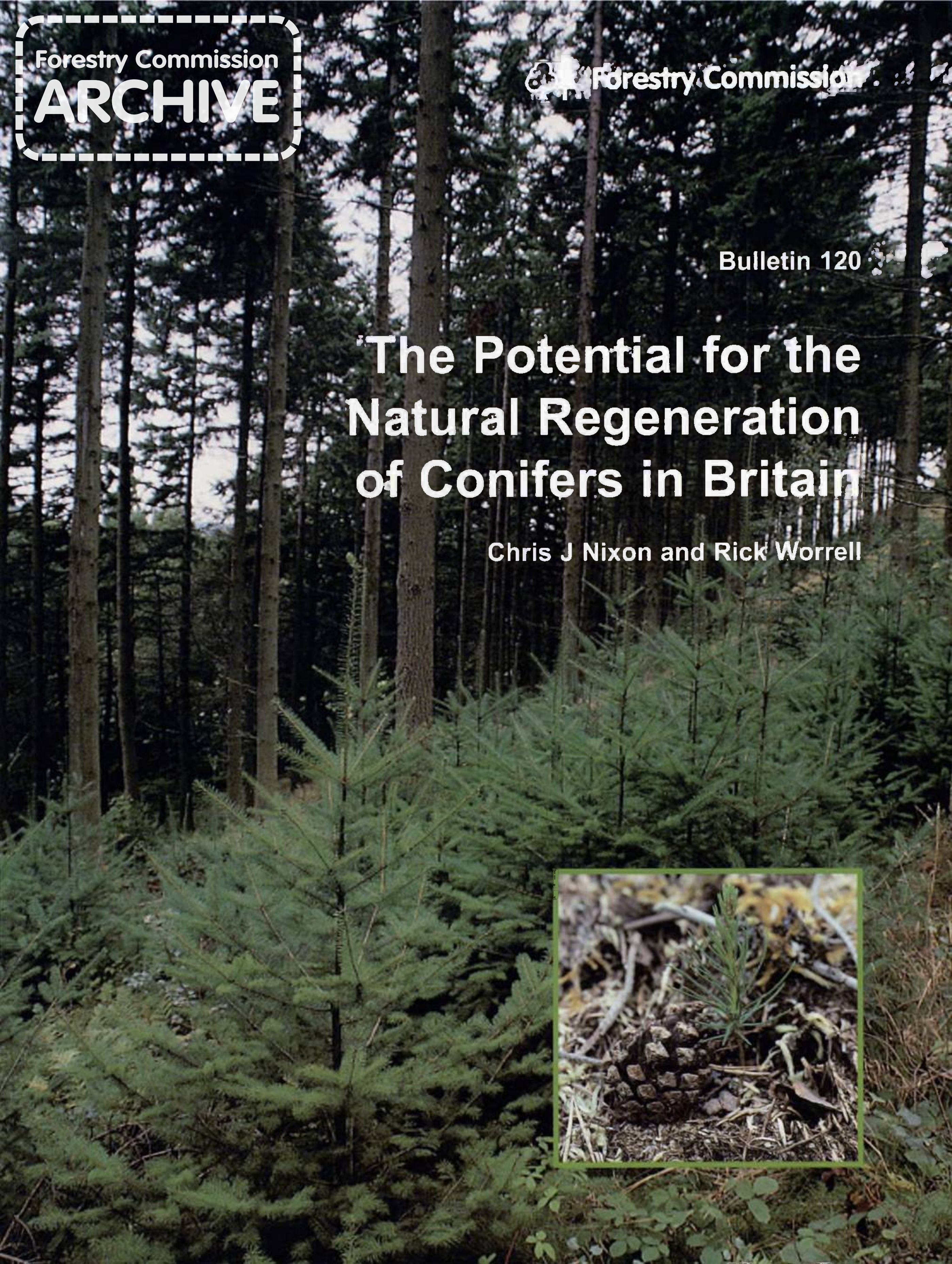
Forestry Commission

Bulletin 120

The Potential for the Natural Regeneration of Conifers in Britain

Chris J Nixon and Rick Worrell



FORESTRY COMMISSION BULLETIN 120

The Potential for the Natural Regeneration of Conifers in Britain

Chris J. Nixon[1] *and Rick Worrell*[2]

[1] *Forest Research, Silviculture (North) Branch, Northern Research Station, Roslin, Midlothian EH25 9SY*

[2] *Institute of Ecology and Resource Management, University of Edinburgh, EH9 3JU*

Forestry Commission, Edinburgh

ISBN 0 85538 401 8

Nixon, Chris J. and Worrell, Rick 1998. The Potential for the Natural Regeneration of Conifers in Britain. Bulletin 120. Forestry Commission, Edinburgh.

FDC 231:174.7:(410)

KEYWORDS: Forestry, Natural regeneration, Conifers, Seed

Cover Photo – Douglas fir natural regeneration beneath mature stand at Thornthwaite Forest in Cumbria. *(39215)*

Inset – Caledonian pine seedling growing in cleared area in Glen Garry, Lochaber. *(Forest Life Picture Library, 1011390040)*

Please address enquiries about this publication to:
The Research Communications Officer
Forest Research
Alice Holt Lodge, Wrecclesham
Farnham, Surrey GU10 4LH

Contents

List of plates

List of figures

Page

List of tables

The Potential for the Natural Regeneration of Conifers in Britain

Summary

An introductory chapter notes the historic and current use of conifer natural regeneration in Great Britain, listing the advantages and disadvantages of its use in forest management.

Coning levels vary markedly from year to year, so it is often desirable to predict the onset of particularly favourable years for seed production. Early thinning helps to promote crown development, which will lead to enhanced seeding from trees in stands when they reach optimum productivity at 25–40 years of age. The majority of seed dispersed from mature trees of around 20 m in height will fall within 100 m, equivalent to the radius of a circular coupe of 3 ha.

Conifer seed rarely remains viable on the forest floor for more than one year. Germination normally occurs in spring with the onset of warm moist conditions following an overwintering period where chilling helps to break the shallow physiological dormancy.

Silvicultural operations to promote rapid establishment of dense natural regeneration must be planned to coincide with years when good quantities of seed are produced. Cultivation to mix the mineral soil with the litter layers helps to provide the favourable seedbed conditions of adequate soil moisture and lack of vegetation competition. When thinnings occur, canopy cover should be carefully manipulated because of its influence over forest floor conditions. Conifer species vary in the ability of their seedlings to tolerate shade, but good light levels are necessary to promote strong growth. Management aimed at producing high densities of regeneration is recommended as the best approach in order to compensate for heavy seedling losses due to a host of damaging agents.

The spring of the third year following germination is considered to be the earliest time at which a reliable estimate of established seedlings, and hence the success of natural regeneration, can be made. Supplementary planting to modify the balance of species or to infill gaps can then be undertaken. Dense regeneration may require respacing early in the rotation. Timing is very important and should be linked to the identification of potential crop trees when trees reach 1.5–2 m in height. A target density of 2500 trees/ha is appropriate at this stage.

In making an economic comparison between use of natural regeneration and planting, the probability of success needs to be considered along with operational details. The use of natural regeneration can be more cost-effective due to operational savings, and can enhance the non-market benefits of the forest. However, after clearfelling there may be costs involved with the delayed establishment of natural regeneration relative to that achieved by planting. Respacing costs are commonly in the order of £350–400/ha.

Under British conditions, natural regeneration will generally be a less certain means of establishing trees than planting, but it has sufficient benefits to make it the preferred option for some combinations of crops and sites. The probability of success can be increased by adopting forest management practices which incorporate the principles and advice contained in this Bulletin.

Possibilités de régénération naturelle des conifères en Grande-Bretagne

Résumé

Un chapitre d'introduction fait état de l'utilisation passée et présente de la régénération naturelle des conifères en Grande-Bretagne, énumérant ses avantages et inconvénients au niveau de la gestion forestière.

La formation de cônes variant sensiblement d'année en année, il est souvent désirable de prédire quand commenceront les années particulièrement favorables à la production de semences. Pratiquées tôt les éclaircies contibuent à encourager le développement des houppiers, ce qui amènera une meilleure production et dissémination des semences chez les arbres en bouquet lorsque ceux-ci atteindront leur productivité optimale à 25-40 ans d'âge. La majorité des semences dispersées, provenant d'arbres adultes ayant environ 20 m de haut, tombera à moins de 100 m, ce qui équivaut au rayon d'une coupe circulaire de 3 ha.

Sur le sol de la forêt, les semences de conifères restent rarement viables au-delà d'un an. La germination se déroule normalement au printemps lorsque s'installent des conditions humides et assez chaudes faisant suite au passage de l'hiver, période où le gel aide à briser la faible dormance physiologique.

Des opérations de sylviculture visant à favoriser l'établissement rapide d'une dense régénération naturelle doivent être planifiées pour coïncider avec les années où de bonnes quantités de semences seront produites. Le labourage ayant pour but de mélanger le sol minéral avec les couches de litière aide à fournir un lit de germination présentant des conditions favorables – humidité du sol et manque de compétition végétale. Au moment de l'éclaircissage, la densité du couvert devrait être manipulée avec soin du fait de son influence sur les conditions du sol forestier. Chez les semis de conifères, la capacité de tolérer l'ombre varie suivant les espèces, toutefois un bon niveau d'éclairage est nécessaire pour promouvoir une croissance vigoureuse. Une gestion visant à produire de hautes densités de régénération est recommandée comme étant la meilleure façon de compenser les fortes pertes de semis dues à une multitude d'agents nuisibles.

Le printemps de la troisième année suivant la germination est considéré comme la première date à laquelle on pourra procéder à une estimation fiable des semis établis, et donc à l'évaluation du succès de la régénération naturelle. Des plantations supplémentaires visant à modifier l'équilibre des essences et à remplir les vides pourront alors être entreprises. Une régénération dense pourra nécessiter un ré-espacement, tôt dans la rotation. Le choix du moment est très important et devrait être lié à l'identification des sujets éventuels du peuplement final lorsque les arbres atteindront 1,5–2 m de haut. Une densité cible de 2500 arbres/ha est appropriée à ce stade.

Pour comparer d'un point de vue économique l'utilisation de la régénération naturelle et le recours à la régénération naturelle et le recours à la plantation, il est nécessaire de considérer les probabilités de succès en même temps que les détails opérationnels. Le recours à la régénération naturelle peut être plus rentable du fait des économies réalisées sur les coûts opérationnels, et peut mettre en valeur les atouts non-commercialisables de la forêt. Néanmoins, après une coupe rase, des coûts peuvent être encourus du fait du retard de l'établissement de la régénération naturelle par rapport à celui de la plantation. Les coûts de ré-espacement sont généralement de l'ordre de £350–400/ha.

Dans les conditions existant en Grande-Bretagne, la régénération naturelle s'avérera généralement un moyen moins sûr d'établir les arbres que la plantation, mais elle présente des mérites suffisants pour en faire l'option de prédilection dans certaines combinaisons de peuplements et de sites. Les probabilités de succès peuvent être accrues par l'adoption de méthodes de gestion forestière incorporant les principes et conseils contenus dans ce bulletin.

Das Potential für natürliche Regeneration von Nadelbäumen in Britannien

Zusammenfassung

Die Einführung vermerkt die historische und heutige Verwendung von natürlicher Nadel-baumregeneration in Britannien, zusammen mit ihren Vor- und Nachteilen für die Forstpflege.

Da Zapfendichte von Jahr zu Jahr sehr unterschiedlich sein kann, ist es oft wünschenswert, den Beginn von besonders günstigen Jahren zur Samenproduktion vorherzusagen. Frühes Durchforsten kann die Kronenentwicklung fördern und dies führt zur verstärkten Aussaat von Bäumen in Beständen, wenn diese, im Alter von 25–40 Jahren, ihre optimale Produktivität erreichen. Die Mehrzahl der Samen, die von schlagbaren Bäumen von etwa 20 m Höhe, verteilt werden, fallen innerhalb von 100 m, entsprechend dem Radius einer runden Hiebsfläche von 3 ha.

Nadelbaumsamen bleibt, auf dem Waldboden, selten länger als ein Jahr keimfähig. Das Keimen erfolgt meist im Frühjahr mit dem Beginn von feuchtwarmen Bedingungen, die einer Öberwinterungsperiode folgen, in welcher die Kälte zum Abbruch der Samenruhe betrug.

Waldbauliche Maßnahmen, um schnelle Etablierung eines dichten, natürlichen Regenerationsbestandes zu fördern, müssen so geplant werden, daß sie mit Jahren von guter Samenproduktion übereinstimmen. Bodenbearbeitung, indem man den Mineralboden mit dem Waldstreu mischt, fordert die bevorzugten Saatbettbedingungen – ausreichende Bodenfeuchtigkeit und wenig Vegetationskonkurrenz. Beim Durchforsten sollte der Beschirmungsgrad sorgfältig manipuliert werden, da dieser einen Einfluß auf die Bodenbedingungen hat. Die Sämlinge von unterschiedlichen Nadelholzarten haben verschiedene Schattenerträglichkeit, aber gute Lichtwerte sind nötig um starkes Wachstum zu fördern. Es wird empfohlen, den Wald im Bezug auf Hohe Regenerationsdicht zu bewirtschaften, da dies die beste Methode ist, um die schweren Sämlingsverluste durch eine Reihe von schädlichen Einflüssen, auszugleichen.

Der Frühling des dritten Jahres nach der Keimung gilt als der früheste Zeitpunkt zu welchem eine verläßliche Schätzung der etablierten Sämlinge, und damit des Erfolgs der natürlichen Regeneration, gemacht werden kann. Zusätzliche Pflanzungen, um die Artenbilanz zu ändern oder Lücken zu füllen, können dann unternommen werden. Dichte Regeneration benötigt Umordnen möglicherweise früh im Umtrieb. Der richtige Zeitpunkt ist sehr wichtig hier und sollte mit der Identifizierung potentieller Zukunfstbäumen verbunden werden, wenn die Bäume etwa 1.5–2 m Höhe erreichen.

Will man einen wirtschaftlichen Vergleich zwischen natürlicher Regeneration und Pflanzung anstellen, so muß die Erfolgswahrscheinlichkeit zusammen mit den betrieblichen Details betrachtet werden. Natürliche Regeneration ist kostengünstiger aufgrund niedriger Betriebskosten, außerdem kann es die nicht-wirtschaftlichen Nutzen des Waldes bereichern.

Nach dem Kahlschlag können jedoch Kosten entstehen, durch die relativ verspätete Etablierung von natürlicher Regeneration im Vergleich zu Pflanzung. Umordnungskosten liegen allgemein im Bereich von £ 350–400/ha.

Unter britischen Bedingungen ist natürliche Regeneration, im Vergleich zur Pflanzung, allgemein eine weniger verläßliche Methode zur Baumetablierung, aber sie besitzt genügend Vorteile, um sie bei gewissen Kombinationen von Kultur und Lage, zur bevorzugten Methode zu machen. Die Erfolgsrate kann verbessert werden indem man forstwirtschaftliche Methoden benutzt, welche die Grundsätze und Ratschläge in diesem Bulletin beinhalten.

Chapter 1

Introduction

As Britain's new conifer forests have matured there has been increasing interest in the use of natural regeneration for restocking after felling. While achieving successful natural regeneration can reduce costs and provide environmental benefits the uncertainties associated with its use can make it difficult for forest managers to decide when and where to rely on natural regeneration in preference to planting.

This Bulletin aims to reduce these uncertainties by providing fundamental information on the reproductive cycles of our major conifer species and by outlining factors which affect seed germination and seedling establishment. The management of existing regeneration is also considered. Guidance is given on the identification of forest sites suited to natural regeneration and on the planning and implementation of forest operations which will enhance the likelihood of success. The focus is on the use of natural regeneration to promote regular, even-aged stands. However, the principles can also be applied to irregular, uneven-aged stands.

The historical use of natural regeneration in British conifer forests

To date, the major coniferous forest type in Britain where natural regeneration has been used has been in the Scots pine forests particularly in northern Scotland. During the last century there were many instances of the successful encouragement of native pinewood regeneration through deliberate stand management (Steven and Carlisle, 1959). Natural regeneration has been used in the management of Scots pine stands in southern Britain, such as the New Forest (Jones, 1947) and the Crown Estates at Windsor (Hart, 1995).

However, the majority of British conifer forests are composed of non-native species which date from 1920 or later. The initial establishment and more recently the restocking of these forests has traditionally been accomplished by planting. As these forests develop, more trees are reaching seed bearing age, and there is greater potential to utilize natural regeneration in the management of a larger proportion of the stands.

The potential for using natural regeneration more widely in these conifer forests was appreciated from the early 1950s but the uncertainty of success restricted its use (MacDonald and Lockhart, 1953; McNeill, 1962). Natural regeneration first began to figure in silvicultural practice during the 1960s when high densities of Sitka spruce seedlings were found to be developing spontaneously after windthrow and clearfelling in the forests of south and west Scotland and Wales (Davies, 1954; Dannat and Davies, 1970).

The current extent of natural regeneration

Sitka spruce regeneration now occurs widely on clearfelled areas in western districts of Britain (Nelson, 1990). For example, a survey of 47 restocking sites in southern Scotland and northern England found natural regeneration of Sitka spruce occurring on 68% of sites (Nixon *et al.*, 1994). Natural seedlings of Sitka spruce are often recorded at densities of over 2500/ha and examples of over 400 000 seedlings/ha have been noted on favourable sites. Nevertheless across the whole country, the occurrence and density of Sitka spruce regeneration tends to be very variable both between and within sites.

Natural regeneration of other conifer species is often less prolific but there are numerous examples of small pockets of regeneration occurring on receptive sites where there are parent trees of seedbearing age. A separate survey of Douglas fir regeneration in Wales and south-west England found regenerating seedlings on over 90% of sites with an average density of 38 000 seedlings/ha (Blackhall and Nixon, 1992). There was considerable variation around this average density underlining the degree to which regeneration success differs with site. However the relative scarcity of naturally regenerating seedlings of species such as larch, western hemlock and Douglas fir is more often a result of forest management practices than ecological adaptation.

Surveys of the native pinewoods have highlighted the overall scarcity of established Scots pine seedlings (Bunce and Jeffers, 1977). However, the presence of smaller seedlings indicates that many pinewoods remain capable of regenerating. One of the main barriers to regeneration of Scots pine and other species is often grazing and browsing animals (Staines, 1995). Deer numbers in particular have increased dramatically in Scotland over the last century (Watson, 1983) and in many areas the number of sheep has also remained high.

Advantages and disadvantages of using natural regeneration

The decision to use natural regeneration needs to consider various factors including the advantages and disadvantages listed below:

Table 1.1

Advantages	Disadvantages
Emulates natural processes	Relies on the presence of parent trees of acceptable quality
Involves less dramatic environmental change	The time of seedling establishment can be less easily predicted
Introduces greater structural, species and visual diversity	Does not allow for the use of genetically improved plant material
Can be a less expensive method of restocking than planting	Can involve a delay in woodland establishment compared with planting
Provides a natural mechanism for rejuvenating and extending native woodlands	Can result in patchy, variable tree stocking densities
	Possible requirement for respacing where seedling densities are too high

Forest management utilizing natural regeneration

Natural regeneration may arise spontaneously or as a result of deliberate management to encourage it. In both cases the use of natural regeneration can have advantages and disadvantages compared with planting (Table 1.1). The successful use of natural regeneration presents the forest manager with a number of challenges requiring care, skill and flexibility in the timing of forest operations.

The clear definition of the objectives of management for any given area, together with consideration of the stand and site type, will be the first stage in deciding whether or not the forest can be managed to encourage natural regeneration. The presence of advanced regeneration either beneath or at the edges of stands is also a useful indication of receptive sites for regeneration.

Despite the uncertainty surrounding the wider use of natural regeneration, there are good examples of the successful encouragement and use of natural regeneration in conifer stands throughout Britain. Particularly noteworthy examples are the naturally regenerated Sitka spruce in the forests of Kielder, Ae and Fernworthy; larch, Douglas fir and other conifers at Longleat Estate in Wiltshire; Douglas fir at Coed-y-Brenin in Wales; larch in the northern Lake District and Scots pine at Rothiemurchus, Glentanar and Glen Dye.

These examples show that, given suitable parent trees, with appropriate management all our major coniferous species are capable of successful natural regeneration provided certain key aspects like seed supply and site receptivity are ensured. The challenge to the forest manager is to develop the knowledge and skill necessary to promote natural regeneration in a successful and predictable manner. This requires an understanding of the principles of seed and seedling physiology and their interaction with site and other factors. These principles are outlined in the following chapters.

Chapter 2

Seed production and dispersal

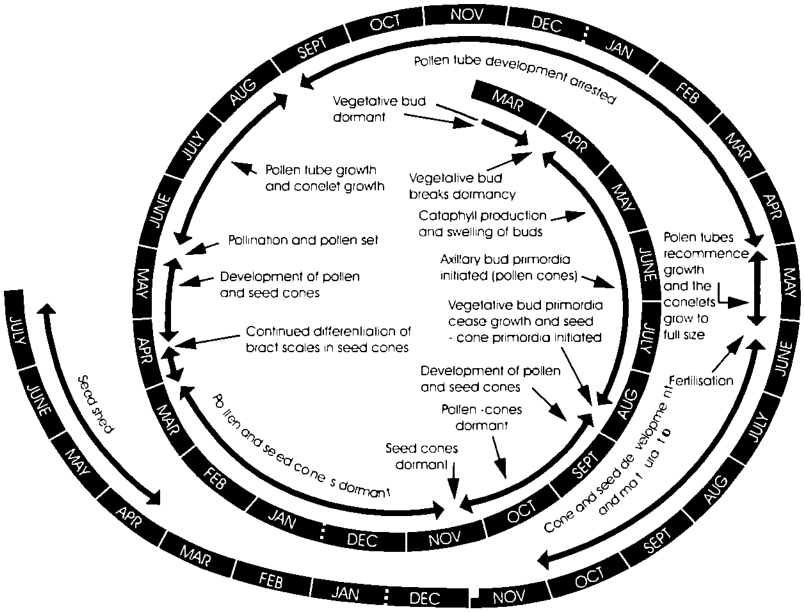


Figure 2.1 *The cycle of flower and cone development in Scots pine (Gordon, 1992)*

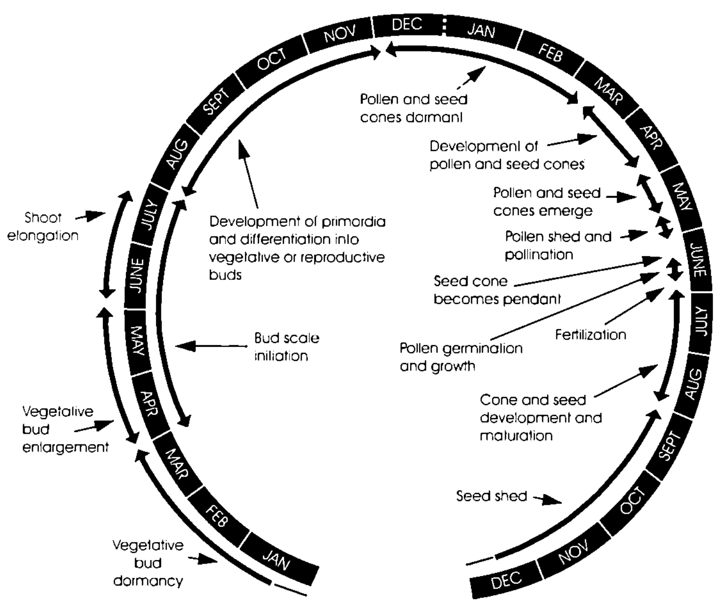


Figure 2.2 *The cycle of flower and cone development in Sitka spruce (Gordon, 1992)*

Successful management of natural regeneration must use the natural patterns and timing of seed production to maximize the available seed supply to a given site during the period of greatest site receptivity.

The timing of flowering and seed production

Most conifers, except the pines, have a two-year reproductive cycle. This starts with bud initiation in the spring of the first year and leads on to flowering and cone maturation during the spring and summer of the following year. Pine species take three years to complete the cycle of seed production (Wareing, 1958). Details of the various stages of development are shown in Figures 2.1 and 2.2 for Scots pine and Sitka spruce respectively.

The frequency of good seed years

Seed production in conifers varies markedly from year to year. A number of authors (Matthews, 1954; Brown and Neustein, 1970) suggest typical intervals between years with very high seed production (seed or 'mast' years) for some species. The production of large seed crops is mostly dependant upon favourable climatic conditions which can occur in successive years or alternatively not occur for many years. Whilst external environmental conditions play a role at the stand level, individual trees tend not to bear a heavy cone crop in successive years due to the drain on their carbohydrate reserves (Brown and Neustein, 1970). Therefore the concept of regular intervals between seed years, or seed production cycles, is only indicative of the return period which might be expected. It cannot be used to predict the next occurrence of a good supply of viable seed.

Variation in seed production also occurs between single trees, between stands in a forest and on a regional scale. These differences are more pronounced in some species than others. Scots pine, for example, often exhibits a more uniform level of seed production than the spruces (Bergman *et al.*, 1981; Sarvas, 1962). The periodic production of very large quantities of seed is thought to be part of an advantageous evolutionary strategy to reduce the loss of seeds to predators in mast years (Fenner, 1991).

Table 2.1 shows the pattern of seed production recorded in surveys of Forestry Commission forests over the period 1930–1948 on a national basis. More recent data are unavailable.

Table 2.1 Record of seed production in Forestry Commission forests 1930–1948

Species	*Year of crops*																		
	1930	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Scots pine	a	a	a	a	a	g	f	g	g	p	g	g	g	p	p	g	p	a	p
Douglas fir	p	p	g	p	g	p	g	f	g	g	na	g	g	f	g	g	p	f	p
Sitka spruce	p	p	p	f	p	a	g	g	f	g	g	g	g	g	p	a	p	a	f
Japanese larch	a	f	p	g	a	f	p	a	g	f	g	p	a	p	p	p	p	a	g

a: abundant – extensive coning on both edge trees and trees within the stand.
g: good – extensive coning on edge trees and some coning on trees within the stand.
p: poor – small numbers of cones on edge trees. Negligible coning on trees within the stand.
f: failure – no coning.
na: data not available.
(Forestry Commission, 1948)

Table 2.2 Number of cones and seeds produced in good seed years by 40–50 year old trees of the major British conifers in stand conditions

Species	*Number of cones/tree*	*Number of seeds/cone*	*Number of seed/tree*	*Seed viability %*
Sitka spruce	3000	100	300 000	70–80
Corsican pine	2500	12	30 000	70–80
Scots pine	800	15	12 000	50–70
Lodgepole pine	700	11	7 700	80–90
Douglas fir	1500	10	15 000	70–80
Norway spruce	700	15	10 500	75–85
Larches	4500	10	45 000	15–25
Western hemlock	5800	10	58 000	50–65

(adapted from Gordon,1992 and Aldhous, 1972)

The quantity of seed produced

During good seed years the quantity of seed produced by a mature stand of trees is very high, often exceeding one million seeds/ha. Occasionally extremely large numbers of seeds may be produced; up to 22 million seeds/ha have been recorded under Sitka spruce stands in western Scotland (Neustein, 1966, 1967, 1968, 1969; Mair, 1973). Table 2.2 gives approximate figures for the number of cones and seeds produced in good seed years by mature dominant trees in stand conditions (*c.* 40–50 years old) of the main conifers. These figures are much less than those for old open-grown trees. For example Garman (1951) recorded an average number of 14 000 cones per tree on scattered old growth Douglas fir trees on Vancouver Island in British Columbia, Canada.

Factors affecting seed production

Tree age

The flowering, coning and seed production of young trees is often sparse and sporadic but increases rapidly with age (Matthews, 1963) and continues to increase throughout the rotation up to a very late stage, providing that the crowns of the trees are free to develop.

Table 2.3 Average age of first good seed crops in conifers in Britain

Species	*Age of first good seed crop*
Sitka spruce	25–35
Scots pine	15–20
Douglas fir	30–35
European larch	25–30
Japanese larch	15–20
Western hemlock	25–30
Corsican pine	25–30
Lodgepole pine	15–20
Norway spruce	30–40
Noble fir	30–40
Grand fir	35–45

(adapted from Philipson, 1990)

In dense stands, particularly where they are unthinned, it is common for the production of seed to stabilize in mid rotation (30–40 years). Sitka spruce, for example, begins to produce seed crops around the age of 20–25 but does not normally produce very large quantities of seed until after 35–40 years of age (Brown and Neustein, 1970).

Crown development and stand density

Provided there is an ample pollen supply, isolated trees will flower and seed more abundantly than those in closed canopy conditions. Flowering is largely confined to those parts of the tree crown which are fully exposed to sunlight (Mair, 1973). Seed production is greatest on dominants, codominants and edge trees. Therefore, the release of the crowns of trees in stands by thinning promotes increased flowering and hence seed production. For instance, Jones (1943) found that, in Scots pine, selecting and promoting the growth of dominant trees was critical to obtaining successful natural regeneration. This was not compensated for by leaving a greater number of smaller trees since the level of coning on dominant trees was 4.5–6 times that of intermediate and suppressed trees.

Important site characteristics

Climate

Climate exerts a strong influence on flowering and seed production at both a regional and local scale. Broadly, warm and dry conditions tend to encourage flowering. Higher temperatures are normally required for flower bud initiation than for the formation of vegetative buds. High temperatures and low rainfall in June and July appear particularly important in flower bud formation years as this corresponds to the time of initiation of reproductive buds. However, seed production may not just be determined by a single subperiod of the growing season (e.g. during the differentiation of the flower buds) but by the nature of the whole growing season prior to flowering (Leikola *et al.*, 1982).

Even where the climatic conditions leading up to flowering are optimal, the weather conditions during flowering and subsequent cone development may also influence the production of viable seed (Van Vredenburch and La Bastide, 1969). High rainfall during pollination, early spring frosts and a cool summer and autumn following flowering can all reduce the final quantity of fertile seed produced. As a result the prediction of good coning years on a site by site basis using climatic data is unreliable and not recommended.

Location, elevation and aspect

Within any climatic zone there is local variation imposed by elevation, aspect and exposure.

Variation in seed production with elevation has been described by many European authors (Piussi, 1967; Bergman *et al.*, 1981). At higher altitudes cones tend to be smaller, with fewer and lighter seeds which have lower average viability levels. Increasing elevation can also influence the periodicity of good seed years with the intervals between good seed years being longer and more irregular at higher elevations compared with lower elevation sites. Although the range of site elevation included in many of these studies was greater than that to be found in Britain, it is likely that similar, if smaller, effects could be demonstrated here.

Seed production is also often higher in stands on sites with a southerly aspect, particularly in comparison to north-facing slopes (Hagner, 1965; Simpson and Powell, 1981). At the individual tree level, higher cone production is also likely to occur on south-facing parts of the crown (Hagner, 1965; Piussi, 1986; Garman, 1951). This is most commonly attributed to the warmer microsite conditions favouring flower induction.

Prospects for enhancing seed production through cultural treatments

A number of cultural treatments can be used to enhance flowering in conifers in addition to the promotion of good crown development. Those most commonly used are fertilization, branch and stem girdling and shoot pruning.

Fertilization

There is a lack of information on the reproductive response of forest trees to fertilization. However, increases in flowering and fruiting, directly attributable to the addition of nitrogen fertilizer, have been reported in species such as Scots pine (Bergman, 1960) and Douglas fir (Smith *et al.*, 1968).

The quantities and relative proportions of the nutrients necessary to stimulate flowering and seed production varies with the nature of the stand, especially the age and size of the trees, and the site conditions. However, on nutrient-poor sites in Britain, i.e. very poor to poor nutrient status in ESC terms (Pyatt, 1995), seed production may be enhanced by correcting any existing nutrient deficiencies of the trees. Foliage analysis should be carried out to see if fertilizer applications are likely to be beneficial.

The most effective time to apply compound fertilizers for the purposes of stimulating bud formation is in the early spring before the new flower buds are formed, i.e. during the period February–May. It should be remembered that in the pines where seed takes two years to ripen, any effect will not be apparent until two years after application.

Girdling

Treatments, such as girdling, place trees under physiological stress and can promote a shortterm enhancement of seed production. The partial girdling of the stem is one of the most effective methods of increasing flowering in a wide variety of tree species under forest conditions. This is most often achieved by cutting two slightly overlapping half-circles through the bark and cambial layer approx 1–1.5 cm wide, one above the other 5–15 cm apart and is most effective when applied before the end of May. Girdling may be carried out in association with particular silvicultural systems of crop management such as the retention of seed trees on a restocking site to provide increased quantities of seed during a season when a receptive seed bed has been prepared. However, due to the damage caused to the stems of the trees, the operation cannot be repeated.

The use of plant growth regulators

In tree improvement programmes the application of plant growth regulators has often proved more successful in enhancing flowering than cultural treatments such as those described above. The application of the growth hormone gibberellin has been successfully used to induce flowering in a number of conifer species (Pharis and Ross, 1986; Pharis *et al.*, 1987). The most successful treatment is often gibberellin injection timed to coincide with cone-bud initiation and combined with a cultural treatment such as girdling (Philipson, 1990; Tompsett and Fletcher, 1979). However, the method has been developed as a technique for use in tree breeding programmes and is not a practical method of encouraging widespread flowering in forest situations due to the high costs involved.

Predicting good seed years

When attempting to utilize the abundant seed supply in 'mast' years, the earlier that the potential of the crop can be assessed, the sooner appropriate management plans can be made and implemented.

Three methods are often proposed for the early prediction of large cone crops in forest trees:

The use of assumed periodic seed cycles

The limitations to the use of this method are discussed at the beginning of this chapter and it is not recommended as a practical management option.

Prediction using climatic variables

The use of this method for the prediction of good seed years in particular crops is difficult for many reasons (Mencuccini, 1991; Clarke, 1992) and it is not recommended.

The visual assessment of buds and flowers

In some conifer species such as Douglas fir and the larches, an early assessment of the potential size of the cone crop may be made by observing the external morphology of flowering buds as they form in the preceeding autumn (Dobbs *et al.*, 1976; Gordon, 1992; Silen, 1967; Philipson, 1997). In other species this is more difficult, requiring the buds to be dissected and studied under a microscope.

Observation and assessment of buds from the ground is not possible but they can be readily seen on the tips of branches of felled trees in the early autumn. Although a high density of reproductive buds cannot be taken as definite evidence of a large cone crop in the following year, they nevertheless indicate the possibility of good flowering. In most conifer species it is therefore not possible to begin to assess the size of the potential seed crop until the spring flush of foliage has occurred.

The abundance of male and female flowers in spring can be used as an indication of the potential cone crop but unfortunately even high numbers of flowers do not necessarily guarantee a large seed crop due to the influence of the prevailing weather conditions during flower and cone development (Philipson, 1997). Late spring frosts and heavy rainfall during pollination are particularly damaging to some species – for example larches. The optimum period for making an assessment of emerging flowers is given in Table 2.3 and the amount of flowering can be classified using a similar system to that recommended for cone crops (see next section).

This method of early prediction is the only one that offers potential for operational forest management. However, estimates derived by this method need to be correlated with subsequent assessments of cone production. At present the reliability of such estimates is uncertain and therefore the technique cannot yet be generally recommended.

The assessment of cone and seed crops

Assessments of cone production need to be made so that operations to encourage natural regeneration can be planned. Cone crop assessment involves making visual estimates of the numbers of cones borne on the crowns of trees. The best time for assessment varies with species (Table 2.4). However, care must be taken with Scots pine, Corsican pine and European larch to distinguish between the current year's mature cones and the spent ones of the previous season. To make an estimate, binoculars are used to observe the crowns of the trees or stand in question from a suitable vantage point. Good, clear weather is essential to allow cones to be distinguished from the background foliage. An estimate is made of the numbers of cones on a given proportion of the trees. Gordon (1992) suggests the following general classification for recording the size of cone crops, although the categories of light, moderate and heavy cone production will vary with species. This has been adapted to help predict the potential for natural regeneration as follows:

- ***Absent*** No cones on any trees.
No potential for natural regeneration.

- ***Light*** A few cones (<50) on about one tree in every 50.
Encouragement of natural regeneration difficult.

- ***Moderate*** A significant number of cones (50–100) visible on about 25–50% of the trees.
Good potential for natural regeneration providing site conditions are conducive to establishment.

- ***Heavy*** Very many cones (>100) on some (5–10%) trees, a significant number of cones on many others trees and at least a few cones on nearly every other tree.
Very good potential for natural regeneration.

Table 2.4 Period for assessment of flowering and coning

Species	*Flowering*	*Coning*
European larch	March – April	April – May
Japanese larch	March – April	April – May
Hybrid larch	March – April	April – May
Sitka spruce	End of May	July – Aug
Scots pine	June – July	Aug – Sept
Douglas fir	Mid May – Mid June	June – July
Western hemlock	June	July – Aug
Norway spruce	End of June	July – Aug
Corsican pine	June – July	Aug – Sept
Lodgepole pine	June – July	Aug – Sept

(adapted from Gordon, 1992)

The yield of viable seed

In order to assess the number of full or viable seeds in the crop, a random sample should be taken in the early autumn of at least five cones from the mid to upper crown of at least 20 trees. These should be cut in half vertically with a sharp blade and the number of full and empty seeds in the surface of one half counted. The minimum number of full seeds per cut surface which represent good crops is in the order of:

Pines	3–4
Spruces	8–10
Firs	5–6
Larches	2–3

Assessing the proportion of full seed in this way is necessary to ensure that the cones contain a high proportion of viable seed. This is particularly important when silvicultural operations to promote natural regeneration are being planned in years with light or moderate cone production levels.

Seed dispersal

The timing of seed dispersal

In Britain, the shedding of seed of many conifer species may be spread over a long period of the year. Seed dispersal commonly begins during the autumn, continues through the winter and extends well into the following spring. Peak periods of seed fall vary both within and between species and there is often no clear peak of the pattern of release. Exceptions to this rule are Corsican pine, Scots pine and European larch whose cones do not develop to the point of releasing seed until the spring following cone development (European larch cones may not open properly for two or three years). Table 2.5 gives the period over which seed fall occurs for the common conifer species.

Cone opening is caused by a reduction in the moisture content of the cone with no appreciable opening often occurring before perhaps 50% of the moisture content has been lost. Cones will naturally open and close several times before total seed fall takes place due to variations in climatic conditions. Periods when no seed dispersal takes place are often associated with long wet spells of weather (e.g. mid-winter), whilst seed shed is favoured by drying winds (Mair, 1973).

Distance of dispersal

The major vector of seed dispersal in conifers is the wind. The distance seed travels from the parent tree varies with seed size and weight, tree height, and wind speed. Consideration of the likely distance over which significant quantities of viable seeds will be dispersed is vital when natural regeneration depends on

Table 2.5 Period of conifer seed dispersal

European larch	Feb – May
Japanese larch	Oct – April
Hybrid larch	Oct – April
Sitka spruce	Nov – April
Scots pine	April – July
Douglas fir	Oct – April
Western hemlock	Sept – April
Norway spruce	Nov – April
Corsican pine	Mar – June
Lodgepole pine	Nov – April

Sept Oct Nov Dec Jan Feb Mar Apr May Jun Jul

(adapted from Gordon, 1992)

seed supply from adjacent stands.

Conifer seeds vary greatly in size, weight and shape, and in the surface area and characteristics of the wing. In general heavy seeds tend to have a faster rate of fall than light ones but weight alone is not the only determining factor (Siggins, 1933). Falling seeds usually rotate about their centre of gravity due to the curvature of the wing. Variation in the speed of rotation also affects the rate of fall of the seed and the size of the wing changes the seeds' wind resistance. Each tree species produces seeds having a characteristic average rate of fall although this rate will vary between trees and stands. Table 2.6 gives details of the average weight of Sitka spruce, Douglas fir, western hemlock, European larch, lodgepole and Scots pine seed and estimates of seed dispersal distances. Data for other species are unavailable.

Table 2.6 Tree seed weight and potential dispersal distance – estimates of distance from mature trees (~20 m in height) within which 80% of seed will fall

Species	*Average weight of seed (mg)*	*Estimated dispersal distance (m)*
Western hemlock	1.54	100
European larch	5.88	80
Sitka spruce	2.50	60
Douglas fir	11.36	40
Scots pine	6.06	20
Lodgepole pine	3.33	70

(adapted from Gordon, 1992; Mair, 1973; Booth, 1984; von Lupke, 1972; Isaac, 1940);

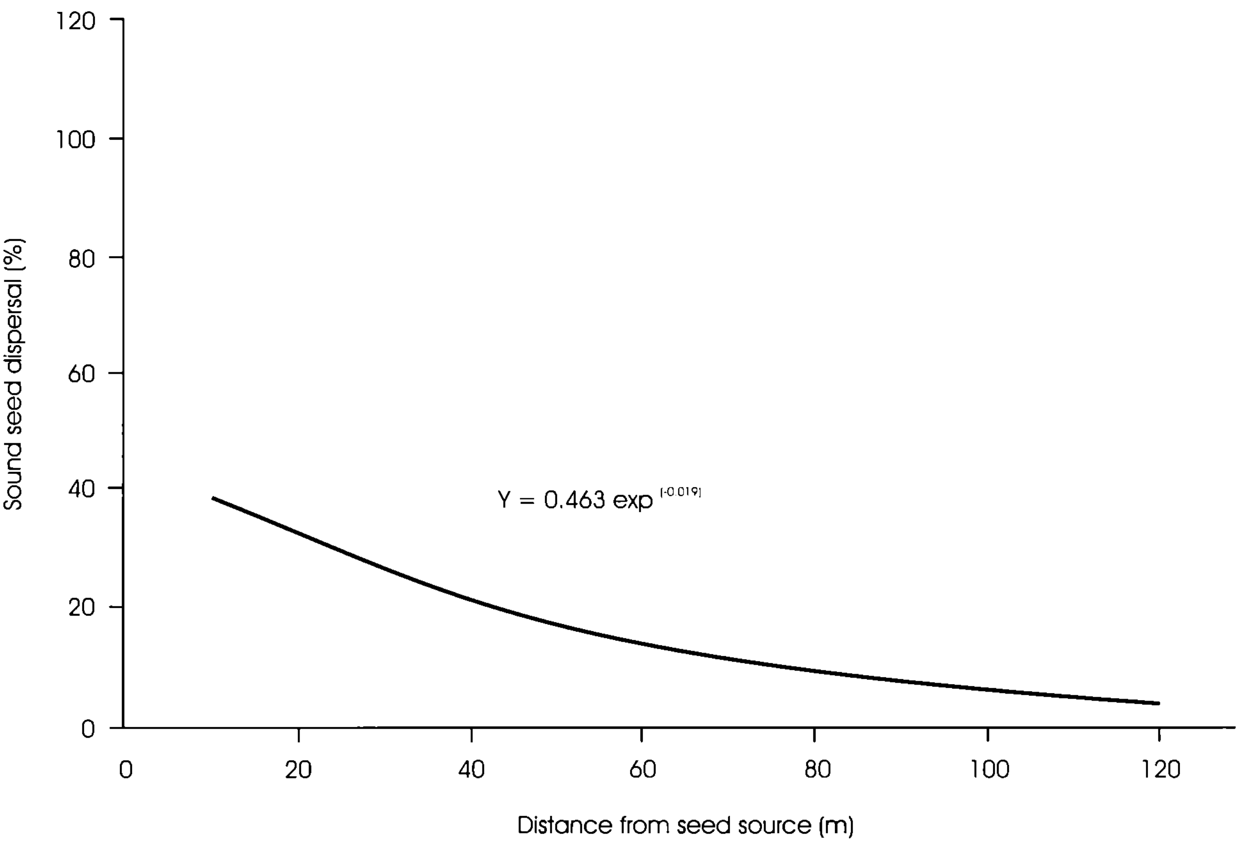


Figure 2.3 *Dispersal of white spruce seed (Youngblood and Max, 1992)*

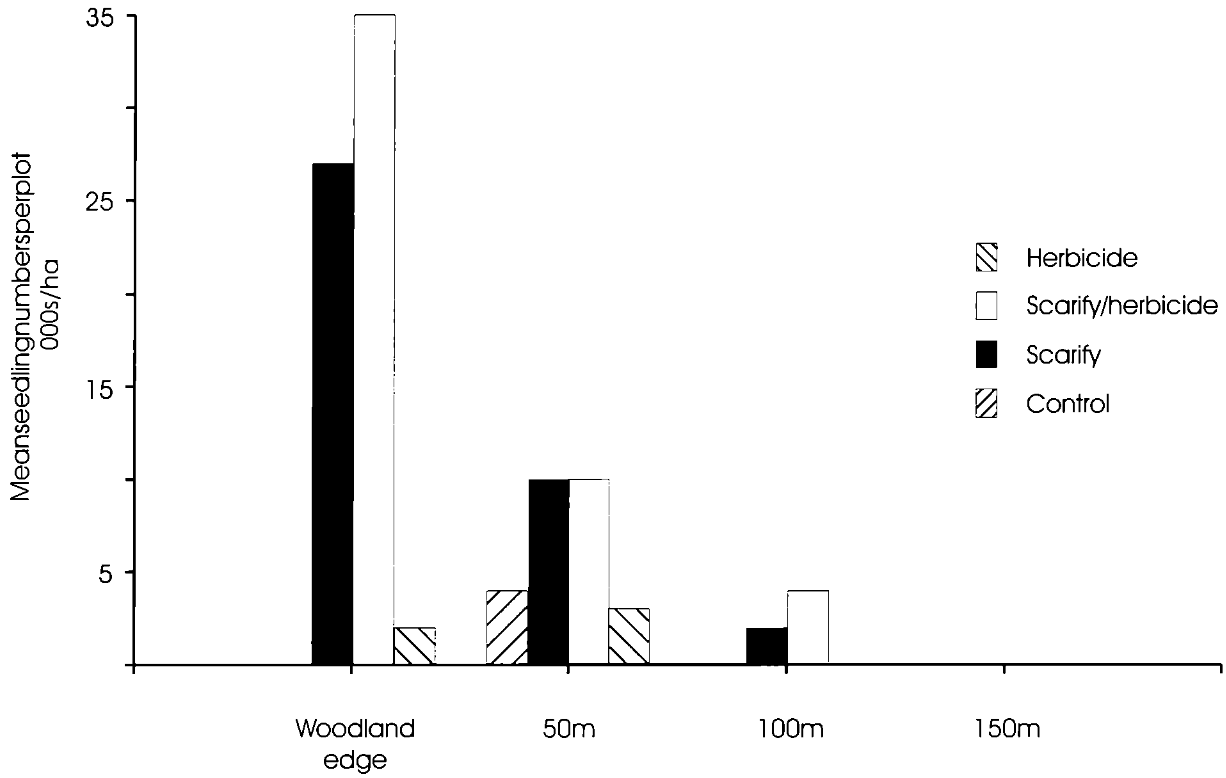


Figure 2.4 *Numbers of natural regenerated Scots pine seedlings in 4 m x 2 m experimental plots at and beyond the edge of a native pinewood two years after the application of different ground preparation treatments. All plots were fenced against browsing animals. (From Nixon, 1997)*

Dispersal distances can be increased by factors such as wind turbulence as well as seeds blowing over frozen ground surfaces and snow cover. Several measurements of seed dispersal have been made in the field and most have recorded a negative exponential relationship between the amount of sound seed and distance from seed source, e.g. Youngblood and Max (1992); Figure 2.3. In order to generalise this relationship, assessments of the consistency of the exponential form would be required over a range of tree or stand heights.

Clearly the important question is how far from the parent trees sufficient seed for successful regeneration can be expected to carry. Given the seed dispersal distances listed in Table 2.6, dense regeneration derived from a stand of mature trees of around 20 m in height is unlikely to occur beyond 100 m from the forest edge. This limits the maximum size of coupe that could be effectively restocked by natural regeneration to around 3 ha.

An example of seed dispersal and subsequent regeneration out from the edge of a Scots pine forest is shown in Figure 2.4. This experiment was established on a heathland site at the Braemoray Estate in Speyside in 1995. Establishment of seedlings was studied at 50 m intervals from the forest edge and related to four different treatments of the regeneration site (i.e. no treatment, scarification, herbicide application and scarification plus herbicide). The parent trees ranged from 15–20 m in height. After two years natural regeneration of Scots pine was concentrated within 50 m of the woodland edge. Even this close to the parent trees soil disturbance was necessary to promote densities greater than 5000 seedlings/ha.

Direction of dispersal

In addition to considering seed dispersal distance it is also necessary to take account of the direction in which the seed will be blown. Since low moisture levels encourage the opening of seed cones, a greater proportion of seed is often released during periods when trees are exposed to continental or drier winds. Working with Sitka spruce, Mair (1973) trapped over 10 times more seed released by dry easterly winds compared with the moister prevailing westerly winds (Table 2.7).

Table 2.7 The number of seeds trapped along three transects downwind of the edge of a Sitka spruce stand in Argyll, Scotland over a seven month period November 1969–May 1970

Wind direction	*Total number of seeds trapped*	*Number of days **
Westerly	55	27
North-easterly	546	24
South-easterly	79	6

* Number of days with wind from each direction
(adapted from Mair, 1973)

Summary

Consideration of the patterns of seed production is essential to achieving successful natural regeneration. Coning levels vary markedly from year to year and as a result it is desirable to predict the onset of particularly favourable years for seed production. Predictions made on the basis of climatic data or assumed typical periodic seed production cycles are unreliable. Therefore it is necessary to assess coning on parent trees prior to undertaking operations to promote regeneration.

- The seed production of young trees is often sparse and erratic and trees in closed stands must reach 25–40 years of age before large quantities of seed are produced. Early thinning helps to promote crown development which will in turn enhance seed production.

- For most conifer species seed dispersal begins during the autumn and extends through to the following spring. Exceptions are Scots pine, Corsican pine and European larch which release seed in the spring and early summer.

- Consideration must also be given to the likely distance and direction of seed dispersal from the parent trees. The majority of seed dispersed from mature trees of around 20 m in height will fall within 100 m which is equivalent to the radius of a circular coupe of about 3 ha. Since drying winds facilitate seed release from cones, the direction of the bulk of seed dispersal is often different from that of the prevailing south-westerly winds.

Chapter 3

Seed dormancy and germination

Once the seed is released from the cones, the process of natural regeneration enters a new phase. When the seed reaches the forest floor a number of environmental factors interact to break the dormancy of the seed and trigger germination. During this period conifer seed is vulnerable to many damaging agents which can greatly reduce the quantity of viable seed which finally germinates. The microsite conditions of the forest floor have a critical influence on the process of natural regeneration and the careful manipulation of these conditions, where possible, can significantly improve the prospects for success.

Seed viability and longevity

Seeds may be nonviable for a number of reasons including poor pollination, infertile pollen and the failure of the embryo to fully develop. Viability can vary between species, sites and season.

It is also possible for seeds to lose their viability before conditions become conducive to germination. This can result from prolonged periods of waterlogging on the forest floor, particularly when anaerobic conditions persist. Seed overwintering in moist litter on the forest floor can experience viability losses of between 50 and 80% (Howells, 1966). Fungi are often a principle agent of seed deterioration.

Seed that has fallen to the ground rarely remains viable for more than one year (Isaac, 1940; Scarratt, 1966; Hill and Stevens, 1981; Hetherington, 1965). This was supported by a study at Kielder Forest where Sitka spruce seed was collected at intervals from October 1992 to February 1994 and stored in the surface litter for periods ranging from 24–61 weeks. Despite high germination potential at time of collection, germination after storage was nil or negligible (Table 3.1). This implies that seed germination will take place during the spring and early summer following dispersal (Clarke, 1992) although periods of drought may delay the onset of germination.

The absence of a long-term viable seedbank requires managers to respond to individual years with high seed production levels to achieve successful natural regeneration.

Table 3.1 Germination percentage of Sitka spruce seed collected at different times from a stand in Kielder Forest before and after varying periods of storage in the litter layer (Edwards, unpublished)

		Sitka spruce seed longevity		
Date collected	*Date buried*	*Initial germination at burial (%)*	*Burial period in weeks (date)*	*Germination after retrieval (%)*
Oct 1992	Oct 1992	90	37 (Jun 1993)	5
Nov 1992	Jan 1993	92	24 (Jul 1993)	0
Jan 1993	Feb 1993	94	35 (Oct 1993)	0
Oct 1993	Nov 1993	96	33 (June 1994)	26
Dec 1993	Dec 1993	95	34 (Aug 1994)	0
Feb 1994	Mar 1994	86	61 (May 1995)	0

Factors affecting germination

Germination may occur whenever the conditions are favourable following seed fall. Viable seeds which do not respond quickly to conditions which favour germination are said to be dormant. Most conifer species exhibit shallow physiological dormancy. The exposure of seed to a period of chilling or stratification helps to break dormancy and results in higher seed germination capacity over a wide range of conditions. Japanese larch and Scots pine are the main exceptions as seed of these species appears to reach similar germination capacities (although not germination rate) with or without stratification. Under forest conditions, the need for stratification of most conifer species is more than satisfied during the winter.

Temperature

Given adequate moisture, low temperatures are likely to be the most significant factor governing the start of germination in the spring. Poor germination and/or the retardation of germination can result from low temperatures. The threshold soil temperature for germination in most conifers is around 10°C. At temperatures above this threshold germination proceeds more quickly with the majority of seeds having germinated within 7 to 14 days (Scarratt, 1966). Since the main effect of temperature is on the rate of germination rather than the germination capacity, i.e. the total percentage of seed which finally germinates, site treatments that increase soil temperature during germination, such as cultivation, should therefore improve the rate of germination. Figures 3.1 and 3.2 show the faster rate of germination of stratified seed of Sitka spruce and Japanese larch as temperature increases from 10–20°C.

Moisture

All seeds require moisture to allow germination to proceed so the optimum conditions are provided by a moist substrate with a high

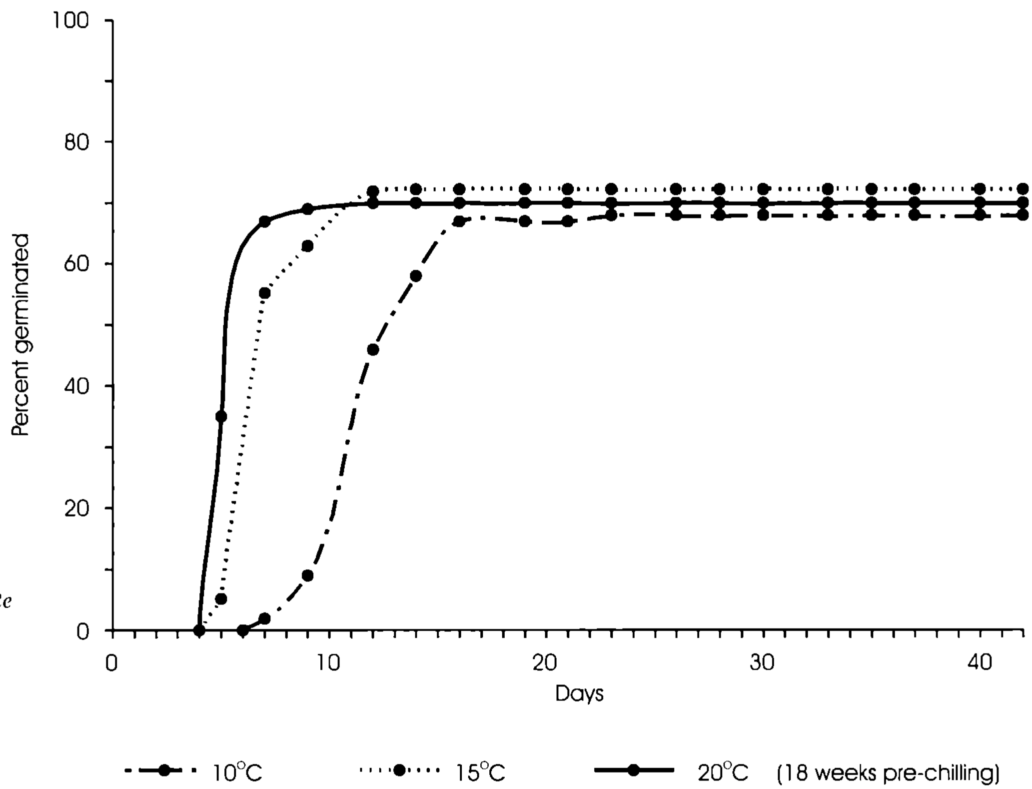


Figure 3.1 *The rate of germination of stratified Sitka spruce seed at three different temperatures. (from Jones and Gosling, 1991).*

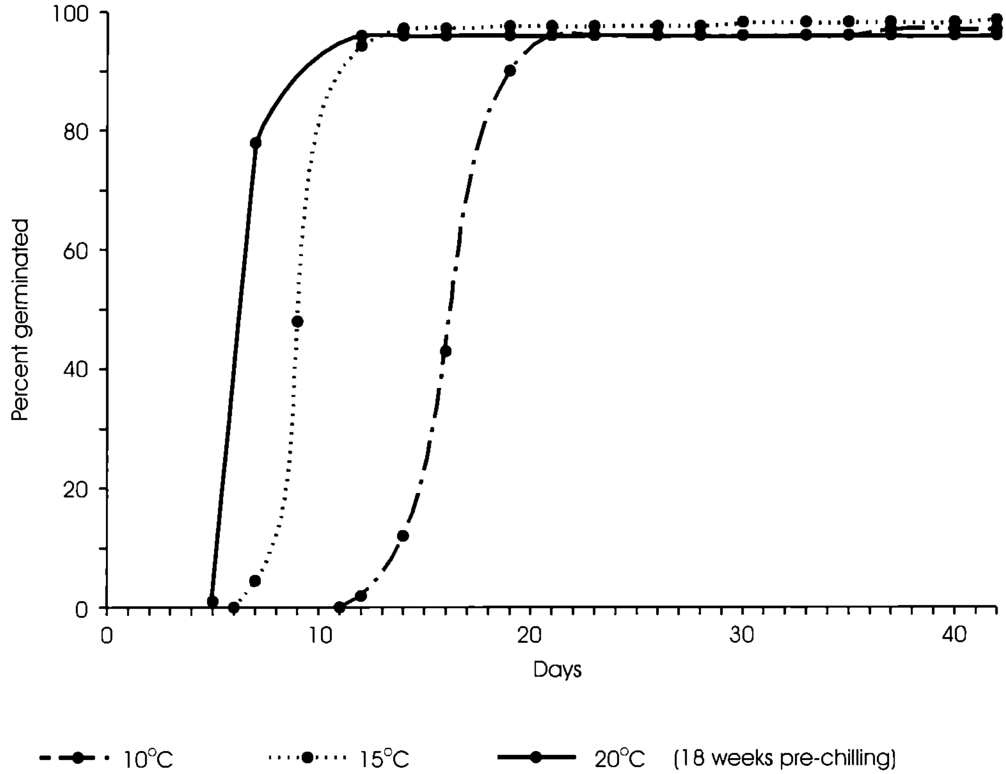


Figure 3.2 *The rate of germination of stratified Japanese larch seed at three different temperatures. (from Jones and Gosling, 1991).*

relative humidity. Dry spells of weather in the spring, depending upon the type of seed bed, may result in moisture becoming a limiting factor restricting or preventing germination. Desiccation can be particularly harmful to seeds as it tends to retard the rate of germination which leaves the seed more exposed to damage. Dormancy may also be induced in seed which has begun to develop but then experiences a period of desiccation due to dry weather. In this instance, germination can be delayed for several weeks (Aldhous, 1972). For example, Edwards (1981) reported a drop in the germination rate of Scots pine in Glen Tanar during a dry spell in June but an increase in July after the dry period had ended.

Creating a favourable seedbed environment

The forest manager needs to assess the regeneration site to identify the factors that are likely to limit the suitability of the seedbed for seed germination. Such factors can be separated into ground conditions and stand environment.

Ground conditions

The most important features of the site that can affect germination are the soil type, the vegetation, the litter layer, and the presence of brash.

Provided the seed is in contact with the soil surface and there is no competition for moisture from ground vegetation, soil type is unlikely to be limiting to germination other than on sites with very dry or very wet soil moisture regimes (Pyatt, 1995). On these particular site types cultivation is desirable to create a suitable microsite for germination: a scarified patch or trench in the first instance, and a raised mound in the second.

Where ground vegetation occurs it can prevent the seed reaching the soil surface and can compete with germinating seedlings for soil moisture and light. Although there is considerable variation in vegetation competition between soil types it is unrealistic to expect good germination on a site which has more than 75% dense vegetation cover. Both herbicides and cultivation can be used to reduce vegetation competition. However, experimental evidence with Scots pine (Figure 2.4; Edwards, 1981) suggests that cultivation is much more effective in improving germination than herbicide application. This is because chemical or manual weed control does not disturb the litter layer (see below). The potential speed of vegetation re-establishment has also to be considered since on more fertile soil types a bare site can be completely recolonized within one year. This limits the length of time that a site remains receptive to regeneration.

Needle litter can be a very favourable substrate for germination but loses moisture readily during dry spells because of a lack of capillary water movement from the deeper soil layers. Therefore mixing litter with the upper soil horizons through cultivation will improve seedbed conditions. The presence of a thin layer of litter covering the seed will improve the seedbed moisture conditions but, following germination, the emerging shoot may have difficulty in reaching the surface.

The presence of brash can also reduce germination success. For example a study in Kielder Forest between 1992 and 1994 compared the number of seedlings that developed where brash had been removed with those found under 5–15 cm depths of brash cover (Table 3.2). Although initial germination was higher under a light brash cover, by the end of two years survival, it was nearly double where the brash had been removed. The germination under the heaviest brash cover was consistently poor. Thus, minimizing the area of a restocking site that is covered by dense brash should improve the success of regeneration.

Stand environment

Stand density may greatly modify and influence the nature of the seedbed vegetation and microclimate. The principal effect of stand density is on the temperature and moisture status of the seedbed environment. Light levels are much less influential at this early stage and the stimulating effect of light is likely to be small compared with the effect of temperature variation.

The need for a certain minimum temperature to be reached before germination can proceed often leads to germination occurring later and more slowly under closed canopy conditions compared with open ground where temperatures rise more quickly in the early spring (Rowe, 1955). Thinning can help to raise ground surface temperatures and hasten germination. Sitka spruce has a higher optimum temperature for germination than western hemlock with the result that under cool, closed stand conditions the hemlock is favoured (Allen, 1941). In seeking to improve the conditions for seed germination under a closed canopy it is necessary to reduce the crown cover without allowing sufficient light to reach the forest floor to promote vigorous growth of competing vegetation.

Predation and seed losses

In considering the predation and loss of seed it is convenient to distinguish between the seed

Table 3.2 Germination of Sitka spruce under differing depths of brash on a peaty gley soil in Kielder Forest. Values are expressed as a percentage of the highest germination after 24 months

Treatment	*Months after initial germination*		
	2 months	*10 months*	*24 months*
Brash removed	80	115	100
Brash depth 5cm	112	92	54
Brash depth 15cm	69	76	51

which overwinters in the cone and that which lies on the forest floor.

Loss of seed within or from the cone

Conifer seed is at risk from a range of cone and seed feeding insects. However, only seed wasps of the genus *Megastigmus* have posed a significant problem so far in Britain. At least three species are well established:

M. spermotrophus (Wachtl) which attacks seed of Douglas fir; *M. pinus* (Parfitt) which attacks *Abies* spp.; and *M. pictus* (Foester) on *Larix* spp.

Seed-trapping studies from 1965–69 (Stoakley, unpublished) demonstrated that when seed production is low, the percentage of potentially sound seed infested is generally high, frequently in the order of 80–90%, but that in good seed years infestation is only 20–30% (Figure 3.3), as the local seed wasp population is unable to fully exploit the increased amount of seed available (Bevan, 1966–69). These results indicate that silvicultural operations intended to encourage natural regeneration of Douglas fir are only worthwhile in heavy cone years. Although our knowledge of the impact of other *Megastigmus* species is limited, the same approach should also be beneficial in the regeneration of *Abies* and *Larix* species.

Seed losses on the forest floor

There have been few studies of the loss of seed from the forest floor up to and during germination. It is possible that such losses are considerable and represent a potential barrier to regeneration success. Losses are likely to be due to voles, mice, fungi, insects and birds. Rodents have been recorded destroying large quantities of directly sown Scots pine seed (McVean, 1961). Seeds exposed on bare mineral soil may be particularly vulnerable and even buried seed may be heavily predated in years which coincide with peaks in the cycle of rodent populations. Soil dwelling saprophytic fungi have been reported as causing considerable damage to Sitka spruce seeds, particularly during periods of slow germination (Scarratt, 1966).

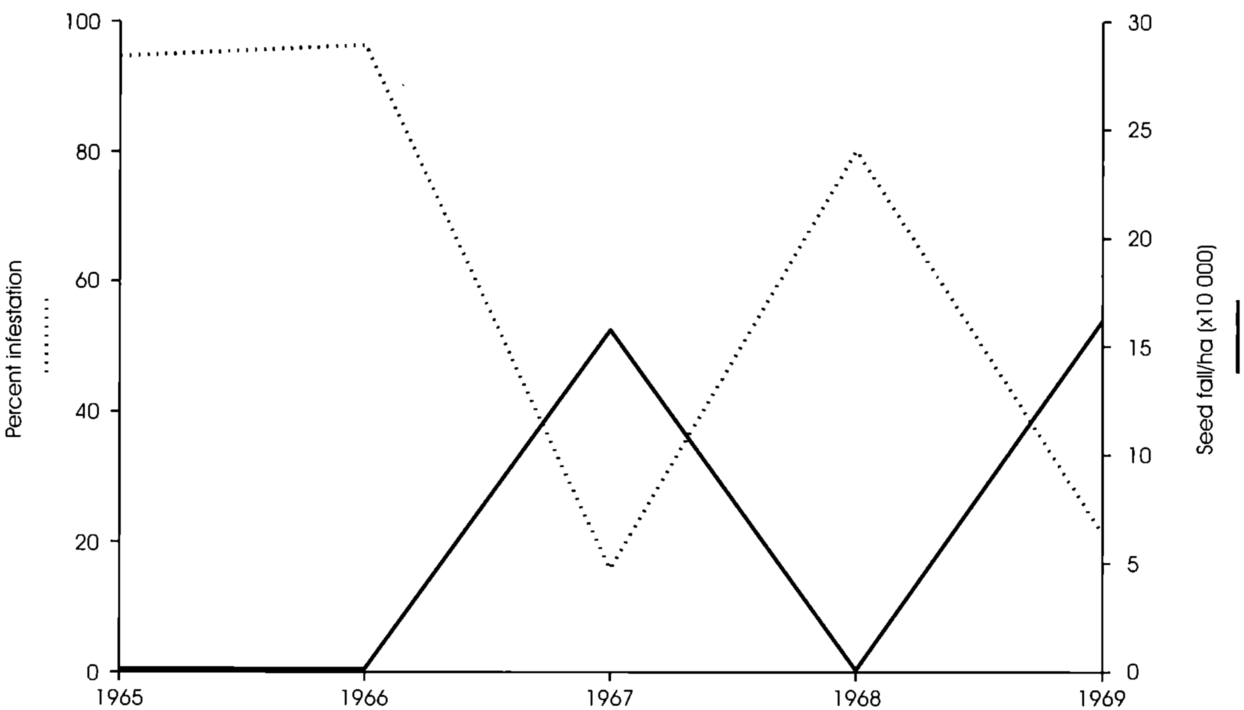


Figure 3.3 *The percentage infestation of Douglas fir seed by* Megastigmus *wasps from 1965–69 in relation to seed fall.*

Summary

- The seed of most conifer species exhibits shallow physiological dormancy and will normally germinate quickly under warm, moist conditions. In the forest, germination usually occurs in the spring following an overwintering period when the seed is subject to chilling which helps to break the dormancy.

- Under most circumstances, conifer seed rarely remains viable on the forest floor for a period of more than one year.

- The absence of a seed bank of viable conifer seed on the forest floor makes it necessary to plan silvicultural operations to promote natural regeneration to coincide with years when the parent trees are producing good quantities of seed.

- The most favourable seedbed environment combines adequate soil moisture with a lack of vegetation competition. Cultivation that mixes the mineral soil with the litter layers is generally the best way of providing such a seed bed.

- The structure and density of forest stands greatly influence the nature of the vegetation and microsite conditions of the forest floor. Where thinning or preparatory seeding fellings are being carried out, the canopy cover must be carefully manipulated to encourage seed germination whilst restricting the growth of other vegetation.

- Conifer seed may be lost through damage from birds, rodents, insects and fungi. Seed exposed on the soil surface is particularly vulnerable to predation and may be removed or destroyed before it has an opportunity to germinate.

Chapter 4

Seedling establishment

Once germination has occurred the process of natural regeneration enters a further phase. The main environmental factors influencing seedling growth and survival are light, moisture, temperature and nutrient supply. Because of the increasing influence of light and nutrient supply, the conditions which promote maximum seedling survival and development are not the same as those for successful germination. Since smaller seedlings are more vulnerable to damage, rate of growth plays an important role in survival.

Microsite variables

Moisture

Although seedling growth may be limited by low light levels, it is not often the most important factor in determining early seedling survival. Of all the site related factors, the level of soil moisture is the most critical for the success of natural regeneration and many instances of young seedlings being lost through drought and desiccation have been noted (Gregory, 1956; Soos and Walters, 1963). Most losses occur during the first season following germination due to desiccation of the upper soil layers in which the developing roots of the seedlings are concentrated.

Light

For most conifer species the capacity to endure shade varies with age with shade tolerance being significantly greater in the early stages of seedling development (Baker, 1945; Fairbairn and Neustein, 1970, Howells, 1966). An estimate of the relative shade tolerance of young seedlings of a range of conifer species is given in Table 4.1 and typical light levels (expressed as a percentage of full light intensity) under varying densities of tree cover are given in Table 4.2.

The estimates in Table 4.1 are approximate and based on published data (Brown and Neustein, 1970; Fairbairn and Neustein, 1970) and modified by field observations. The estimates suggest that conifer species can be divided into three broad categories: those that are intolerant of shade (larches, pines); those that have limited tolerance to light shade (Sitka spruce, Douglas fir); and others that are shade tolerant (i.e. can persist under woodland shade).

The practical implication of these categories is that it will be the more shade tolerant species which will tend to colonize small gaps in mature stands. The relative light levels that are found beneath existing stands, or in gaps, are dependant upon the canopy species and the number of stems per hectare. Examination of

Table 4.1 Estimates of minimum light levels (relative to full light) for establishment of conifer natural regeneration

			Percentage of full light			
60	—	*50*	—	*30*	—	*10*
Larches	Lodgepole, Corsican and Scots pines	Sitka spruce	Douglas fir	Grand fir, Norway spruce	Western hemlock	Western red cedar

Table 4.2 Percentage of full daylight in different gap sizes and beneath various crown cover densities

Species	*Age*	*Number trees/ha*	*Gap size (ha)*	*% Full daylight*
Norway spruce	46	3000	-	1
Norway spruce	46	1700	-	8
Norway spruce	46	500	-	13
Sitka spruce	40	250	-	26
Sitka spruce	40	-	0.04	35
Sitka spruce	40	-	0.12	39
Sitka spruce	40	-	0.40	48
Sitka spruce	40	-	4.0	100
Japanese larch	26	500	-	50
Japanese larch	26	300	-	55
Japanese larch	26	150	-	63
Japanese larch	26	75	-	66

Light intensity figures are mean values of several measurements made throughout each stand by photometer in mid summer.
(Adapted from Fairbairn, 1963 and unpublished Forestry Commission data)

data in Table 4.2 suggests that most conifers would develop satisfactorily under larch, but only the most shade tolerant species, e.g. western hemlock and western red cedar would grow under Norway spruce and then only at the low stem densities. Another useful point apparent from Table 4.2 is that even under a well-thinned spruce stand close to normal rotation age the relative light levels are low compared with a small sized gap. This suggests that a strategy to promote advance regeneration under a mature stand of a densely crowned species will require either extending the rotation, heavy thinning or the deliberate creation of gaps. If gaps are being created, a useful rule of thumb is that the diameter of the gap should be one to two times the height of the surrounding trees to provide regeneration niches for both shade tolerant and intolerant species.

Once established, seedlings require considerably more light to promote fast growth. Therefore, where thinning is carried out to promote seed germination, provision must be made to remove a greater proportion of the overstorey to release the seedlings soon after they become established. This will be particularly important for regeneration under densely crowned species such as firs and spruces.

Temperature

Because of their small initial size, young regenerated seedlings are vulnerable to damage from both heat and cold. High ground surface temperatures during the growing season, particularly in the first year may kill young seedlings through heat girdling and associated bark necrosis. Litter substrates are more prone to lethal surface temperatures than mineral soils because of their dark colour and lower reflectivity (Maguire, 1956; Day, 1963).

At the other extreme, cold temperatures can result in frost heave particularly on fine textured soils. This leads to exposure of the roots and consequent dessication and seedling death. Unseasonal frosts may also damage the actively growing shoots. Stand conditions will modify temperatures at ground level (Chen, Franklin and Spies, 1993) and consequently the frequency and severity of frosts (Figures 4.1 and 4.2). In these examples, seedlings developing close to a mature stand, or under a shelterwood, were at a lower risk of frost damage.

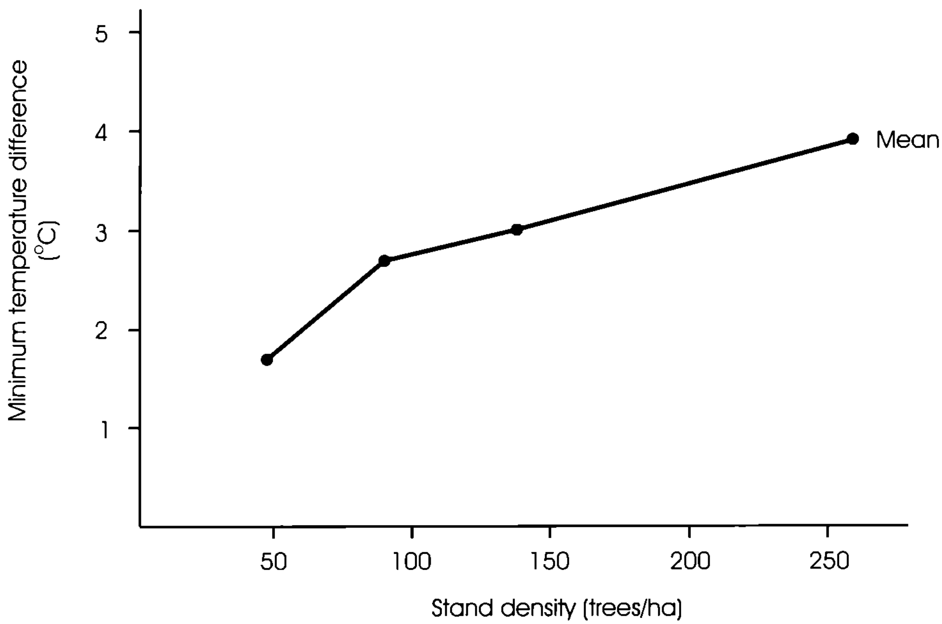


Figure 4.1 *Minimum temperature differences between shelterwoods of different densities and an open clearing during calm and clear nights. Mean values from 14 selected readings May–Sept. 1984. (Figure after Ottoson Lofvenius, 1987)*

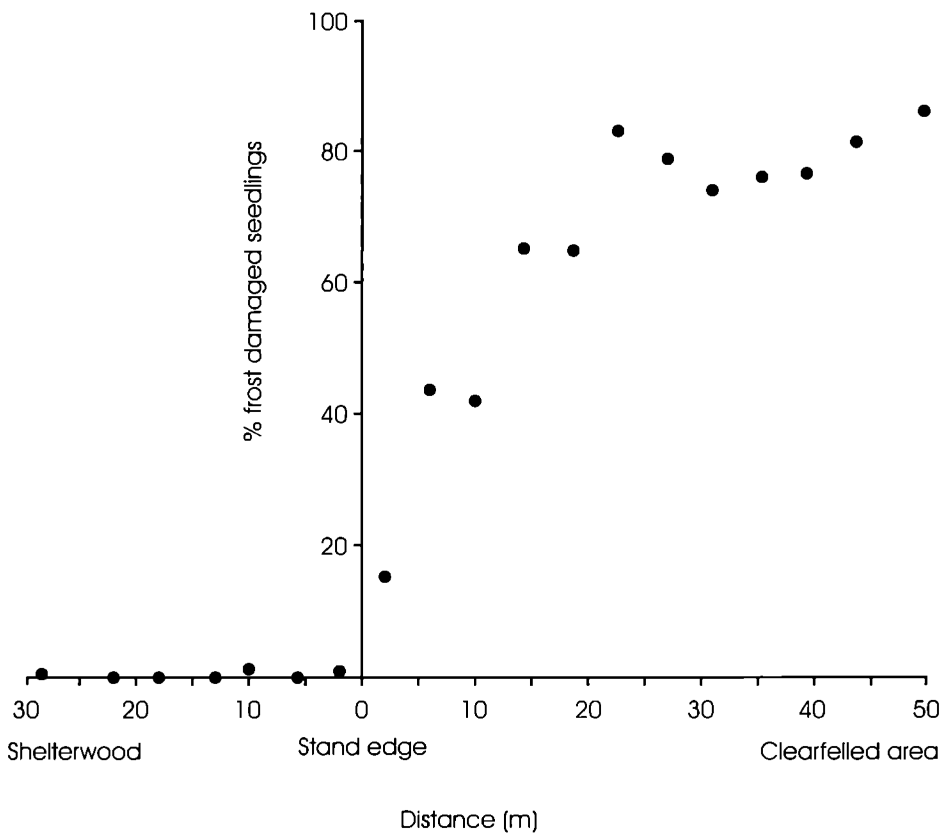


Figure 4.2 *Occurrence of frost damaged spruce seedlings in a shelterwood of Scots pine and on a clearfelled area, at various distances from the edge of the shelterwood. (Figure after Hagner, 1965)*

Site variables

Soil type

Natural regeneration can occur on most soil types since the early establishment phase is more dependent upon the microsite conditions of the germination substrate at the soil surface than on the soil type itself.

In the absence of dense competing vegetation, seedling establishment of many conifer species occurs most frequently on fresh to very moist soils with very poor to medium nutrient regimes (Figure 4.3). However, the occurrence of regeneration is not a guarantee that the species is ecologically adapted to the site. Thus, Sitka spruce can be found regenerating under Scots pine on dry, nutrient poor soils where it is at best considered as 'suitable' (Pyatt and Suárez, 1997).

Surface vegetation

Where germination is successful, the influence of vegetation becomes increasingly important as the seedbed becomes recolonized. This may be extremely rapid on soils with medium to very rich nutrient regimes. Brown earths and surface water gley soils are recolonized more quickly

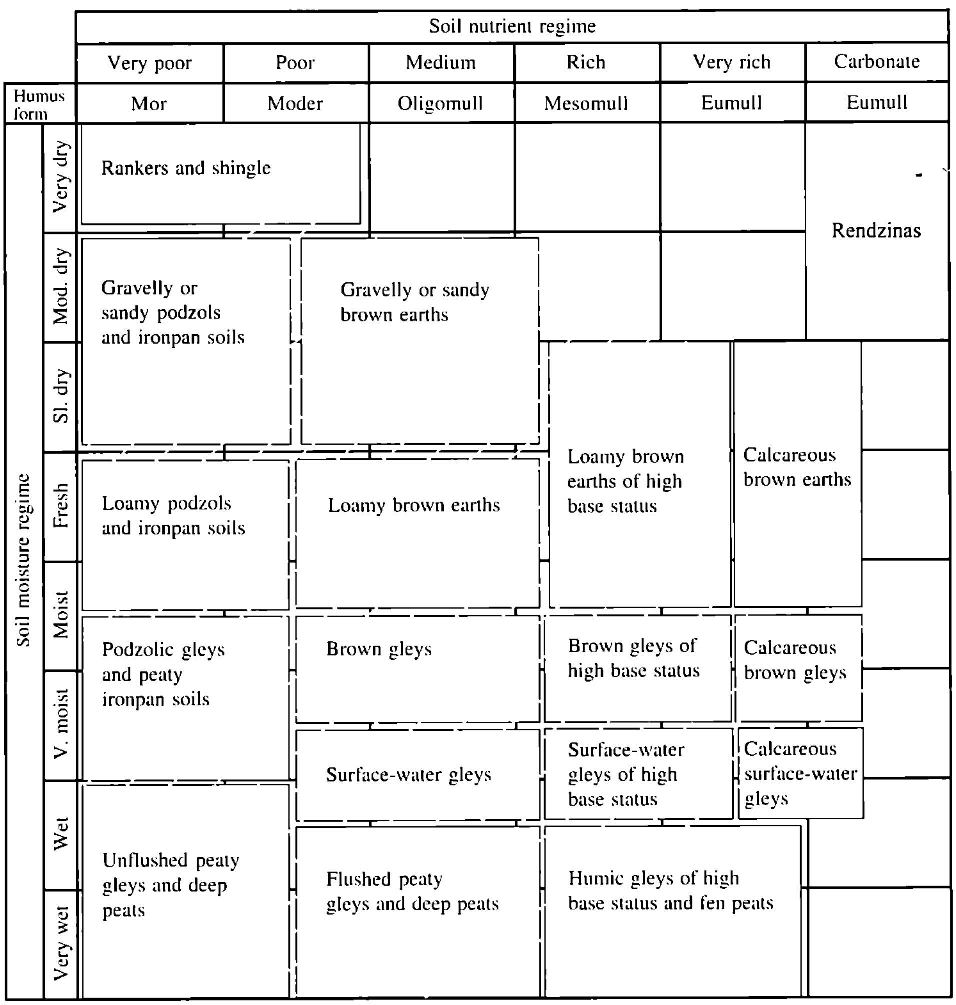


Figure 4.3 *The potential for conifer natural regeneration in relation to the soil types used in the ecological site classification (Pyatt, 1995). Solid hatching = soil types good for natural regeneration. Broken hatching = natural regeneration unlikely to occur or difficult to encourage on these soil types. (After Pyatt and Suárez, 1997.)*

than peaty soils. Fertile site types are frequently colonized by species such as bracken and grasses which are generally very competitive and can seriously hinder or even prevent regeneration. The vegetation-free period may be drastically reduced making the encouragement of natural regeneration difficult.

On less fertile sites, *Vaccinium* and *Molinia* can be strong competitors to conifers such as Scots pine (Jones 1947; McNeill, 1955; Henman, 1961). Other species, e.g. *Calluna*, provided it is not rank, may be less detrimental. Figure 4.4 presents data showing the correlation between Douglas fir seedling density and different vegetation types from the range of sites sampled by Blackhall and Nixon (1992). Successful regeneration was positively associated with the presence of mosses and brash, but negatively correlated with bracken, bramble and grass. However, thick moss cover can restrict root penetration and also dry out quickly. Greater losses of seedlings have been found to occur on dense mosses such as *Mnium hornum* and *Dicranum scoparium* compared with the less compact moss species, e.g. *Hypnum cupressiforme* (Howells, 1966).

The age of the vegetation sward is also an important factor. Seedlings which survive their first season on weed-free surfaces are often able to compete successfully with other vegetation, whereas those germinating in pre-existing vegetation often struggle to survive.

Aspect

South and south-west facing slopes tend to be drier and experience higher maximum summer temperatures. On some sites this may encourage earlier germination of seeds as temperatures rise in the spring and this initial advantage may persist throughout the first season. Conversely, higher temperatures later in the season may result in the death of greater numbers of first year seedlings, particularly on coarse textured soils. Where this is a problem retaining a larger proportion of the overhead canopy to provide more shade may improve survival.

In contrast, north and north-east facing slopes tend to be cooler and more humid. In this case germination may be delayed but the loss of seedlings through desiccation and heat girdling is commonly lower.

Although in extreme cases the effects of aspect can be clearly reflected in the success of natural regeneration, these extremes are only rarely encountered under British conditions. The few studies carried out in the British Isles have not demonstrated a significant relationship between success of natural regeneration and aspect (Blackhall and Nixon, 1992; Oliver, 1993; Von Ow, 1992).

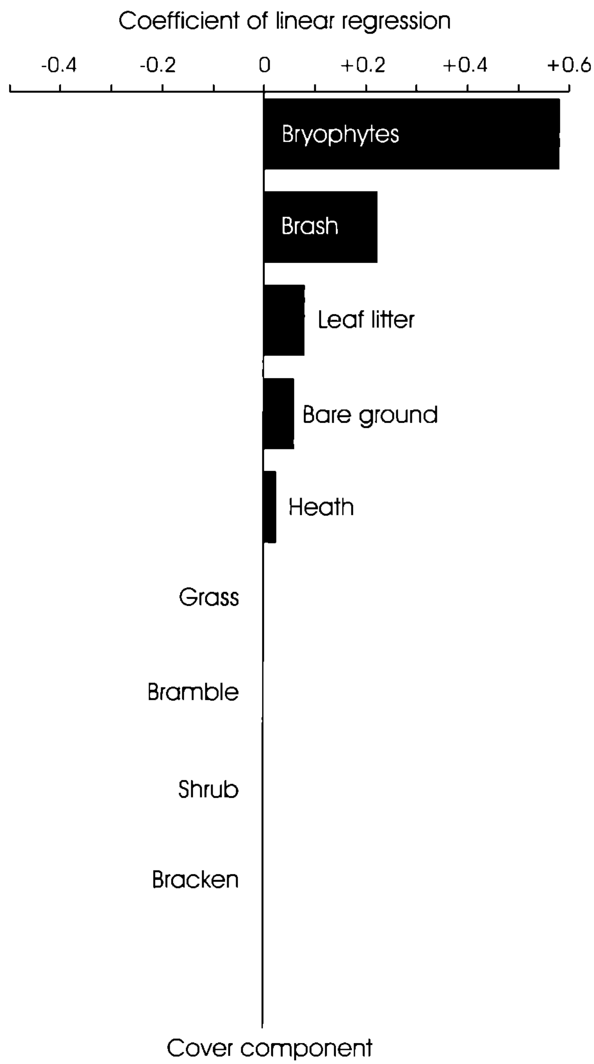


Figure 4.4 *The relationship of Douglas fir seedling density with percentage cover of various ground and field layer components.*

Predation and seedling losses

Seedling mortality and losses through the activities of rodents, insects, birds and fungi can be very high. Seedling susceptibility is greatest immediately following emergence and also when seedlings are weakened by adverse environmental conditions.

Fungi

Grey mould (*Botrytis cinerea*) can invade dead or damaged tissues of young seedlings, particularly where regeneration is dense, and can then spread to infect healthy plants. Infection can occur on shoots and foliage damaged by frost. The disease becomes less important as the plants become woody with age although occasionally the fungus will kill transplant-sized conifers (Aldhous and Mason, 1994).

Two other fungi may also be locally important. These are *Lophodermium seditiosum* on Scots pine and *Meria laricis* on European and to a lesser extent hybrid larch. Both these fungi attack needles and may cause complete defoliation. Existing trees act as reservoirs of inoculum and thus attacks are often more serious adjacent to and beneath an overstorey of the same species. In a similar manner, natural regeneration of susceptible European larch provenances may be infected by canker (*Lachnellula willkommii*) leading to the early death of regenerating trees.

Insects and slugs

Young conifer seedlings are susceptible to attack from a wide range of insect species. The most common and serious attacks involve the caterpillars of noctuid moths (*Agrostis segetum, Agrostis exclamationas, Noctua pronuba*), springtails such as *Bourletiella hortensis* and chafer grubs of Scarabeid beetles – the most common of which are *Melolontha* and *Serica brunnea* (Gribbon, 1989).

Insect pests such as pine weevils (*Hylobius abietis*) and black pine beetles (*Hylastes* spp.) will damage young conifers by gnawing their bark and causing death when ringing of the stem occurs. Whilst this damage may be severe, it rarely results in the loss of all regenerated seedlings and as such tends to be less serious than attacks on planted trees. Infestations of the defoliating aphid *Elatobium abietinum* occur on Sitka and Norway spruce, especially under conditions of partial shade, and can result in the death of apparently well established seedlings up to ten years old (Brown and Neustein, 1970).

Slugs (*Arion ater* and *Arion subfuscus*) have been recorded as the most important reason for mortality in both Scots pine (McVean, 1963) and Sitka spruce (Scarratt, 1966). Losses due to slugs are particularly high where moist conditions prevail.

Rodents

Rodents are one of the most potentially damaging agents to young seedlings. Losses are often most severe during the succulent cotyledon stage and usually decline as soon as primary needle development commences. Rodents were responsible for 40–60% of germinant losses in Sitka spruce (Scarratt, 1966) with damage being particularly high on sites with an established cover of grasses and other vegetation. Bank voles (*Clethrionomys glareolus*), field voles (*Microtus agrestis*) and field mice (*Apodemus silvaticus*) were all responsible for heavy losses (Scarratt, 1966), although the bank vole caused the majority of damage. In upland conifer forests, populations of field voles show a 3–4 year cycle of abundance (Petty and Fawkes, 1997) and years with high populations could result in appreciable damage to young seedlings.

Rabbits will also browse young seedlings and, if populations are high, areas of regeneration may need to be fenced to prevent damage.

Birds

There are very few published reports of bird damage to conifer regeneration in Britain although it is known that many bird species will peck or clip young seedlings (Evans, 1988). Chaffinches and other small song birds damage seedlings during the early stages of germination (Brown and Neustein, 1970).

Deer

Browsing by deer will prevent the establishment of natural regeneration where deer numbers are high. The effects of deer browsing may not become apparent until the plants become large enough to be palatable to deer (i.e. after 2 or 3 years).

In Scots pine forests the importance of browsing by red deer has often been stressed (Booth, 1984; Malcolm, 1976; Dunlop, 1975), and its limiting effect upon growth of regeneration is clearly demonstrated by exclosure plots. Often the total number of Scots pine seedlings is not influenced by fencing as the major effect is in releasing existing seedlings to achieve unhindered height growth (McVean, 1963, Fenton, 1985). Malcolm (1995) reported a 14 year study in Perthshire which showed that in the first four years after germination growth of seedlings was similar inside and outside a deer fence, but thereafter browsing prevented any further height growth of the unfenced trees. A recent study of the development of Sitka spruce regeneration in Kielder Forest showed 30% lesser height growth in unfenced plots exposed to roe deer browsing. This demonstrates that even regeneration of reputedly less palatable conifers can be damaged by deer.

Where small areas are being regenerated it will rarely be desirable to fence individual coupes. However, where browsing cannot be controlled by other means, a ring fence surrounding a larger area of forest can be effective. The immediate exclusion of deer following harvesting is not always necessary as a low level of browsing, particularly on fertile sites, may help to retard recolonization by weed growth and help to promote the early establishment of seedlings (Dunlop, 1983).

Protection will need to be maintained as long as the trees remain vulnerable. With red deer, freedom from browsing is not reached until the majority of trees have reached 3–4 m in height, and bark stripping may continue until trees reach about 12–14 cm breast height diameter. Roe deer may also cause damage until the trees reach approximately 1 m in height. Even at relatively low densities of deer (<5 km^{-2}), the selective browsing of tree seedlings and herbaceous plants can affect the pattern of regeneration since more palatable species (e.g. Douglas fir, larch) may be preferentially browsed so favouring less palatable species such as Sitka spruce (Ratcliffe and Mayle, 1992).

Summary

- The moisture status and the surface temperature of the regeneration substrate critically affect the early survival of young seedlings.

- The light environment is critical for subsequent seedling growth. Conifer species vary in their ability to tolerate shade. Shade intolerant species (e.g. pines, larches) require full light to achieve vigorous growth. More shade tolerant species such as Douglas fir and western hemlock can benefit from greater overhead shade which also helps to avoid moisture loss and dessication.

- Young seedlings can survive for some time (commonly two to three seasons depending on species) under quite dense stands. Following this initial period higher light levels are required to promote strong growth. Care is needed less sequential fellings encourage vigorous growth of other vegetation which can smother young seedlings.

- Heavy seedling losses may occur due to a host of damaging agents including frost, fungal attack, insect and animal damage. Many methods exist for protecting seedlings against animal damage such as fencing, individual tree guards and direct pest control. Although seedlings may be protected from larger animals such as deer, sheep, and rabbits, little can be done to avoid losses from some other agents such as slugs. Management aimed at promoting high densities of regeneration will be the best approach in order to absorb subsequent seedling losses.

Chapter 5

The assessment and management of established seedlings

Where the aim of utilizing natural regeneration is to achieve stocking levels similar to those in plantations, relatively high seedling densities will be required. Ideally the seedlings should be uniformly scattered across the area and a minimum density of established seedlings will be the aim (e.g. one seedling per 4 m^2 to provide 2500 plants/ha) where timber production is important. Uniform distribution of seedlings rarely occurs on a large scale although in some circumstances, very few seedlings may be required to ensure continuity of tree cover or to improve the structural diversity of the stand.

Assessing regeneration success

The timing of assessment

When making estimates of the density of regeneration it is essential that account is taken of the mortality which will occur before seedlings can be classed as safely established. Mortality levels are very difficult to predict as the death of seedlings can occur for many reasons (drought, frost, animal predation, etc.). It is common for fewer than 25% of the original number of germinants to be present by year 4. A good example of this high early mortality is provided by a study of the survival of Sitka spruce seedlings on a peaty gley soil at the forest of Ae (McNeill and Thompson, 1982; Figure 5.1).

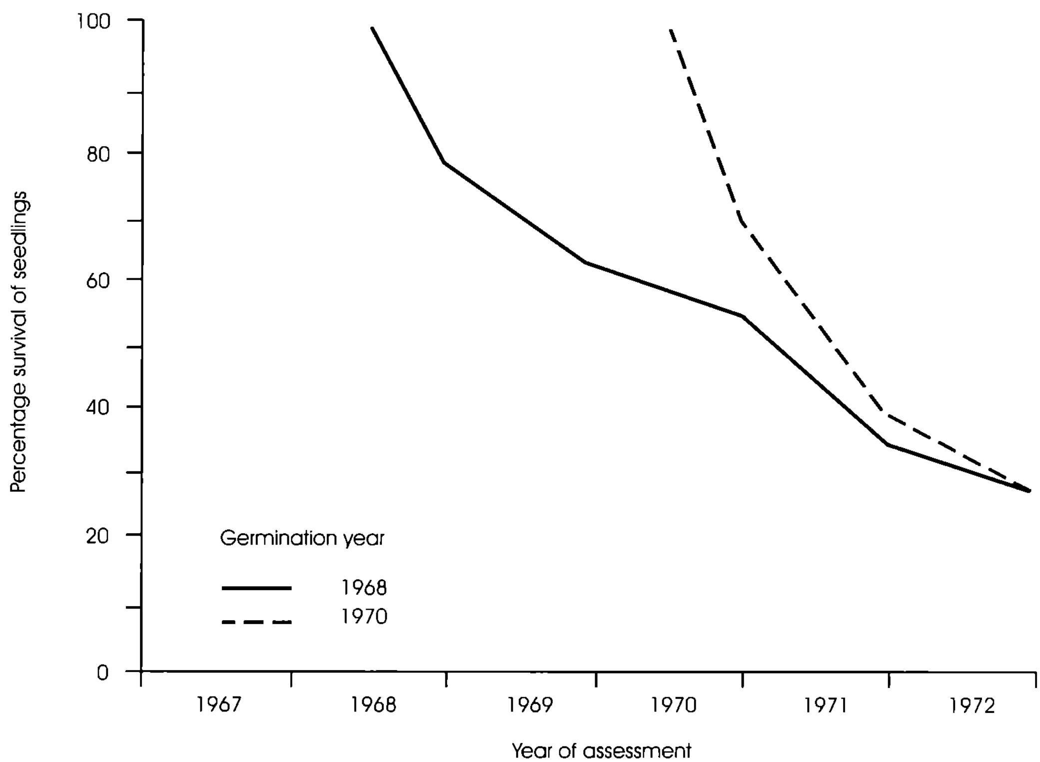


Figure 5.1 *Percentage survival at the end of year 3 of Sitka spruce seedlings germinating in 1968 and 1970. (McNeill and Thompson, 1982)*

In the absence of browsing and heavy vegetation competition naturally regenerated conifer seedlings should have a high chance of survival when they reach more than 50 cm tall. Where the impact of browsing and/or weeds is important the seedlings may need to be at least 1 m in height before they can be considered to be established.

A preliminary evaluation of the likely success of regeneration can be made in the first summer following germination. It will be sufficient to walk a site noting the presence or absence of young germinants. However, due to inevitable losses, the variability of mortality on different sites and also annual climatic differences, the longer any detailed assessment of seedling numbers can be delayed the more reliable will be the final estimate. *For this reason the assessment of one- and two-year-old seedlings should be avoided.* However, since the level of mortality normally declines each year following germination, the earliest that reliable sampling can be carried out is probably in the summer of the third year following germination (this is not necessarily the third year following the completion of stand or ground preparation operations). Even at this stage further losses may occur but dramatic reductions in seedling densities are unlikely.

Assessment procedure

Normally the primary aim in making an assessment is to record the number of seedlings per unit area. An efficient way to achieve an estimate of stocking density is to use the desired number of seedlings per hectare to determine the size of sample plots. For example, for many conifers full stocking would be achieved at 2500 plants/ha. This requires at least one seedling to be present in each 4 m^2 area. Thus, sample plots of 4 m^2 are used and a plot is 'stocked' if at least one established seedling is recorded within the plot. Following this rationale a stocking of 1100 plants/ha would require sample plots of 9 m^2.

Table 5.1 Relationship between overall seedling density and sample plot stocking

Percentage of 'stocked' sample plots	*Estimated minimum seedling density (no./ha) †*	
	Sample plot size	
	9 m^2	*4 m^2*
10	115	260
15	155	350
20	245	560
25	300	700
30	400	900
35	440	1000
40	570	1300
45	660	1500
50	750	1700
55	880	2000
60	1000	2300
65	1150	2600
70	1320	3000
75	1540	3500
80	1760	4000
85	2070	4700
90	2550	5800
95	3300	7500
100	>3300	>7500

†Predicted seedling density assumes the number of seedlings in a plot is described by a Poisson distribution.

The Poisson distribution can be used to describe the number of seedlings/ha over the site as a whole. This assumes that individual sample plots receive a large number of seeds (n) with a low probability of germination (p). Table 5.1 gives the predicted seedling density over the site as a whole based on the proportion of 'stocked' sample plots (i.e. the number of 'stocked' plots divided by the total number sampled).

Variation in the uniformity of the regeneration over an area can be described by locating stocked/unstocked plots on a map. This allows each area to be subdivided into parts requiring supplementary planting and those already fully stocked. Notes may also be made at this stage of areas which require respacing. Large areas (perhaps >10 ha) can be stratified into homogenous sections and sampled separately.

For areas up to 10 ha the minimum sampling intensity required to provide reliable results is in the order of 1% of the area. The sample also needs to be representative of the whole area in question. The most straightforward method of achieving this is to walk over the site in a systematic manner laying down assessment plots along transects. To achieve a 1% sample would require the area to be traversed at 40 m intervals with sample plots being assessed at the rate of 10 for every 100 m of transect. To avoid the problems associated with repetitive changes in the site (e.g. brash lanes) the plots should be randomly located. Unplantable areas such as very deep brash, rock outcrops, etc., should be excluded.

Supplementary planting

Supplementary planting provides an opportunity to modify the balance of species on a site and to introduce more desirable species and/or provenances. It may be necessary where there is poor stocking or in areas where regeneration has failed. In almost all instances waiting for further seedfall and germination to restock gaps is not practical. In some instances natural seedlings taken from nearby regeneration may be used as in conventional beating up operations.

The direct sowing of seed to supplement regeneration is rarely worthwhile. It is quite likely that the sown seed may fail for the same reasons as the original naturally dispersed seed and as such large quantities are often required to achieve adequate numbers of plants (Evans, 1988). If this method is used, it should also be borne in mind that the growth of the trees in the sown areas would be at least one and possibly several years behind the rest of the regeneration.

Respacing

Successful natural regeneration often results in very high numbers of seedlings which are well in excess of conventional planting densities. As a result of these high seedling numbers, respacing is often necessary to reduce the amount of competition within the stand at an early stage. This operation has the effect of concentrating the growth potential of the stand on a smaller number of selected trees. As a rule of thumb managers should consider respacing regeneration if there are substantial areas with densities in excess of 5000 stems/ha. The decision to respace will be influenced by species and site characteristics. For example, in light demanding species such as larch a lower critical density would be appropriate.

Methods of respacing

There are a number of possible ways of removing trees from dense stands. These can be separated into manual, mechanical and chemical methods.

Manual methods

Most respacing work is currently carried out manually. This commonly involves the selection of future crop trees and the cutting of all competing trees by brushcutter or chainsaw. Careful planning of working method is required to ensure maximum productivity. In particular, operators need to be aware of site features such as direction of slope, drains and streams, blank areas and the direction of the prevailing wind (Dauncey *et al.*, 1992). Brushcutters are safer and ergonomically more satisfactory. Trials have indicated that the ideal crop height for motor manual respacing is between 2 and 3 metres as by this stage the better formed and dominant trees can be identified. For species such as Sitka spruce, it is also very important to ensure that no live branches remain on the stumps of cut trees since these can regrow and compete with those that have been released. When working in small regeneration it is often difficult to ensure that the trees are cut below the lowest live whorl.

Mechanical respacing

This involves the use of machines such as forwarders fitted with rotary cutters or flails to cut swathes through the regeneration (Plate 9). The use of machines in this way provides good access to the site, reduces the amount of manual cutting required and also potentially reduces the overall cost. The most common cutting patterns are strip and checkerboard patterns. Higher outputs can be achieved using horizontal shaft flails compared with vertical shaft flail configurations although rack widths can be wider than ideal. In a test of the Berti horizontal shaft flail in Kielder Forest, the average rack width after follow up motor manual respacing averaged 2.6 m which was unacceptably wide when the target density was 2500 stems/ha (Harding, 1996). Further development work is therefore required to maximize the potential of mechanized respacing methods.

Chemical respacing

The application of chemicals to control young regeneration (<0.5 m in height) can be done at low cost but effective control can be difficult with some species, e.g. Sitka spruce. It is also difficult using present methods of application to achieve any degree of selection and thus the main potential is in the control of trees in blocks or swathes. As with mechanical control, this normally means that some follow up work by manual methods will be required. Further development work is needed on the effective deployment of chemicals and the control of spray widths during the application process.

Glyphosate (applied as a foliar spray at 10 l product ha^{-1} + adjuvant) has been found to be moderately effective in controlling small Sitka spruce natural regeneration (Nelson, 1990). However, Sitka spruce, Norway spruce, Scots, Corsican and lodgepole pine can tolerate overall sprays with glyphosate during dormant periods. Imazapyr is the only herbicide which has given consistent control (applied as a foliar spray at 12 l product ha^{-1} + adjuvant), but can only be used as a pre-planting treatment prior to establishing conifers (Willoughby and Dewar, 1995). The optimum time for herbicide application is during the early summer (June/July) and before any new growth on the trees has hardened.

The timing of respacing

The timing of the respacing operation is very important. Ideally it should be carried out as soon as potential crop trees can be identified. This is generally not possible in the first five years after germination as at this stage it is only possible to select for vigour and not form (Rollinson, 1988). It is therefore necessary to undertake the operation at a stage when trees can be checked for stem straightness and form. In dense conifer stands this means delaying until a mean height of around 1.5–2 m has been reached which is normally at 5–10 years of age, depending on the rate of growth (Plate 10).

Delaying the respacing operation further, beyond the point at which natural thinning begins, results in decreased growth of the crop trees. A period of growth check may also be induced by respacing older crops during which the remaining trees develop poorly and fail to utilize the favourable growth conditions which are created. The delay in achieving canopy closure may also allow further natural regeneration and regrowth to occur in some species, e.g. Sitka spruce.

The loss in future timber production due to competition in the early stages of stand development, although often overlooked, can be substantial in close spaced conifer stands (Furey, 1984)

The benefits of respacing

The competition for light between seedlings in dense stands is so great that death through natural self-thinning will occur over time. However, this occurs at the expense of the growth of the trees which eventually form the final crop. By spacing out the trees at an early stage the full growth potential of the selected trees can be realized. Following selective respacing, the potential size of the final crop trees is increased and the range of tree size reduced. This can be a particular benefit on high windthrow hazard class sites where rotation lengths may be reduced.

An experiment with Sitka spruce carried out at the Forest of Ae illustrates some of these points. This experiment compared different methods of respacing dense (27 000 stems/ha) Sitka spruce regeneration. At time of respacing the trees were about 5 years old with an average height of 1.6 m. Selective and systematic respacing methods were compared: the selective favoured vigorous trees at 2 m spacing; the systematic cut 1 m swathes at 2 m intervals with a second set of swathes cut at right angles to the first. After 20 years, mortality had reduced stocking density in all treatments. The trees in the selective treatment were significantly larger than those in the systematic or in the control (Table 5.2). Regrowth in the systematic treatment has meant that the density was equivalent to that in the control. The control plots (Figure 5.2) were characterized by larger numbers of small spindly trees. These have proved more vulnerable to snow damage with 14% of trees in the control plots being damaged by heavy snow in February 1996 compared with 5% for the selective and 2% for the systematic treatments respectively.

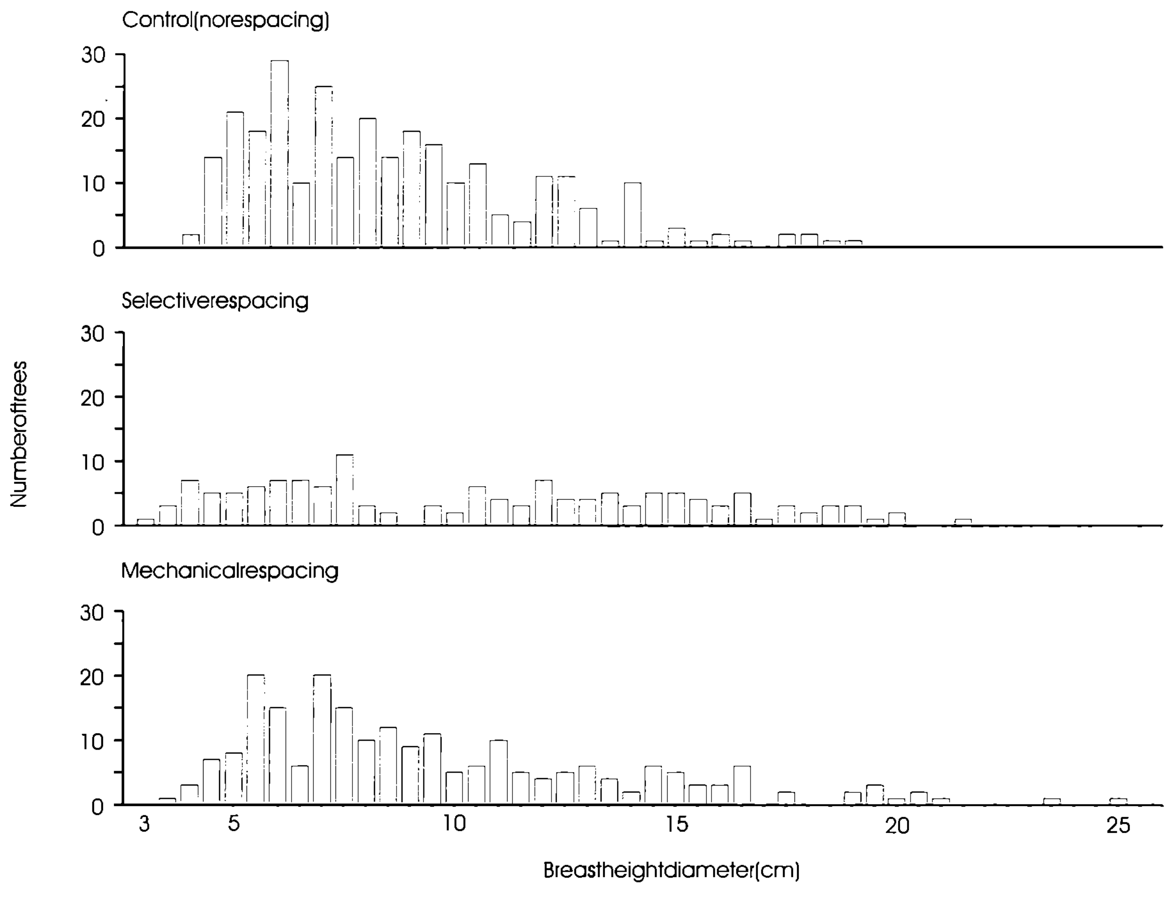


Figure 5.2 *Size distribution of Sitka spruce in respaced experimental plots at the Forest of Ae after 20 years*

Table 5.2 Respacing of Sitka spruce natural regeneration: development after 20 years in the Forest of Ae

	Control (no respacing)	*Selective respacing*	*Systematic respacing*
Stocking (stems/ha)	4963	2825	4650
Basal area (m^2/ha)	48.0	44.9	48.4
Top height (m)	16.8	16.4	15.5
Mean DBH (cm)	12.8	14.3	11.5

During respacing, the opportunity can also be taken to influence the composition of the stand for various reasons. Where selection is made on the basis of stem quality, damaged trees, trees of poor form and/or diseased trees can all be removed. Where mixed species regeneration has occurred the species composition of the stand may also be altered by retaining a greater number of the desired species.

Target spacings for reduction of crop density

Although respacing to low densities can improve the subsequent growth of the trees, the potential effect on timber quality must also be considered. Wide inter-plant spacing can result in a higher proportion of juvenile wood, larger and more frequent knots and increased stem taper (Haygreen and Bowyer, 1996). All of these characteristics have the effect of reducing wood quality. The aim therefore should be to release trees from strong competition whilst avoiding significant reductions in timber quality associated with periods of open or free growth.

Wood quality studies in Sitka spruce have shown that plant spacing greater than 2 m can significantly reduce the production of structural quality timber (Brazier, Hands and Seal, 1985). Thus, in respacing dense conifer regeneration at an early age, a target density of around 2500 stems/ha (2 m x 2 m) would appear most appropriate where timber quality is important. Where respacing is being carried out later in the rotation the target density may be lower.

Later crop development

There are few reports of the effects of respacing upon growth later in the rotation. However, it has been shown

(Reineke, 1933) that any pure, fully stocked stand of a given average stem diameter has the same number of stems/ha as any other pure, fully stocked stand of the same species with the same mean diameter, i.e. independent of age. Therefore as the mean number of stems/ha decreases, the mean diameter increases in a predictable way (3/2 power law of self-thinning – Yoda *et al.*, 1963). Respaced stands can be assumed to grow at a similar rate to planted trees once inter-plant competition occurs (Nelson, 1991). Thus the development of a dense even-aged naturally regenerated stand can be predicted from existing yield models.

Summary

- In making an assessment of the success of natural regeneration the timing of the assessment is important in order to allow for seedling mortality. Commonly the spring of the third year following germination is the earliest a reliable estimate of established seedlings can be made. Systematic point sampling techniques provide an efficient way of estimating seedling density and also allow the distribution of seedlings to be recorded.

- Where the stocking of regeneration is less than that desired, supplementary planting provides an opportunity to modify the balance of species and to infill gaps. The direct sowing of seed under these circumstances is rarely successful as it is likely to fail for similar reasons as the original natural regeneration.

- Very dense regeneration often requires respacing to reduce inter-plant competition early in the rotation. This operation can be carried out manually by clearing saw or chemical application or by mechanized flail. The timing of the respacing operation is very important and should be linked to the identification of potential crop trees. In dense conifer stands this is commonly possible when the trees reach around 1.5–2 m in height.

- Respacing encourages a period of increased diameter growth on the remaining trees prior to crown closure. A balance needs to be struck between releasing crop trees from competition and encouraging too long a period of free growth which can reduce timber quality. In general a target density of 2500 trees/ha at a crop height of 1.5–2.0 m is appropriate. Once direct inter-tree competition resumes it is likely that respaced stands will develop in a similar way to planted crops of the same stocking density.

Plate 1. Extensive natural regeneration of Sitka spruce on a site at Glasfynydd, Wales. *(39194)*

Plate 2. Visitors to Whinlater Forest in the Lake District enjoying a walk through regenerating stands at Comb Woods. *(Forest Life Picture Library, 1015157020)*

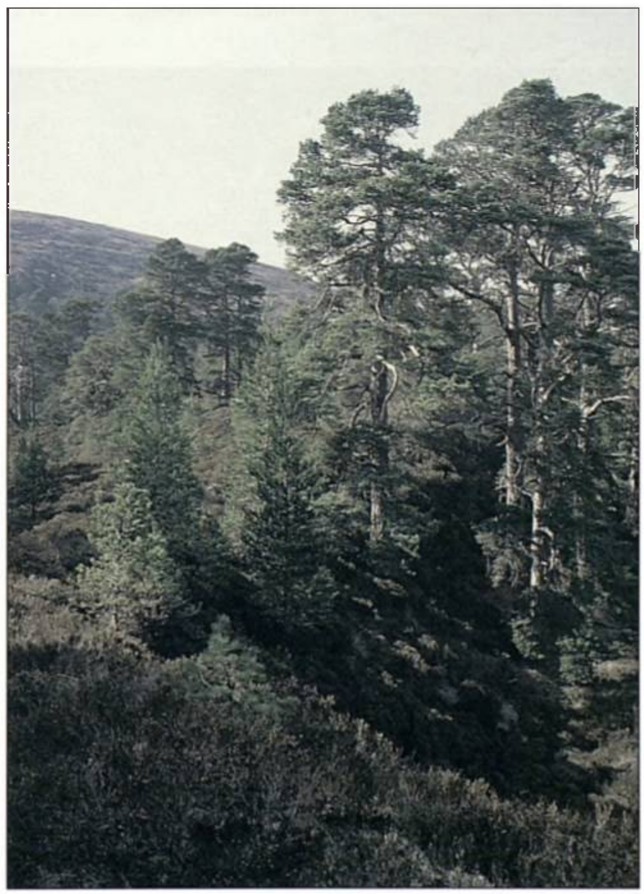


Plate 3. Natural regeneration of a relict native pinewood in a gorge at the Beinn Eighe National Nature Reserve in Wester Ross. *(50773)*

Plate 4. Heavy coning on dominant and edge trees of Sitka spruce in stands at Kielder Forest, Northumberland.

Plate 5. Cut cone of Corsican pine showing numbers of full, viable seed. *(38852)*

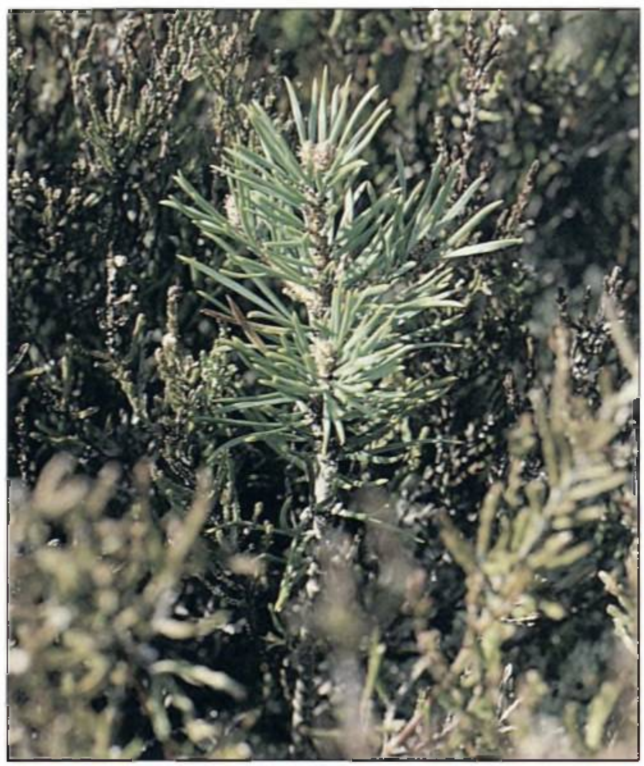


Plate 6. Young Scots pine seedling growing in dense heather at Mar Lodge Estate, Deeside. *(50776)*

Plate 7. Damage to young seedlings of Corsican pine by field mice. *(17407)*

Plate 8. Fencing to exclude deer and promote natural regeneration at Glen Affric Pinewood. *(Forest Life Picture Library, E4744)*

Plate 9. Mechanical respacing of dense Sitka spruce seedlings by forwarder mounted flail. *(Forest Life Picture Library, WAL/0/93/2–47)*

Plate 10. A young Sitka spruce crop following respacing. *(Forest Life Picture Library, 112/0/94/4–2)*

Plate 11. Scarification of a Scots pine restocking site by a TTS Delta scarifier.

Chapter 6

Economics

The cost of using natural regeneration will often need to be compared with conventional planting. Careful consideration of the crop and site potential for regeneration needs to be made in addition to the financial analysis in order to make an informed decision about the most appropriate approach on a particular site.

Comparing the cost of natural regeneration with planting

To compare the use of natural regeneration for restocking with more traditional planting methods requires the quantification of the cost of any materials and operations which are specific to each approach. Costs common to both establishment systems, e.g. fencing, roading and overheads can be treated as fixed costs and omitted from any calculations.

The main variables involved in the comparison of planting with natural regeneration include: the preparation of the ground prior to regeneration or planting; the purchase of plants and other establishment operations associated with planting; the need for pre-commercial respacing of dense regeneration; and any establishment delay associated with the encouragement of natural regeneration.

For example, assuming no differential costs of residual stand management, Tables 6.1 and 6.2 show the relative costs of restocking compared with natural regeneration of Sitka spruce on a peaty gley soil in upland Britain. It is assumed that good forestry practice results in quick establishment with limited beating up and weeding. Further assumptions include the need for additional operations of ground cultivation and weeding associated with planting as compared with an establishment delay and respacing costs incurred with natural regeneration. Finally, it is assumed that good coverage of natural regeneration will occur leaving only a few areas requiring supplementary planting.

Table 6.1 Costs/ha associated with restocking by planting

Year	*Operation*	*Actual cost £/ha*	*Discounted cost £/ha**
0	Cultivation	260	260
0	Plants	260	260
0	Planting	160	160
1	BU plants	65	62
1	BU plants	45	42
1	Weeding	55	52
1	*Hylobius* spray	45	42
Total discounted cost			£878

(*Discount rate = 6%) (£1996/7)

Table 6.2 Costs/ha associated with restocking by natural regeneration

Year	*Operation*	*Actual cost £/ha*	*Discounted cost £/ha**
2	Regeneration delay	-	115
3	Supplementary plants	65	55
3	Supplementary planting	45	38
7	Respacing	370	246
Total discounted cost			£504

(*Discount rate = 6%) (£1996/7)

Following germination, natural regeneration commonly takes two and sometimes three years to reach the size of a freshly planted tree. This delay reduces the net revenue from the rotation as compared with planted crops. With a 6% discount rate, a two-year delay in establishment will result in a discounted revenue (DR) loss of around 11% from the subsequent rotation. Assuming a discounted revenue of £1500/ha (for a Sitka spruce stand growing at YC12) then this is equivalent to a cost of £115/ha. Regeneration delay will be less on sites with less competitive vegetation and immediately following a good seed year.

In this example the use of natural regeneration shows a net cost of £504/ha compared with £878/ha for planting, a difference of *c.* £375/ha. However, each case will vary and there may be instances where planting would be the more cost-effective approach, e.g. where there are costs associated with overstorey treatment, the intention is to restock a site with genetically improved planting material or there is a very significant delay in the establishment of natural regeneration.

Respacing costs

The cost of respacing dense conifer crops is a significant element of the expenditure required to successfully manage natural regeneration. The actual cost depends upon the number of stems to be removed per unit area and the height of the trees at the time of respacing. The direct cost of respacing dense Sitka spruce crops at around 1.5–2.0 m in height by manual methods is commonly in the order of £350–400/ha (1996/7).

The expected financial benefits from carrying out the operation are dependent upon yield class, predicted future prices and the planned rotation length. Using a price size curve derived from timber sales in Great Britain during

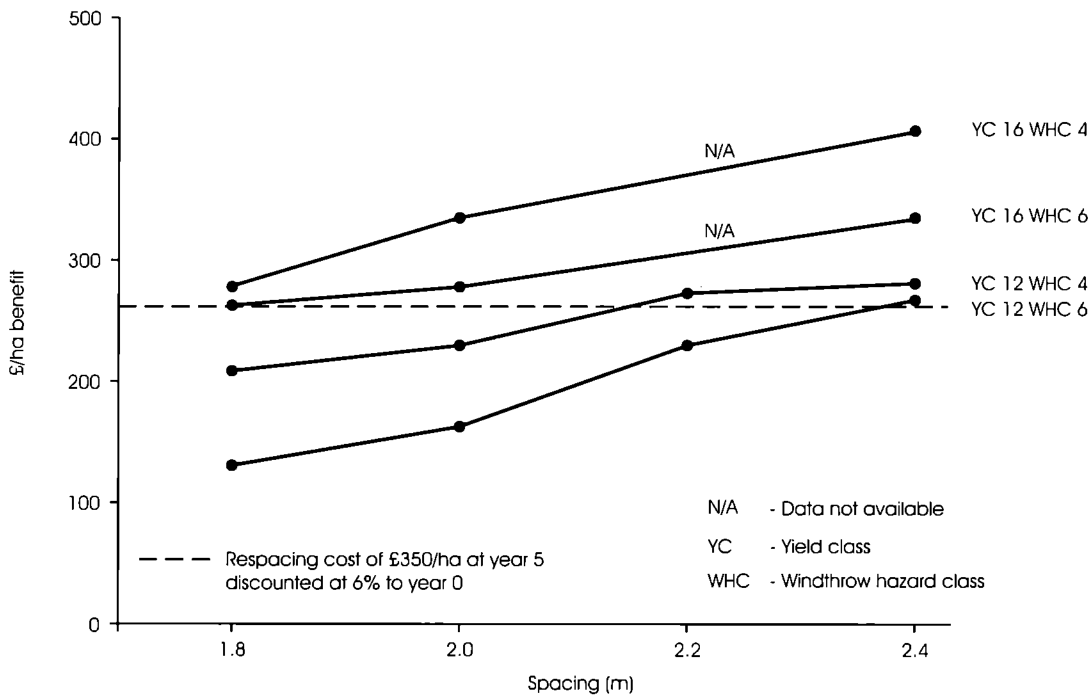


Figure 6.1 *Potential improvements in discounted revenue at year 0 by respacing Sitka spruce seedlings from 0.9 x 0.9 m initial spacing.*

1993/4, and following the methods used by Nelson (1991), crops growing at GYC 12 or above could be profitably respaced at a cost of £370/ha. However, this calculation is also critically influenced by the estimate of windthrow hazard (Figure 6.1).

Susceptibility to windthrow restricts the benefits to be gained from respacing, particularly of higher yielding crops, due to the reduced rotation length over which the trees can respond to the favourable growth conditions.

When deciding upon the order in which existing stands should be respaced the potential benefits of the operation should be considered in each case and work should give priority to sites with:

- the densest regeneration;
- the crops of highest yield class;
- the lowest windthrow risk.

Summary

- In making an economic comparison of encouraging natural regeneration and planting, the probability of success needs to be considered along with operational details. In operational terms, the main differences associated with the use of natural regeneration are the costs or savings associated with ground preparation, plant purchase, respacing and any delay in establishment.

- Cost comparisons will vary with circumstances but the use of natural regeneration can be more cost-effective than planting. The use of natural regeneration can also enhance the non-market benefits (e.g. landscape, species diversity) of the forest. However, where clearfelling is carried out natural regeneration may nevertheless involve costs associated with a delay in establishment relative to that which could be achieved by planting.

- Where respacing is necessary, this commonly costs in the order of £350–400/ha although the actual cost will vary with the initial stocking of trees and the proportion of the crop to be removed. The initial stocking density, the predicted rate of growth of the trees and the danger of early windthrow are all factors which can be used to prioritize areas for treatment.

Chapter 7

Forest management to encourage natural regeneration

A number of conditions must be fulfilled if successful natural regeneration is to be achieved. These are:

- the presence of parent trees of acceptable quality;
- site conditions which are or can be made receptive for seedling establishment;
- adequate coning or seed production on the parent trees;
- a suitable microclimate for seed germination and seedling growth;
- the absence of significant browsing pressure.

Meeting these preconditions requires the manager to make a series of decisions which will influence the likelihood of achieving successful conifer natural regeneration. These steps are shown in the form of a decision model in Figure 7.1. Key points are discussed in the following sections which cross reference as necessary to earlier chapters.

Stand quality

The first consideration is to decide whether the parent trees on the site are of the desired quality. If the trees are of poor form and vigour, there will be little to gain by encouraging natural regeneration, particularly where the production of quality timber is a concern. Parent trees should also be in good health and of a seed bearing age. Most conifer species produce plentiful seed for much of their life but in the periods leading up to reproductive maturity, and when trees become very old, seed yields may be significantly smaller (Chapter 2).

Preparatory thinning

Assuming the parent trees are of an acceptable quality, the main objective should be to ensure that preparatory thinnings are commenced early in the life of the stand (normally between 25–35 years) to promote crown development on the future parent trees. As the majority of coning occurs on the exposed parts of the crown it is important to release crowns early in the rotation to retain deep, full crowns for seed production in later years. The aim should be to maintain a live crown depth of at least half the total height of the trees. This is particularly important as many conifers have a limited ability to redevelop crown depth once it is lost. Preparing stands in this way is a normal procedure on the European continent and has long been recognized as an important prerequisite to achieving good regeneration. Crown thinning can be used to favour the future parent trees. The number of thinnings and their intensity will vary according to the site exposure and vulnerability to windthrow (Table 7.1).

Where conventional thinning is not possible due to high risk of windthrow, other approaches may be taken to promote seed production. On these sites the creation of windfirm stand edges through the early respacing of some parts of the stand can help to promote crown development on a proportion of the trees whilst also allowing them to develop greater stability.

Table 7.1 Number of thinnings in relation to site exposure

Preparatory thinning	
Windthrow hazard	*Number of thinnings*
I-III	Normal thinning cycle
IV-V	Single thinning
VI	Single early respacing

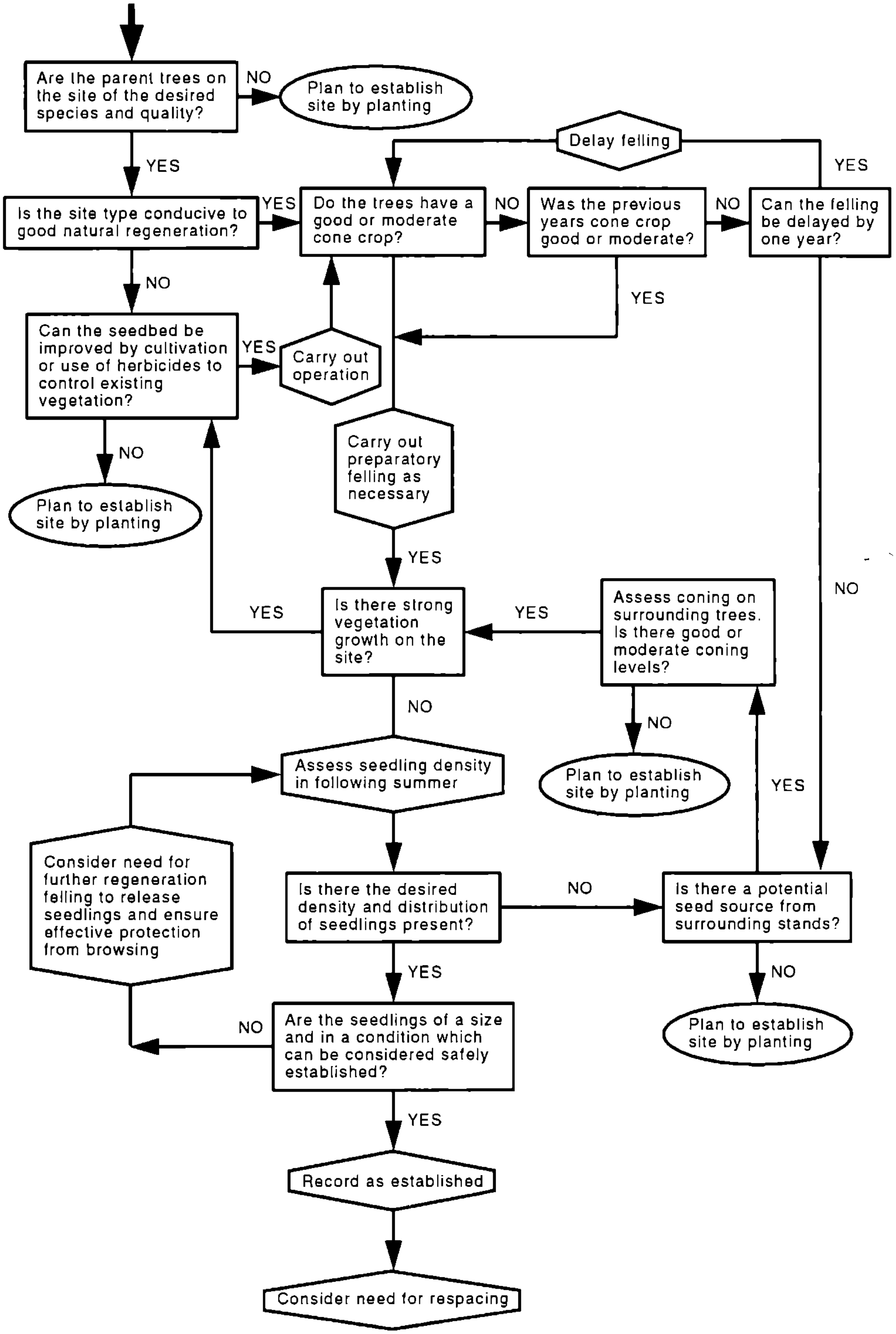


Figure 7.1 *A decision model showing the major factors influencing the management of conifer stands to encourage natural regeneration prior to and following preparatory felling.*

Site suitability for natural regeneration

To achieve successful regeneration the condition of the forest floor must be suitable for the germination and growth of seedlings. Seedling establishment can occur in the absence of special management action and the presence of seedlings on a site can often be a good indicator of regeneration potential. Sites with low nutrient status often regenerate well due to their slow recolonization by competing vegetation following tree felling. As a result, sites with dry sandy soils often support regeneration of Scots and lodgepole pine and larch, whilst moist peaty soils commonly provide suitable seedbeds for Sitka spruce and lodgepole pine. Dense Douglas fir regeneration is not often found in the absence of site disturbance due to the nature of the sites upon which it thrives, i.e. fresh and rich soils with potentially vigorous weed growth. Figure 4.3 shows the general relationship between soil type and regeneration potential.

Improving site conditions for regeneration

Competing vegetation

Natural regeneration can be encouraged by operations which remove or disturb existing vegetation and also areas of deep, undecomposed needle litter which are prone to drying out. A combination of humus and mineral soil provides the best surface conditions for regeneration and this mixing of the surface soil layers can be achieved by cultivation. On many sites patch or strip scarification is to be preferred to more extensive disturbance.

Ground preparation measures will be most effective when carried out in the autumn or early winter period prior to seedfall. This minimizes the time available for competing vegetation to become established prior to the germination of tree seedlings. Depending on the fertility of the soil, prepared regeneration areas may only remain receptive for a short period (1–2 years) before competing vegetation recolonizes the site.

Where sites have become dominated (i.e. >75% cover) by vigorous weeds such as bracken, bramble or grasses, the potential for natural regeneration will be significantly reduced and conventional methods of site preparation and planting should be preferred.

Felling residue

The distribution of felling residue or brash on a site can affect the subsequent pattern of natural regeneration. Areas covered with brash of >15 cm depth are unlikely to regenerate well due to the creation of unfavourable conditions for seed germination and/or seedling growth. Spreading brash thinly, or raking brash into piles can help to increase the proportion of a site which is suitable for regeneration establishment.

The burning of brash was a common practice in Nordic countries, especially Finland and Sweden, until the development of mechanical scarifiers about 20 years ago (Bergman *et al.*, 1981). Controlled burning, mimicking the effects of wildfires, has also been used to encourage the regeneration of Scots pine in Britain on sites with a dense cover of *Calluna*. However, burning is not recommended for several reasons. Firstly, controlled burning, particularly beneath existing seed trees, is difficult and expensive. There is also a risk of damage to seed trees and any existing regeneration. On sites with a thin humus layer nutrients (especially nitrogen) may also be lost.

Coning and seed production

Assessing the potential

A good quality stand on a receptive site, which has been prepared for regeneration through careful thinning, will have very good natural regeneration potential. However, the timing and quantity of seed production by the parent trees will still be critical to the ultimate success of regeneration. Assessments of flowering in early spring, and cone numbers in summer will provide indications of the level of seed production in any given year (Chapter 2). It is unrealistic to expect good regeneration unless the cone crop has been assessed as moderate or heavy.

Timing the felling

Figure 7.2 illustrates the optimum period for timing felling to encourage regeneration in species such as spruces, firs and Japanese larch which release most of their seed over winter. Felling the mature stand much before October reduces the potential for regeneration because the seed in the cones will not have fully matured. Felling later than April in the year following a large cone crop risks damaging the new seedlings germinating on the forest floor. Exceptions to this rule are Corsican pine, Scots pine and European larch which release seed in the spring and early summer. With these species late spring felling is most appropriate.

Managers can also use the information on the optimum seed dispersal period to time fellings so that the occurrence of regeneration is minimized. This can be particularly useful if seeking to replace existing tree species or retain permanent open space.

Preparatory regeneration fellings and silvicultural systems

Where natural regeneration is being encouraged beneath an overstorey, the task in promoting regeneration is initially to allow in sufficient light to allow the young seedlings to survive, at least for the first season. Following this, it is essential to increase the light reaching the seedlings without fostering excessive competition from ground vegetation.

Preparatory regeneration fellings will be required where tree canopy density is too great to allow successful seedling establishment beneath the existing stand. The levels of canopy cover beneath which seedlings can establish varies between species, and also the height of the surrounding parent trees. Estimates of critical canopy cover (plan view) for mature stands (i.e. 25–30 m tall) of a range of species are given in Table 7.2.

Table 7.2. Critical canopy cover for seedling establishment under mature stands of different conifer species

Tree species	*Critical canopy cover for seedling establishment**
Pines/larch	40–50%
Sitka spruce	45–55%
Douglas fir/Norway spruce	60–65%
Western hemlock	70–75%

*Estimates for stand conditions unaffected by significant sidelight.

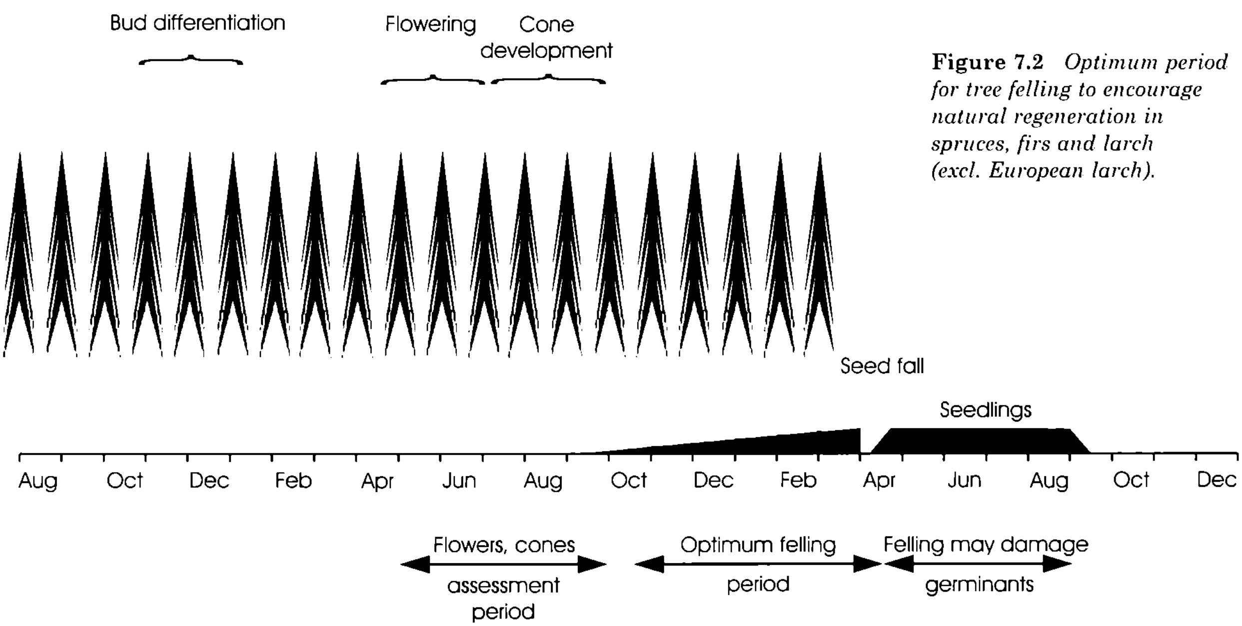


Figure 7.2 *Optimum period for tree felling to encourage natural regeneration in spruces, firs and larch (excl. European larch).*

For most conifers preparatory regeneration fellings must be undertaken during the autumn and early winter period in a moderate or heavy coning year to maximize the quantity of tree seed reaching the forest floor (see Figure 7.2).

Successful regeneration will often be the first phase of the introduction of a new silvicultural system. In plantation forests, careful consideration is needed of the desired future goal in terms of stand structure and future regeneration. Alternative silvicultural systems will not be covered in detail here, but where the objective is to utilize natural regeneration to sustain forest cover, the characteristics of the species in question will help to define the range of possible approaches to stand management. In general the more shade tolerant species such as Sitka spruce, western hemlock and Douglas fir lend themselves to more intensive management within selection and group shelterwood systems, whilst light demanding species such as the pines and larches are more suited to shelterwood and seed-tree systems. (For further information on silvicultural systems, see Hart, 1995).

Monitoring seedling establishment

Visual checks for young seedlings can begin during the summer following seed dispersal. However, seedlings will not normally become safely established until the third growing season. Assessment of established seedlings can be made by noting the presence or absence of seedlings in a series of temporary sampling plots (see Chapter 5). If the density of seedlings is low or patchy, consideration will need to be given to supplementing the regeneration by planting. This is also an opportunity to manipulate the proportion of particular species in mixed stands. Under these circumstances a careful appraisal of the likelihood of further natural regeneration occurring on the site needs to be made. This commonly occurs as a result of seed dispersed from adjacent stands.

Where regeneration proves to be poor or absent a reassessment of the future potential for regeneration will be needed. Where site and/or stand conditions appear unfavourable planting may well prove a more reliable option (Figure 7.1).

Protection of regeneration

Young seedlings will require protection, particularly from browsing animals such as deer, sheep and rabbits, if they are to become safely established. For example, red deer densities above 5 animals km^{-2} can prevent Scots pine regeneration and above about 10 animals km^{-2} regeneration of less palatable species such as Sitka spruce will be seriously checked or prevented. Under circumstances where there are likely to be a significant density of grazing animals either fencing or a sustained cull or reduction in animal numbers will be essential in order to achieve successful regeneration.

Respacing

Where dense regeneration occurs, respacing of young conifer seedlings will often be necessary to encourage the diameter growth of the remaining trees and to reduce stem densities in line with planted crops. This operation is normally carried out when the trees reach a height when it becomes possible to identify the more vigorous and dominant trees (Chapter 5).

Summary

While natural regeneration will generally be a less certain means of establishing trees than planting it has sufficient benefits to make it the preferred option for some combinations of crops and sites. Where natural regeneration is both desirable and feasible, the probability of success can be increased by:

- stand treatment to increase the bud and frequency of seed production and the microclimate of the site; site treatment to improve germination, seedling survival and early growth;

- vegetation management to ensure adequate light and moisture for the young seedlings;

- pest management to limit subsequent losses;

- respacing where necessary to achieve optimum spacing.

However, given the variability of seed production, foresters need to be flexible in their approach to natural regeneration. They must be prepared to wait for an abundance of seed, be flexible in making the most of opportunities and be willing to adopt alternative methods when natural regeneration is too uncertain or is failing to achieve the objectives of management. By application of the general principles stated in this Bulletin and the development of local knowledge an increasing proportion of sites can be regenerated by natural means.

Appendix 1

Notes on natural regeneration by species

Sitka spruce

Many Sitka spruce crops are capable of producing large quantities of seed within relatively short rotation lengths and the seed often has a high viability.

The seed has a high moisture requirement for successful germination and therefore germinants are often most successful on peat soils and in damp hollows and wet flushes on other soil types. The distribution of felling residue on harvesting sites often restricts dense regeneration to brash-free areas. The treatment of brash is therefore important in the encouragement of regeneration in this species.

Sitka spruce is commonly found regenerating naturally following clearfelling of crops on sites in the border regions of north England and south Scotland, in western Scotland and also in Wales. There is estimated to be at least 1000 ha of young natural regeneration present on sites in Forest Enterprise forests in these areas. The moderate shade-tolerance of young seedlings makes it possible to encourage regeneration beneath well-thinned stands of mature trees as an alternative to clearfelling systems. However, once the seedlings have reached 1m in height they require releasing to maintain satisfactory growth. If this is not done growth stagnates and they can become vulnerable to defoliation by *Elatobium.*

Due to its ability to regenerate very densely, there are many occasions when the respacing or pre-commercial thinning of young regeneration will be necessary. The timing and methodology used must be carefully considered.

The larches

Larch species tend to produce good quantities of seed almost every year making it simpler to plan regeneration operations. However, the seed has quite low viability levels and so very good coning levels are needed to provide sufficient seed to make good natural regeneration possible. The seed has a very low requirement for cold stratification and can therefore germinate throughout the year whenever conditions are favourable.

As pioneer species larch seedlings are very light demanding and need very open canopy conditions in order to establish successfully. This lends itself to silvicultural systems which involve patch or clearfelling and strip shelterwood.

Due to the low moisture requirement of the seed during germination, young seedlings are often found on disturbed soil, sand or even roadside spoil. Thus ground preparations which disturb the soil surface and expose mineral soil are generally most successful. Although larch seedlings often begin to establish on many nutritionally poor sites, subsequent fertilization may be necessary to maintain satisfactory growth.

As with other light demanding species such as Scots pine, early respacing of dense seedlings is needed to ensure the final crop trees are given sufficient space to develop before damaging competition occurs.

Scots pine

Scots pine trees produce some seed almost every year making the timing of regeneration operations less critical than with species such as Sitka spruce and Douglas fir. The seed has a lower moisture requirement for germination than spruce and fir and as such young germinants often occur on drier soils such as sands and gravels, roadside spoil, etc. Scarification or some other form of ground disturbance which reduces the competition from vegetation is often needed to achieve dense regeneration.

The seed is relatively heavy which restricts the potential for dense regeneration far beyond the edge of existing woodlands. This characteristic makes systems of management involving the retention of seed trees the most appropriate in many circumstances.

Young seedlings need light open conditions to grow successfully making it necessary to remove any overhead canopy once young seedlings are established. As with all regeneration, protection from grazing animals is essential to allow seedlings to grow beyond the height of the matrix vegetation. In the native pinewoods protection from deer is often the most significant requirement.

Where regeneration is dense, early respacing will be needed to ensure the release of final crop trees as with other light demanding species such as larch. Fertilization may be necessary on nutritionally poor sites to achieve successful development beyond the initial establishment phase.

Douglas fir

Seed production in Douglas fir tends to be erratic with often long gaps between mast years. In poor years many seeds can be infected by the seed wasp *Megastigmus spermotrophus* rendering them non-viable. This can make the successful encouragement of natural regeneration very difficult unless operations are timed to coincide with a mast year.

Douglas fir grows best on more fertile, sheltered sites which also support vigorous vegetation. This often makes it difficult for germinating seedlings to establish. The control of competing vegetation by a gradual opening up of the overhead canopy is possible where mature stands are sufficiently dense. In cases where strong vegetation growth is already established the use of herbicides or scarification operations will be necessary to create a receptive seedbed.

Seedlings of Douglas fir are moderately tolerant making it possible to manage stands to create a multi-storied structure. Protection will be required in the early years, particularly from roe deer which find Douglas fir very palatable.

Western hemlock

Western hemlock is normally only a minor component of most forests. However, where mature trees occur, seed production can be prolific and good seed years are frequent. The very shade tolerant seedlings can establish beneath most tree canopies making it potentially invasive. This same characteristic makes it an ideal component of stands where selection and shelterwood systems of management are employed.

Seedlings establish best on disturbed soil with little vegetation competition. Seedling

Table A1 Frequency of occurrence of natural regeneration of Britain's major conifer species

	Frequency of occurrence		
Species	*Frequent*	*Occasional*	*Rare*
Abies grandis		√	
Abies procera		√	
Chamaecyparis lawsoniana			√
Larix decidua	√		
Larix x *eurolepis*	√		
Larix kaempferi	√		
Picea abies		√	
Picea sitchensis	√		
Pinus contorta	√		
Pinus nigra			√
Pinus sylvestris	√		
Pseudotsuga menziesii	√		
Tsuga heterophylla	√		

(adapted from Brown and Neustein, 1970)

densities can be very high requiring respacing operations to be carried out. The timing of this operation is perhaps less critical than with other more light demanding species.

Other conifers

There are a number of other conifer species which can be found naturally regenerating successfully in parts of Britain. These include Corsican and lodgepole pine, Norway spruce and *Abies* species such as grand and noble fir plus a range of other minor species. At present there are few examples of active stand management to deliberately encourage natural regeneration of these species but the presence of young seedlings after stands have been thinned or felled demonstrates the potential to regenerate these species by natural means.

REFERENCES

ALDHOUS, J. R. (1972). *Nursery practice.* Forestry Commission Bulletin 43. HMSO, London.

ALDHOUS, J. R. and MASON, W. L. (1994). *Forest nursery practice.* Forestry Commission Bulletin 111. HMSO, London.

ALLEN, G. S. (1941). A basis for forecasting seed crops of some coniferous trees. *Journal of Forestry* **39**, 1014–1016.

BAKER, F. S. (1945). Effects of shade upon coniferous seedlings grown in nutrient solutions. *Journal of Forestry* **43**, 428–435.

BAKER, R. M. (1990). Observations on the natural regeneration of western hemlock in south-east Wales. *Quarterly Journal of Forestry* **84**, 94–98.

BERGMAN, F. (1960). Seed ripening and seed quality of pine in Norrland. *FS Information, Foreningen for Skogstradforadling,* Uppsala, 9. (2pp.)

BERGMAN, F., BORSET, O., and LEIKOLA, M. (1981). Natural regeneration of conifers in Fennoscandia. *Proceedings XVII IUFRO Congress, Div.* 1, 381–401.

BEVAN, D. (1966). Douglas fir seed wasp, *Megastigmus spermotrophus. Forestry Commission Report on Forest Research 1965*, 65. HMSO, London.

BEVAN, D. (1967a). Douglas fir seed wasp, *Megastigmus spermotrophus. Forestry Commission Report on Forest Research 1966*, 75. HMSO, London.

BEVAN, D. (1967b). Douglas fir seed wasp, *Megastigmus spermotrophus. Forestry Commission Report on Forest Research 1967*, 103. HMSO, London.

BEVAN, D. (1968). Douglas fir seed wasp, *Megastigmus spermotrophus. Forestry Commission Report on Forest Research 1968*, 112–113. HMSO, London.

BEVAN, D. (1969). Douglas fir seed wasp, *Megastigmus spermotrophus. Forestry Commission Report on Forest Research 1969*, 112. HMSO, London.

BLACKHALL, S. R. and NIXON, C. J. (1992). *Factors affecting the natural regeneration of Douglas fir.* Forestry Authority internal report. Unpublished.

BOOTH, T. C. (1984). Natural regeneration in the native pinewoods of Scotland, a review of principles and practice. *Scottish Forestry* **38**, 33–43.

BRAZIER, J. D., HANDS, R. G. and SEAL, D. T. (1985). The influence of plant spacing on structural wood yields from Sitka spruce. *Forestry and British Timber* **14**(9), 34–37.

BROWN, J. M. B. and NEUSTEIN, S. A. (1970). Natural regeneration in the British Isles. *Proceedings of the Royal Horticultural Society 3rd Conifer Conference*, 29–39.

BUNCE, R. G. H. and JEFFERS, J. N. R. (1977). Native pinewoods of Scotland. *Proceedings of the Aviemore Symposium 1975.* Institute of Terrestrial Ecology, Cambridge.

CHEN, J., FRANKLIN, J. F. and SPIES, T. A. (1993). Contrasting microclimates among clearcut, edge and interior of old-growth Douglas fir forest. *Agricultural and Forest Meteorology* **63**, 219–237.

CLARKE, G. C. (1992). The natural regeneration of spruce. *Scottish Forestry* **46**, 107–129.

DANNAT, N. and DAVIES, E. J. M. (1970). To wait or not to wait ?: spruce regeneration problems at Inverliever. *Scottish Forestry* **24**, 17–20.

DAUNCEY, A. (1992). *Respacing of Sitka spruce natural regeneration.* Forestry Commission Technical Development Branch, Technical Note 3.

DAVIES, F. H. (1954). Natural regeneration at 1200 feet above sea level at Glasfyndd. *Journal of the Forestry Commission 1952–4* **23**, 55–56.

DAY, R. J. (1963). Spruce seedling mortality caused by adverse summer microclimate in the Rocky Mountains. *Publication of the Department of Forestry Canada* 1003. (36pp.)

DOBBS, R. C., EDWARDS, D. G. W., KONISHI, J. and WALLINGER, D. (1976). *Guideline to collecting cones of B.C. Conifers.* British Columbia Forest Service/Canadian Forest Service. Joint Report 3.

DUNLOP, B. M. S. (1975). The regeneration of our native pinewoods. *Scottish Forestry* **29**,111–119.

DUNLOP, B. M. S. (1983). The natural regeneration of Scots pine. *Scottish Forestry* **37**, 259–263.

EDWARDS, C. (1995). *Results of experiments on Sitka spruce seed longevity at Kielder Forest.* Forestry Commission. Unpublished.

EIS, S. (1973). Cone production of Douglas fir and grand fir and their climatic requirements. *Canadian Journal of Forest Research* **3**, 62–70.

EVANS, J. (1988). *Natural regeneration of broadleaves.* Forestry Commission Bulletin 78. HMSO, London.

FAIRBAIRN, W. A. (1963). Some observations on group regeneration. *Forestry* **36**, 113–123.

FAIRBAIRN, W. A. and NEUSTEIN, S. A. (1970). Study of response of certain conifer species to light intensity. *Forestry* **43**, 57–71.

FENNER, M. (1991). Irregular seed crops in forest trees. *Quarterly Journal of Forestry* **85**, 166–172.

FENTON, J. (1985). Regeneration of native pine in Glen Affric. *Scottish Forestry* **39**, 104–116.

FORESTRY COMMISSION (1948). Forestry Commission Annual Research Report.

FUREY, P. F. (1984). *Early growth responses in spaced softwood stands.* Abitibi-Price, Newfoundland. Unpublished.

GARMAN, E. H. (1951). *Seed production by conifers in the coastal region of British Columbia related to dissemination and regeneration.* British Columbia Forest Service, Technical Publication T35.

GARMAN, E. H. (1955). *Regeneration problems and their silvicultural significance in the coastal forests of British Columbia.* British Columbia Forest Service, Technical Publication T41.

GORDON, A. G. (ed.) (1992). *Seed manual for forest trees.* Forestry Commission Bulletin 83. HMSO, London.

GREGORY, R. A. (1956). *The effect of clearcutting and soil disturbance on temperature near the soil surface in SE Alaska.* US Forest Service Station Paper 7.

GRIBBON, P. (1989). *A study of the factors influencing the natural regeneration of Sitka spruce in clearcut areas.* MSc Thesis, University of Lancaster. Unpublished.

HAGNER, S. (1965). Seed production, choice of seed-trees and seedling establishment in a study of natural regeneration. *Studia Forestalia Suecica* 27. (43pp.).

HARDING, J. (1993). *Motor manual respacing by clearing saw.* Forestry Commission Technical Development Branch Report 17/93.

HARDING, J. (1994). *Mechanical respacing by Bruunett/Berti Flail.* Forestry Commission Technical Development Branch Report 6/94.

HART, C. (1995). *Alternative silvicultural systems to clearcutting in Britain: A review.* Forestry Commission Bulletin 115. HMSO, London.

HAYGREEN, J. G. and BOWYER, J. L. (1996). *Forest products and wood science.* Iowa State University Press, Ames.

HENMAN, D. W. (1961). Natural regeneration of Scots pine woods in the highlands. *Scottish Forestry* **15**, 235–242.

HETHERINGTON, J. C. (1965). *The dissemination, germination and survival of seed on the west coast of Vancouver Island from western hemlock.* British Columbia Forest Service, Research Note 29.

HIBBERD, B. G. (ed.) (1991). *Forestry practice.* Forestry Commission Handbook 6. HMSO, London.

HILL, M. O. and STEVENS, P. A. (1981). The density of viable seed in soils of forest plantations in upland Britain. *Journal of Ecology* **69**, 693–709.

HOWELLS, G. (1966). *Some factors affecting the development of natural regeneration of Sitka spruce.* Unpublished PhD thesis. Department of Forestry, University College of North Wales, Bangor.

HUSSEY, N. W. (1952). *Megastigmus* insects attacking conifer seed. *Forestry Commission Report on Forest Research 1951*, 137–138.

INSLEY, H., HARPER, W. and WHITEMAN, A. (1987). *Investment appraisal handbook.* Forestry Commission, Edinburgh.

ISAAC, L. A. (1940). *Life of seed on the forest floor.* USDA Forest Service, Experiment Station Research Note 31.

JEANSSON, E. (1987). Some aspects of site preparation and natural regeneration in Sweden. *Proceedings, IUFRO Symposium in Lapland, Finland, 16–22 August 1987.*

JONES, E. W. (1943). The cone production of Scots pine seed bearers. *Forestry* **17**, 52–54.

JONES, E. W. (1947). Scots pine regeneration in a New Forest enclosure. *Forestry* **21**, 151–178.

JONES, S. K. and GOSLING, P. G. (1991). Unpublished data. Forestry Commission Research Division.

KERR, G. and EVANS, J. (1993). *Growing broadleaves for timber.* Forestry Commission Handbook 9. HMSO, London.

KUOCH, R. VON (1965). Der samenanfall 1962–3 an der oberen Fichtenwaldgrenze im Sergital. *Schweizerische Anstalt fur das forstliche Versuchwesen, Mitteilungen* **41**, 62–85.

LEIKOLA, M., RAULO, J. and PUKKELA, T. (1982). Predictions of variations in the seed crop of Scots pine and Norway spruce. *Folia Forestalia* **537**, 1–43.

LOW, A. J. (1988). Scarification as an aid to regeneration in the Glentanar native pinewood. *Scottish Forestry* **42**, 15–20.

LOWRY, W. P. (1966). Apparent meteorological requirements for abundant cone crops in Douglas fir. *Forest Science* **12**, 185–192.

LUPKE, B. von (1972). The natural regeneration of European larch. *Aus dem Walde* 17, 76.

MACDONALD, J. M. and LOCKHART, S. F. M. (1953). Some early observations in natural regeneration of conifers in Britain. *Scottish Forestry* **7**, 79–82.

MAGUIRE, W. P. (1956). Are ponderosa pine crops predictable? *Journal Forestry* **54**, 778–779.

MAIR, A. R. (1973). Dissemination of tree seed; Sitka spruce, western hemlock and Douglas fir. *Scottish Forestry* **27**, 308–314.

MALCOLM, D. C. (1976). Silvicultural problems in the conservation of natural Scots pine in Scotland. In, *Ecosystems* 14–22, ed. Mayer, H. 16th IUFRO World Congress, Oslo.

MATTHEWS, J. D. (1954). Production of seed by forest trees in Britain. *Forestry Commission Report on Forest Research 1954*, 64–78.

MATTHEWS, J. D. (1963). Factors affecting the production of seed by forest trees. *Forestry Abstracts* **24**, 1–13.

MAZURKIEWICZ, M. (1991). Population dynamics and demography of the bank vole in different tree stands. *Acta Theriologica* **36** (3–4), 207–227.

McINTOSH, R. and HENMAN, D. W. (1981). Seed fall in the Black Wood of Rannoch. *Scottish Forestry* **35**, 249–255.

McNEILL, W. M. (1955). Studies of surface vegetation and natural regeneration in a mature Scots pine wood in Aberdeenshire. *Forestry* **28**, 49–65.

McNEILL, W. M. (1962). Problems and prospects of natural regeneration in coniferous plantations in Scotland. *Supplement to Forestry* **35**, 28–33.

McNEILL, J. D. and THOMPSON, D. A. (1982). Natural regeneration of Sitka spruce in the Forest of Ae. *Scottish Forestry* **36**, 269–282.

McVEAN, J. D. (1961). Experiments on the direct sowing of Scots pine. *Empire Forestry Review* **40**, 217–227.

McVEAN, J. D. (1963). Ecology of Scots pine in the Scottish Highlands. *Journal of Ecology* **51**, 671–686.

MENCUCCINI, M. (1991). *Seed production in Picea abies.* Institute of Sylviculture, University of Firenze. Unpublished report.

NELSON, D. G. (1990). *Chemical control of Sitka spruce natural regeneration.* Forestry Commission Research Information Note 187. Forestry Commission, Edinburgh.

NELSON, D. G. (1990). *Restocking survey 1989.* Forestry Commission report. Unpublished.

NELSON, D. G. (1991). *Management of Sitka spruce natural regeneration.* Forestry Commission Research Information Note 204. Forestry Commission, Edinburgh.

NEUSTEIN, S. A. (1967a). Regeneration of tree stands. *Forestry Commission Report on Forest Research 1966*, 39–42.

NEUSTEIN, S. A. (1967). Regeneration of tree stands. *Forestry Commission Report on Forest Research 1967*, 55–59.

NEUSTEIN, S. A. (1968). Regeneration of tree stands. *Forestry Commission Report on Forest Research 1968*, 57–59.

NEUSTEIN, S. A. (1969). Natural regeneration. *Forestry Commission Report on Forest Research 1969*, 94.

NIXON, C. J. and CAMERON, E. (1994). A pilot study on the age structure and viability of the Mar Lodge pinewoods. *Scottish Forestry* **48** (1), 22–27.

NIXON, C. J. (1997). *Results of a field experiment at Braemoray Estate, Spreyside.* Forestry Commission report. Unpublished.

OLIVER, P. (1993). *Factors which contribute to the presence or absence of natural regeneration on recently felled peaty gley and surface water gley sites in the border region of Britain.* Internal Forestry Commission Report. Unpublished.

OTTOSSON LOFVENIUS, M. (1987). *Effects of high pine shelterwood on temperature near the ground.* Uppsala University, Department of Physical Geography, UNGI Rapport 65, 69–79.

PEINE, H. (1982). Timing of spacing in young balsam fir stands. *Forestry Chronicle*, April 1982.

PETTY, S. J. and FAWKES, B. L. (1997). Clutch size variation in tawny owls from adjacent valley systems. Can this be used as a surrogate to investigate temporal and spatial variations in vole abundance? In, *Biology and conservation of owls of the northern hemisphere: 2nd international symposium*, eds J. R. Duncan, D. H. Johnson and T. H. Nichols. USDA Forest Service, General Technical Report NC–190.

PHARIS, R. P., WEBBER, J. E. and ROSS, S. D. (1987). The promotion of flowering in forest trees by gibberellin A4/7 and cultural treatments: a review of possible mechanisms. *Forest Ecology and Management* **19**, 65–84.

PHARIS, R. P. and ROSS, S. D. (1986). Hormonal promotion of flowering. In, *CRC Handbook on flowering* Vol.5, ed. Halevy, A. H. CRC Press, Boca Raton, FL, 269–286.

PHILIPSON, J. J. (1987). A review of coning and seed production in *Picea sitchensis. Proceedings of the Royal Society, Edinburgh* **93(B)**, 193–196.

PHILIPSON, J. J. (1990). Prospects for enhancing flowering of conifers and broadleaves of potential silvicultural importance in Britain. *Forestry* **63**, 223–240.

PHILIPSON, J. J. (1997). Predicting cone crop potential in conifers by assessment of developing buds and cones. *Forestry* **70** (1), 87–96.

PIUSSI, P. (1967). Characteristics of Norway spruce seed collected at different elevations. Proceedings, *XIV IUFRO Congress. IV Section 23, Munich*, 510–515.

PIUSSI, P. (1986). La rinnovazione della peccata subalpina. *Le Scienze* 58–67.

PYATT, D. G. (1995). *An ecological site classification for forestry in Britain.* Forestry Commission Research Information Note 260. Forestry Commission, Edinburgh.

PYATT, D.G. and SUÁREZ, J.C. (1997). *An ecological site classification for forestry in Great Britain – with special reference to Grampian, Scotland.* Forestry Commission Technical Paper 20. Forestry Commission, Edinburgh.

REINEKE, L. H. (1933). Perfecting a stand density index for even-aged forests. *Journal of Agricultural Research.* **46**, 627–638.

RATCLIFFE, P. R. and MAYLE, B. A. (1992). *Roe deer biology and management.* Forestry Commission Bulletin 105. HMSO, London.

REINEKE, L. H. (1933). Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* **46**, 627–638.

ROLLINSON, T. J. D. (1988). Respacing Sitka spruce. *Forestry* **61**, 1–22.

ROWE, J. S. (1955). *Factors influencing white spruce reproduction in Manitoba and Saskatchewan.* Forestry Branch Canada, Technical Note 3.

RYANS, R. P. F. (1988). *Mechanized precommercial thinning methods: experience to date.* Forest Engineering Institute of Canada. Special Report No. SR–56.

SARVAS, R. (1955). Investigations into the flowering and seed quality of forest trees. *Communications Institute Forestalis Fenniae* **45**, 533–556.

SARVAS, R. (1962). Investigations on flowering and seed crop of *Pinus sylvestris. Communications Institute Forestalis Fenniae* **53**, 1–198.

SARVAS, R. (1968). Investigations into the flowering and seed crop of *Picea abies. Communications Institute Forestalis Fenniae* **67**, 1–79.

SCARRATT, J. B. (1966). *Germination, early growth and survival of Sitka spruce seedlings.* PhD Thesis. University College of North Wales, Bangor.

SHIRLEY, J. L. (1945). Reproduction of upland conifers as affected by root competition and light. *American Midland Naturalist* **53**, 537–612.

SIGGINS, H. W. (1933). Distribution and rate of fall of conifer seeds. *Journal of Agricultural Research* **47** (2), 199–228.

SILEN, R. R. (1967). Earlier forecasting of Douglas fir cone crops using male buds. *Journal of Forestry* **65**, 888–892.

SIMPSON, J. D. and POWELL, G. R. (1981). Some factors influencing cone production on young black spruce in New Brunswick. *Forestry Chronicle* **57**, 267–269.

SMITH, J. H. G., WALTERS, J. and KOZAK, A. (1968). *Influences of fertilisers on cone production and growth of young Douglas fir, western hemlock and western red cedar on the U.B.C. research forest.* University of British Columbia, Faculty of Forestry. Bulletin 5.

SOOS, J. and WALTERS, J. (1963). *Some factors affecting the mortality of western hemlock and western red cedar germinates and seedlings.* Research Paper 56, Faculty of Forestry, University of British Columbia. (12pp.)

STAINES, B. W. (1995). The impact of red deer on the regeneration of native pinewoods. In, *Our pinewood heritage,* 107–114, ed. J.R. Aldhous. FC/SNH/RSPB.

STEVEN, H. M. and CARLISLE, A. (1959). *The native pinewoods of Scotland.* Oliver and Boyd, Edinburgh.

STOAKLEY, J. (1992). *Results of Douglas fir seed wasp research 1965–9.* Internal Forestry Commission note. Unpublished.

STROTHMAN, R. O. and ROY, D. F. (1984). *Regeneration of Douglas fir in the Klamath Mountain Region, California and Oregon.* USDA Forest Service, General Technical Report PSW–81.

SYKES, J. M. and HORRILL, A. D. (1981). *Development of post fire vegetation in the Caledonian Pinewood of Coille Creag Loch, Sheildaig, Wester Ross.* NCC Chief Scientist Report No. 313.

TOMPSETT, P. B. and FLETCHER, A. M. (1979). Promotion of flowering on mature *Picea sitchensis* by gibberellin and environmental treatments. The influence of timing and hormonal concentration. *Physiologia Plantarum* **45**, 112–116.

VAN VREDENBURCH, C. L. H. and LA BASTIDE, J. G. A. (1969). The influence of meteorological factors on the cone crop of Douglas fir in the Netherlands. *Silvae Genetica* **18**, 182–186.

VON OW, F. (1992). *Examination of factors affecting the establishment of natural regeneration of Sitka spruce on clearfelled sites in forest areas of Counties Wicklow and Dublin.* MSc Thesis, University College Dublin.

WAREING, P. F. (1958). Reproductive development in *Pinus sylvestris.* In, *The physiology of forest trees,* 643–654, ed. Thinmann, K. V. Ronald Press, New York.

WATSON, A. (1983). Eighteenth century deer numbers and pine regeneration near Braemar. *Biological Conservation* **25**, 287–305.

WILLIS, C. P. (1914). Control of rodents in field seeding. *Proceedings, Society of American Foresters* **9**, 365–371.

YLI-VAKKURI, P. (1962). Experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands. *Acta Forestalia Fennica* **74**, 1–52.

YODA, K., KIRA, T., OGAWA, H. and HOZUMI, K. (1963). Self-thinning in over-crowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* **14**, 107–129.

YOUNGBLOOD, A. and MAX, T.A. 1992. *Dispersal of white spruce seed on Willow Island in Interior Alaska.* USDA Forest Service, Research Paper PNW–RP–443.

Forestry Commission Bulletin 120 The Potential for the Natural Regeneration of Conifers in Britain

£14