Forestry Commission

Research Note

Understanding the provision of conifer seed for woodland species

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Conifer seed provides an important food resource for many woodland mammals, birds and insects, including some of Britain's rarest species. This Research Note brings together information from a number of sources on cone and seed production by the main conifers planted in Britain. This information can help managers assess the seed resources of their woodlands and manage the woods for the objective of seed production, whether for food or to encourage natural regeneration. Cone and seed crops fluctuate annually and the amount of seed available in good compared with bad seed years, as well as the frequency of good years, depends on a range of factors which include tree species, age of the crop and climatic conditions. Some species such as Scots pine produce moderate but consistent crops of seed every year, whereas others are much more variable. For example, in a good year Japanese larch can provide the greatest amount of seed and energy per area of woodland of any conifer species grown in Britain, whereas in a poor year production is almost negligible. The time of year when seed is released differs between conifer species. Woodland management can influence the continuity of seed supply as well as the quantities of cones and seed produced. Managing to provide a continuous and abundant seed resource involves consideration of woodland age structure and species composition as well as choice of appropriate interventions.

Introduction

This Research Note presents information on coning and seed supply for the main conifer species planted in Britain. It also considers the animals that eat these conifer seeds. Information from published sources and from analyses of unpublished data has been collated and used to address the following six key questions of interest to woodland managers and others involved in nature conservation:

- Which species are dependent on conifer seed as a food supply?
- Do species have seed preferences, and what factors affect their choice?
- How can continuity of seed supply be optimised?
- How can seed and energy production be maximised?
- Does a good cone crop always indicate a good seed crop?
- What methods can be used to assess cone (and seed) crops?

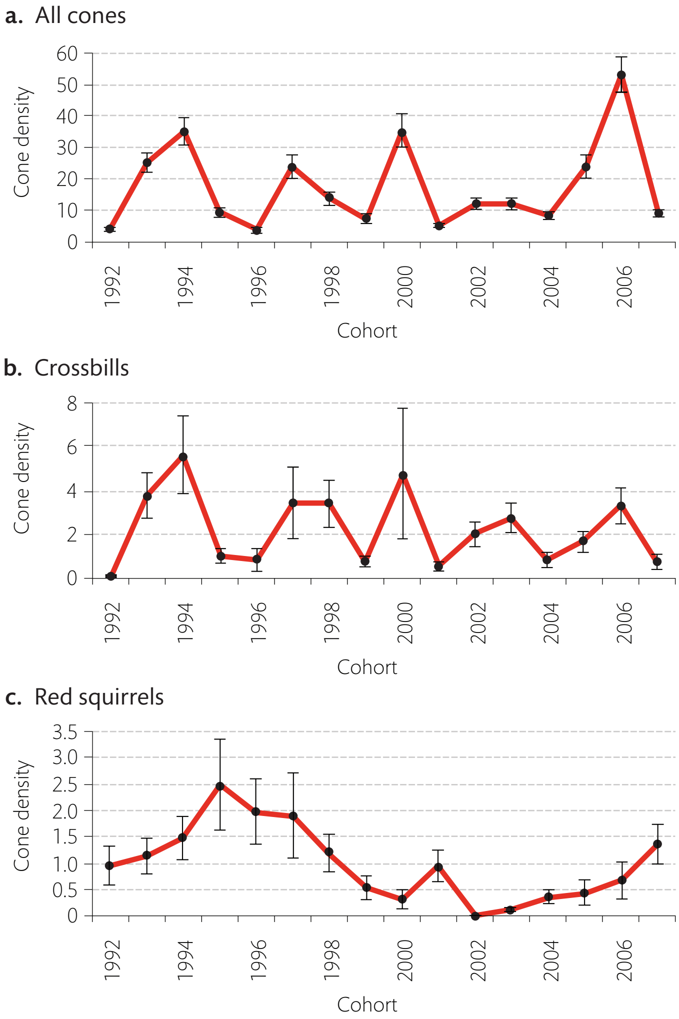
Which species are dependent on conifer seed as a food supply?

Conifer seeds are eaten by a large number of mammals, birds and insects. They may be eaten while still held within the cones (e.g. by crossbills, red squirrels, siskins, tits and great spotted woodpeckers) or after they have been shed (e.g. by voles, mice, chaffinches and beetles).

Crossbills and red squirrels are particularly dependent on conifer seed as a food source. Summers (2011) studied the year-by-year pattern of foraging on Scots pine (*Pinus sylvestris*) cones by crossbills and red squirrels over 16 years in three stands of widely spaced, ancient pines in Abernethy Forest, in Highland Scotland. Box 1 gives details of the methods used. Figure 1a shows the mean densities (number per m^2 averaged across trees and sites) of all cones on the forest floor (fallen naturally plus dropped by crossbills and red squirrels) for each cone cohort (year) as well as densities of cones dropped by crossbills and red squirrels (Figure 1b and c). Vertical bars indicate standard errors. Cones were produced each year but the number of cones varied from year to year. There was a strong correlation between cone removal by crossbills and cone availability. For red squirrels, removal of cones did not vary according to cone availability,as they took a greater percentage of cones in years when there were fewer cones available. The numbers of crossbills which arrive in an area are determined by the annual fluctuations in the size of the seed crop. By contrast, the red squirrel, although it can move 0.5–2 km on a daily basis to exploit cone crops, is unable to track larger scale fluctuations and its numbers are held in check by periods of low seed production unless alternative food sources are available.

Conifer seed is a key food resource in the woodland ecosystem and fluctuations in production have been shown to drive population trends in both the species that consume the seed directly (e.g. finches) as well as their predators (e.g. sparrowhawks (*Accipter nisus*) and merlins (*Falco columbarius*)) (Petty *et al.*, 1995).

Figure 1 Densities of cones fallen naturally (a), dropped by crossbills (b), and dropped by red squirrels (c).



Box 1 Coning, red squirrel and crossbill study methods

Plots under the canopy of Scots pine trees were cleared of all old cones prior to starting the study and any new cones falling were collected at the end of each month. Collected cones were allotted to the year in which they would have shed their seed (their cohort year), running from July prior to seed shed to June the year after shedding. Each cone was examined for distinctive damage by crossbills or red squirrels. An index of total cone production of each cohort by each tree was calculated (number of cones per square metre of forest floor), along with the proportion of these taken by crossbills and red squirrels.

Do species have seed preferences, and what factors affect their choice?

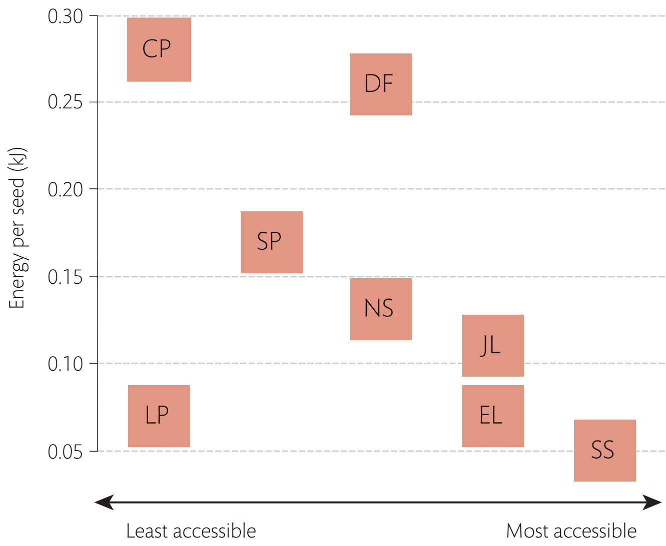
Crossbills are so highly adapted to extracting seeds from cones that they have bill sizes developed for particular conifers. Thus, common crossbills (*Loxia curvirostra*) are adapted to Norway spruce (*Picea abies*) and parrot crossbills (*Loxia pytyopsittacus*) to Scots pine. Most other seed-eating species select the tree species according to availability of the seed, the abundance of the seed crop and the energy value of the individual seeds.

Conifer seeds are protected by a spiral and overlapping array of cone scales, with seeds located behind each scale. The strength (thickness) of the scales affects the accessibility to seed within the cone prior to opening. Sitka spruce (*Picea sitchensis*) has thin, papery scales which afford only poor protection to the seeds (Figure 2) but pines have thick, woody scales (Figure 3) which provide better protection. However, seeds of conifer species with thicker scales are usually larger with more of the energy-rich contents (endosperm) and therefore of higher energy value. Also, the seed coat in some conifer species can be hard and this can affect the time taken for species to reach the endosperm within the seed and process cones. Presence of resin in the cones can also affect accessibility. There is a trade-off between effort and reward for species feeding on different conifers, and Figure 4, based on accessibility data from Staines *et al*. (1987) and Smith (1999) and seed energy values from Gurnell *et al*. (2009) and Lloyd (2003), attempts to show these relationships for the main British conifer species.

Figure 2 Sitka spruce cones and cross-section showing thin scales.

Figure 3 Scots pine cone and cross-section showing thicker scales.

Figure 4 Energy value of individual seeds of different conifer species plotted against the accessibility of seed within the cone to wildlife.



Key to species: Corsican pine (CP), Douglas fir (DF), European larch (EL), Japanese larch (JP), lodgepole pine (LP), Norway spruce (NS), Scots pine (SP) and Sitka spruce (SS).

There is an obvious advantage to feeding on seed when the cones are open just prior to seed shedding. Conifer species shed seed at different times of the year and many seed-eating species (e.g. crossbills, siskins, squirrels) switch between tree species to take advantage of this asynchrony. They will feed on seed in thin-scaled open or closed cones during most of the year but switch to those in thick-scaled cones when they are easily accessible just prior to seed shedding.

Length of cone also affects processing time. A feeding study using Corsican pine (*Pinus nigra* ssp. *laricio*), Scots pine, lodgepole pine (*Pinus contorta*) and Japanese larch (*Larix kaempferi*) cones showed that for cones from all these species it took grey squirrels around 100 seconds on average to process a cone 2.5–3.5 cm long but around 300 seconds to process cones twice as long (Smith, 1999). In Scots pine, longer cones have thicker scales and more effort is required to prise scales apart.

How can continuity of seed supply be optimised?

The main features of woodland that determine the continuity of seed supply are the species of conifer present and the age structure of the stands.

The age of onset of coning and maintaining seed supply over long time periods

Although some conifer trees of less than 10 years old are observed to bear a few cones, large cone crops are not produced until the trees have matured. Coning is linked to the provision of carbohydrate resources generated by photosynthesis and thus to having an adequately large canopy. The age at which the first good cone crop is produced varies with species, with Japanese larch being one of the earliest to mature and Douglas fir (*Pseudotsuga menziesii*) one of the latest (Table 1). Some coastal provenances of lodgepole pine have been reported to produce their first good cone crop as early as 5 to 6 years old (Petty, unpublished).

Table 1 Age of first large cone crop for the common conifers in Britain (Nixon and Worrell, 1999).

Conifer species	Age (years)
Lodgepole pine	15
Japanese larch	15
Hybrid larch	15
Scots pine	25
European larch	25
Sitka spruce	25
Norway spruce	30
Douglas fir	30

Growth rates of conifer stands, for example as indicated by increments in top height, slow as trees age. In line with this, there is assumed to be an age at which cone crop production peaks (this is around 60 years for most species but around 100 years for Scots pine). In managed conifer plantations, however, crops are likely to be felled before cone production declines.

Maintaining seed supply over long time periods (decades) requires a consideration of the age structure of woodlands and planning the crop succession, ensuring that areas being felled are replaced by equivalent areas which are entering the period of maximum cone production.

Continuity of seed supply from year to year and periodicity of annual cone crops

Typically, conifers show large annual variations in cone production (cone density – see Box 2). Production of large seed crops is dependent upon favourable climatic conditions. The production of a large cone/seed crop also drains the carbohydrate reserves so individual trees do not tend to produce large crops in successive years. Of the common British conifers studied by Broome, Hendry and Peace (2007), Norway spruce exhibits the greatest annual variation (Figure 5a), with many years of little or no cone production followed by a year of peak production, known as a 'mast' year. Recent research (Broome and Deioanni, unpublished) shows that cone production in larch also varies annually with years with low cone production, for example in 2003 and 2005 (Figure 5b). Pines tend to be more conservative and produce some cones each year, though the fluctuations can still vary by a factor of 10.

Sitka spruce, Norway spruce and to some extent the larches show synchrony of coning over large areas, as seen from stands of the species sampled across the whole of Britain (Figures 5a and b). High mast years occurred synchronously in Sitka spruce and Norway spruce, with both species showing high cone production in 1996 and low production in 1999. Such fluctuations in production are believed to reflect an evolved strategy in which seed-eaters are swamped with food during 'mast' years, so that some seed is not consumed and therefore has the chance to germinate and produce the next generation of trees. In addition, this strategy controls the size of seed-eating populations because large populations cannot be supported during poor years.

Box 2 Spatial and annual coning variation study methods

In the Broome, Hendry and Peace (2007) study, annual cone production was assessed in up to 80 plots per species of Sitka spruce, Norway spruce and Scots pine, distributed across their planting range in Britain. Cone production was recorded as an index and converted to a range of cone densities (cones per square metre of tree canopy). Cone densities were also directly measured annually on 19 larch plots representative of the range of climate zones where larch is grown in Britain (Broome and Deioanni, unpublished). Mean cone densities for each plot and year from these studies have been interpolated to provide maps of annual cone density (Figure 5).

The number of years separating good seed/cone crops varies with conifer species (Table 2). For example, pines produce a good seed crop on average every 2 to 3 years whereas there tends to be a minimum of 5 years between good cone crops in Norway spruce.

To ensure year-to-year continuity in seed supply, it is important to consider the species of conifers planted. Managers should aim to plant a mixture of species, including some which crop regularly (e.g. Scots pine), and avoid woodlands composed of single species which have infrequent mast years (e.g. Norway spruce) or mixtures of species that mast synchronously (e.g. Norway and Sitka spruce).

Figure 5 Annual and spatial variation in average density of cones in the canopy (cones per m^2) in four conifer species in Britain. (a) from Broome, Hendry and Peace, 2007) and (b) from Broome and Deioanni, unpublished.

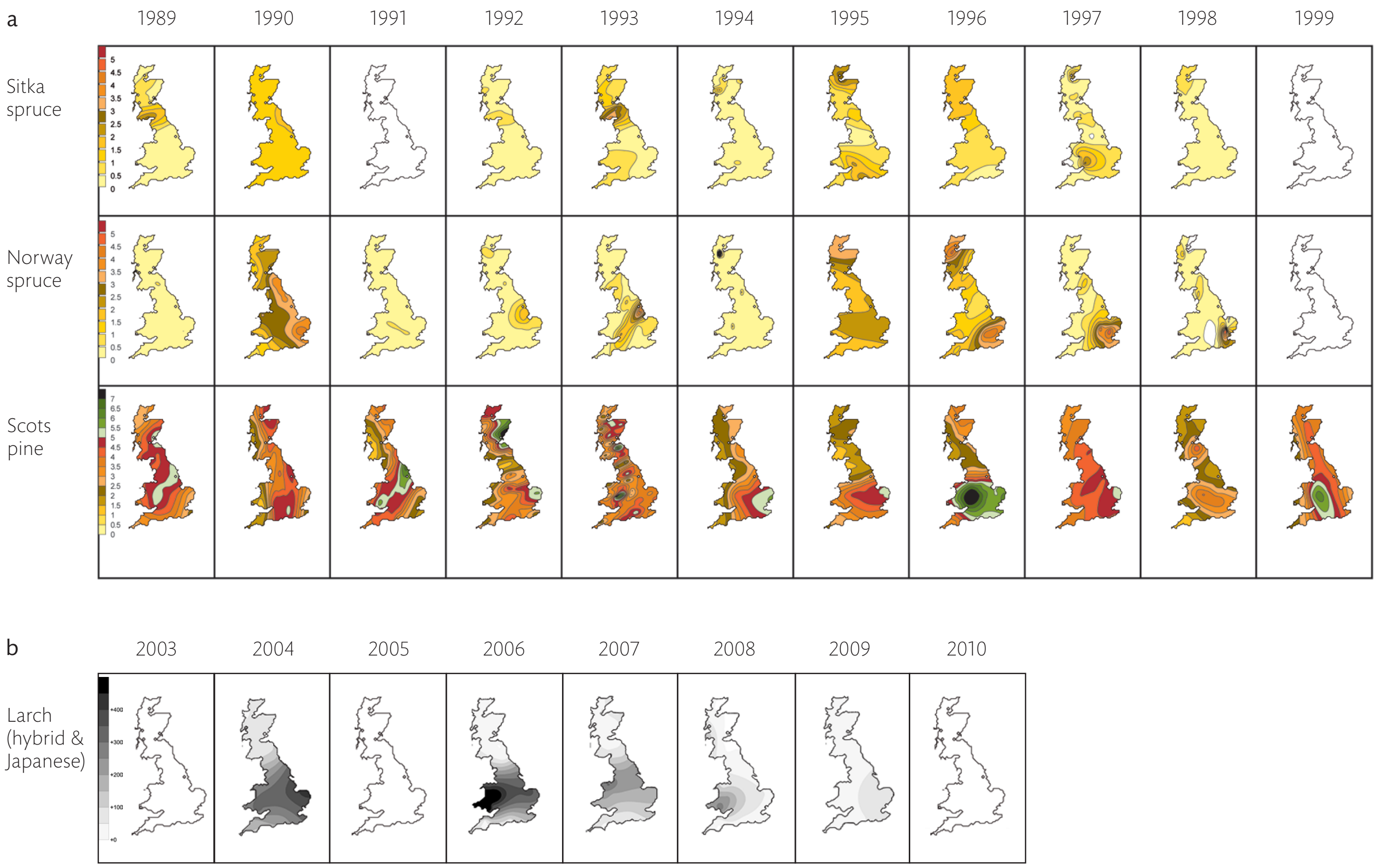


Table 2 Number of years separating large seed/cone crops reported for Britain based on data from Aldhous (1972), Staines, Petty and Ratcliffe (1987), Gordon (1992) and Nixon and Worrell (1999). Numbers in parentheses are from one information source only.

Conifer species	Years
Scots pine	2–3
Lodgepole pine	2–3 (5)
European larch	3–5 (4)
Japanese larch	3–4 (5)
Hybrid larch	3–4 (5)
Norway spruce	4–5 (10)
Sitka spruce	3–5 (6)
Douglas fir	4–6

Maximising seed availability within the same year, and timing of seed shed

Most species that feed on conifer seed do so when the seed has been shed from the cone. The timing of seed shedding varies between conifers (Table 3 and Figure 6). As shown in Figure 6, European larch (Mason, Edwards and Hale, 2011) and Scots pine (Edwards, 2005) shed seed in spring, for the latter when the warming weather causes the scales to spring back. By contrast, Sitka spruce (Forest Research experiments) starts to shed seed in the autumn, and continues through the winter (when there is a lull), with another peak in spring.

Woodlands composed of a mixture of spruces, pines and larches, particularly where European larch and Scots pine are included, are likely to provide a continuous supply of available seed throughout the year.

How can seed and energy production be maximised?

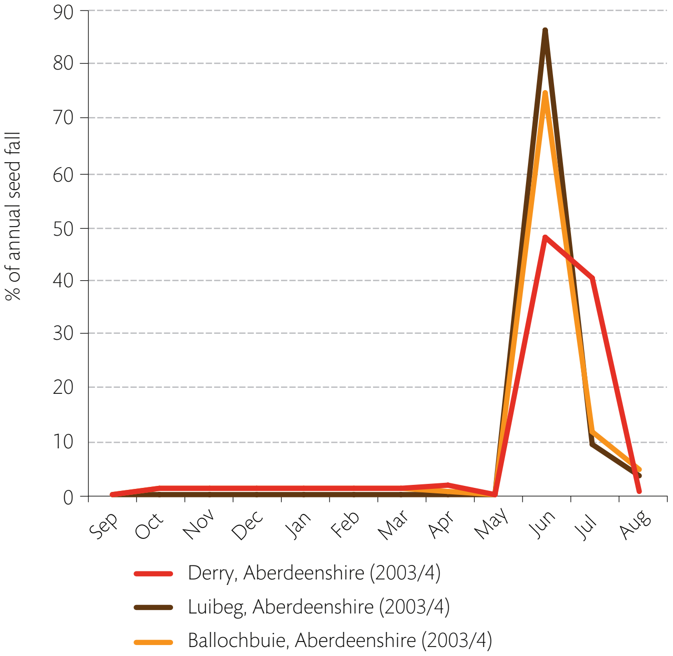
As well as choosing suitable species to maximise seed quantity and energy production woodland managers can also use interventions to encourage cone and seed production (see Table 4). Thinning is likely to be the most readily applied method (see below). Other interventions have been used in seed orchards to promote flowering and coning, including application of fertilisers or hormones, girdling, bending and root pruning. Their applicability in conventional forestry settings is limited, but root girdling/pruning may be effected deliberately during site

Table 3 Months of the year when seed is shed from cones by different conifer species (Nixon and Worrell, 1999).

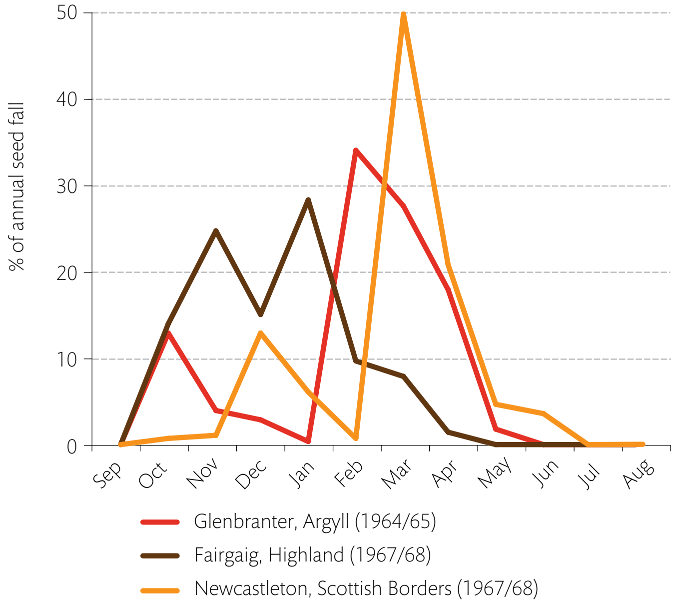
Conifer species	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Scots pine								×	×	×	×	
Lodgepole pine			×	×	×	×	×	×				
European larch						×	×	×	×			
Japanese larch		×	×	×	×	×	×	×				
Hybrid larch		×	×	×	×	×	×	×				
Norway spruce			×	×	×	×	×	×				
Sitka spruce			×	×	×	×	×	×				
Douglas fir		×	×	×	×	×	×	×				
Corsican pine							×	×	×	×		

Figure 6 a–c Percentage of seed fall through the year measured by seed trapping (see Box 3) for three different conifer species in Britain.

a. Scots pine



c. Sitka spruce



b. European larch

Box 3 Seed trapping study methods

The data presented in Figure 6 have been collected from seed trapping. Various collecting devices can be used, from large suspended funnels feeding into animal and bird-proof collection bags to circular plastic pots which are sunk into the ground to the level of the adjacent vegetation. Such pots are usually lined with horticultural fleece and are covered by a wire mesh frame to protect the trap from large debris and reduce the risk of loss of seed to birds and small mammals. Traps are emptied each month and seeds are sorted by species (where possible) and counted. It is important to know the surface area of the trap and the area which the traps are sampling (e.g. five traps of 0.1 m^2 used to sample a 1 ha plot) and from these the seed fall per m^2 or per ha can be calculated.

preparation operations. Success of these interventions in enhancing seed production is variable, often being dependent on which conifer species is treated and/or whether the intervention is carried out in a good seed year (Table 4).

Thinning stands

The production of well-developed seed (i.e. seed with an endosperm) can be increased by encouraging the growth of tree crowns. Trees with long, well-developed crowns flower more prolifically than trees with short, poorly developed crowns. Crown depth is an important determinant of the amount of pollen produced as in most conifer species the male (pollen-producing) cones are located in the lower third of the crown. Production of large quantities of pollen increases the chances of good seed set. Trees respond to thinning by slowing crown base recession. Trees also respond to thinning by increasing crown width, resulting in larger crowns and the potential to produce more cones. Exposure of the tree crown to maximum sunlight by removing adjacent trees which cast shade on them also results in speedier ripening and larger seeds as well as higher cone production, cone length and number of seeds per cone. Several studies have shown the beneficial effects of thinning and of sunlight exposure due to position of trees on the edge of a stand (Table 5).

Stand management in order to optimise seed production therefore aims to establish large, isolated crowns and this is normally achieved through one or two heavy thinnings, focused to release crowns particularly on their south side. If seed production is the main objective, stands should be managed in order to achieve a low stocking density in young to middle age

Table 4 Management interventions to enhance seed supply, mechanism of action and evidence of success by species (Davies, unpublished).

Treatment	Summary of knowledge
Ground preparation	Root damage to remaining seed trees caused by site cultivation might enhance seed supply. Root girdling and root pruning are damaging treatments that affect the movement of nutrients within the tree and which have been shown to have a positive effect on flowering in seed orchards for some species (e.g. Douglas fir, Ross et al., 1985) but not others (e.g. larch, Heitmüller and Melchior, 1960).
Application of fertilisers	Direct application of fertilisers or the flushes of nutrients caused by ground disturbance influence seed production, but the effects are considered very variable. Fertilising with nitrogen reduced flowering in Japanese larch but fertilising with phosphate, potassium or a combination of the two increased flowering (Matthews, 1963). In Douglas fir, both the numbers of trees coning and the numbers of cones per tree may increase with nitrogen fertiliser applications in good seed years, but no benefits have been seen in poor seed years (Puritch, 1977).
Stem girdling	Girdling treatments typically involve making two slightly overlapping semi-circular cuts through the bark of a tree stem (Puritch, 1977) that sever the conductive tissues below the bark to prevent the upward movement of water from the roots and the downward movement of carbohydrate from the crown. Positive effects of girdling on coning in Sitka spruce (Philipson,1985), European and Japanese larches (Melchior, 1960, 1961) and Douglas fir (Puritch, 1977) have been noted but assessment for Douglas fir showed that the number of viable seeds per cone was not enhanced (Woods,1989). For all species, girdling did not have a significant effect in a poor seed year.

References for Table 4 from Davies (unpublished) are available at www.forestry.gov.uk/publications

Table 5 Effects of thinning on cone and seed production for various conifer species (Davies, unpublished).

Conifer species	Treatment/situation of conifer stand	Effects/response	References
Douglas fir	Seed fall measured in differently thinned and unthinned stands	Higher seed production per tree in thinned stands	Burton et al., 2000
Douglas fir	Seed fall measured in differently thinned and unthinned stands	Some benefit from thinning, though not in poor seed years	Reukema, 1961
Douglas fir	Regular scoring of cone crops in seed trees on a clearfell site compared to dominants in a closed stand (375 stems per hectare)	Larger and more frequent cone crops from seed trees	Garman, 1955
European larch	Seed fall measured in differently thinned and unthinned stands	Higher seed production per tree in thinned stands	Mason *et al.*, 2011
Sitka spruce	Density of cones along transects from edge to centre of stand	Higher cone production, cone length and number of seeds per cone for trees in first and second stand edge rows	Lloyd, 2003

References for Table 5 from Davies (unpublished) are available at www.forestry.gov.uk/publications

– the guide figures are 200–300 stems per hectare at tree height 12 m and 100–150 stems per hectare at tree height 22 m (Faulkner, 1962). Management objectives for the stand need to be clear as stands managed to maximise timber production maintain stem densities at least double the 100–150 stems per hectare target value at the age of maximum cone production, as shown in Table 6.

Cones, seeds and energy production, and choice of conifer species

Table 6 uses average or generic figures of cone and seed quantity based on assuming a standard relationship between numbers of seeds produced and size of cone (Box 4). Bearing in mind the variability in number of viable seeds per cone, any extrapolation to numbers of seeds per tree or per area has to be an approximation. However, such figures when multiplied by energy values for seeds are useful in giving a feel for the food resource within woodland and how it can vary between species and between good and poor seed years.

Conifer species differ in the amount of seed produced for a given area of woodland as well as in the amount of energy contained within each seed. Guide figures on seeds produced by stands in 'good' seed years show that the larches are the most prolific (up to 24 million seeds per hectare) followed by Sitka spruce (6 million seeds per hectare) and with the least seeds being produced by Norway spruce, lodgepole pine and Scots pine (1–2 million seeds per hectare). Although energy per individual seed in Scots pine is almost twice that of the larches, the seed crop produced by larches provides more energy per hectare (1–2 GJ ha^{-1}) in a good seed year. Energy from seed production (at 0.1–0.5 GJ ha^{-1}) is much lower in the pines as well as Sitka and Norway spruce. However, unlike the larches and spruces, the pines do provide some seed/energy resources even in poor seed years; for example, a hectare of Scots pine is estimated to produce 20 000–30 000 seeds (equivalent to 0.003–0.005 GJ) per hectare in poor seed years.

Box 4 Calculating seed energy production values per unit area of conifer forest

Maximum cone index score (3) allocated in annual assessments by Forest Research of coning in the major conifers planted in Britain is taken as indicative of the level of coning occurring in a 'good' seed year. The cone density per area of tree canopy for cone index score 3 (Broome and Poulsom, 2006) has been multiplied by 0.66 times the minimum and maximum modelled canopy area (m^2) of a single tree within a plantation setting of the conifer species considered (Broome and Deioanni, unpublished). The resulting range in cone numbers has been multiplied by a standard value of number of seeds per cone (Nixon and Worrell,1999, p. 6) to give the range of numbers of seeds per tree. For the calculation of seeds per hectare, a number of trees per hectare had to be assumed. This figure was drawn from the Forestry Commission yield models for each conifer species, selecting a middle of the range yield class, a normal spacing (2 m) consistent with the canopy area models, an 'intermediate' thinning regime and a stand age representative of age of maximum production. This was close to the recommended felling age when managing the stand for timber production. Energy production in gigajoules per hectare (1 GJ = 106 kJ) was calculated by multiplying species' energy value per seed by number of seeds. Where a range of energy per seed values had been sourced, the upper and lower ones were used in the calculation of maximum and minimum energy per area, respectively.

Table 6 Guide figures for numbers of cones, numbers of seeds and energy produced per year by different conifer species in 'good' seed years in plantations (see Box 4 for details of calculations).

Conifer species	Cones per tree[1]	Seeds per tree[2]	Age of trees (years)	Trees per hectare[3]	Seeds (in millions) per hectare	Energy (in gigajoules per hectare)
Scots pine (YC[3] 8)	150–250	3000–4000	80	330	0.9–1.3	0.21–0.2
Lodgepole pine (YC 10)	400–600	4000–7000	35	880	1.4–2.2	0.1–0.2
Japanese larch (YC 10)	3000–5000	26000–48000	50	290	8.7–16.0	0.9–1.6
Hybrid larch[4] (YC 8)	4000–7000	41000–73000	40	520	13.7–24.2	1.4–2.4
Norway spruce (YC 14)	250–400	4000–6000	55	350	1.2–2.1	0.1–0.3
Sitka spruce (YC 16)	180–200	18000–19000	40	430	6.1–6.4	0.2–0.4

[1] Based on values of cones per square metre of canopy recorded in cone index score validation surveys (Broome and Poulsom, 2006; Broome and Deioanni, unpublished).
[2] Calculated using numbers of seeds per cone (Nixon and Worrell, 1999, p. 6).
[3] Assumes a stocking rate following a standard thinning regime for the stand of indicated Yield Class (YC) which is the annual increment in timber volume (cubic metres) per hectare, at the age of maximum cone production (Matthews, 2008).
[4] For hybrid larch energy value per seed is assumed to be the same as European and Japanese larch at 0.1 kJ per seed.

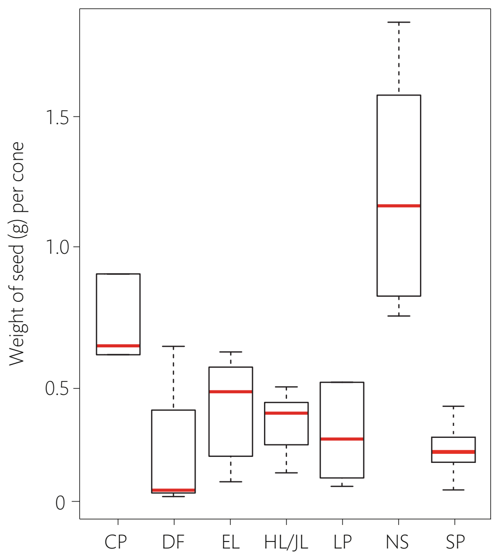
Does a good cone crop always indicate a good seed crop?

Cone and hence seed production is dependent on favourable summer weather as this stimulates flower production. Pollination occurs in the following year when cones start to grow and typically good pollination is achieved when conditions are warm and dry. If seeds are not fertilised, the embryo and endosperm does not develop and the husk (seed coat) remains empty. Therefore, although there is a relationship between cone production and seed production (as the latter is dependent on the former), a good crop of viable seeds does not always result from a large cone crop (Figure 7 and Box 5).

The relationship between number of cones and the quantity of filled seed is very variable and strongly influenced by climatic conditions. Seed yield in Britain will therefore vary from year to year and region to region. Effects of spatial position (longitude and latitude) and climate (accumulated temperature, continentality and moisture deficit) on the seed yield (weight of seed obtained from a set volume of cones) of seven tree species collected from different forests throughout Britain over 40 years were estimated by linear mixed model analysis. Tree species yields were analysed separately using the method of residual maximum likelihood and involved fitting spatial and climatic effects as fixed effects and collection years as random effects. Some weak regional trends were indicated. Relationships between yield and easting and northings, neared significance (p<0.1) for Sitka spruce, Japanese larch, European larch and Scots pine. Sitka spruce showed an increase in yield the further south in Britain cones were collected, Japanese larch the further west and European larch the further southwest. Across its entire range of planting locations in Britain, Scots pine showed an increase in seed yield the further south and east collections were made, but within its Scottish range trend in yield increased with the further north and east sites were. This latter finding is consistent with a study of seed yield from Scottish native pinewoods, with stands in northeast Scotland generally yielding more seed than those in southwest Scotland (Summers and Waddell, 2004).

Figure 7a–b Variability in the quantity of filled or sound seed found within a cone by conifer species. Key to species: Corsican pine (CP), Douglas fir (DF), European larch (EL), hybrid larch (HL), Japanese larch (JL), lodgepole pine (LP), Norway spruce (NS), Scots pine (SP), Sitka spruce (SS).

a



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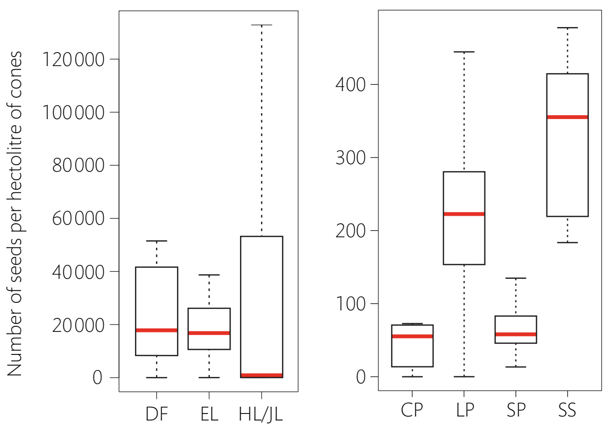

Box 5 Seed quantity versus cone quantity study methods

Two measures of the variability in the quantity of seed per cone can be derived from historical seed extractory and seed testing datasets for Britain. Neither dataset gives a count of seeds per cone but both provide a relative measure of seed quantity in relation to cone quantity. The dataset shown in Figure 7(a) is based on the weight of seed extracted from a known number of cones and that in Figure 7(b) on the number of seeds from a set volume (a hectolitre = 100 litres) of cones. Although cones of the same species vary in length, the number of seeds per unit length is assumed to be consistent as a longer cone will have more scales and usually pairs of seeds are borne at the base of each scale. The same volume of cones of the same species should therefore have the potential to contain an equivalent quantity of seed.

The box and whisker plots in Figure 7 indicate the variability in the relationship between seed quantity per unit measure of cones. Half of the values closest to the median (or central value as represented by the heavier lines) are contained within the boxes, whereas the whiskers are the 25% highest and 25% lowest range of values. Short boxes indicate that the relationship of seed quantity with cone is consistent across many samples (e.g. Scots pine is more consistent than Sitka spruce), and long whiskers indicate that in a few cases the quantity of seed per cone can be very different from the median (e.g. lodgepole pine).

What methods can be used to assess cone (and seed) crops?

Assessment of cone production can provide a proxy for the amount of seed produced. A variety of methods for estimating coning are available and these are applicable in different situations. Cone abundance is usually evaluated by some form of visual assessment and scoring of numbers of cones on the trees (descriptive and cone index methods) or by the number of fallen cones (cone-line method).

The abundance of the cone crop is usually judged by comparing the results of the visual survey or fallen cone count with survey records for the area and conifer species from previous years. However, as a guide, standard descriptions and records from a number of cone studies are given (Table 7) for reference.

In comparison to cone assessment, direct assessment of seed abundance is labour intensive and/or requires specialist equipment. Seed assessments (e.g. seed trapping, see Box 3) are generally only used for research projects.

Visual assessment methods

Visual assessment of cone production is performed in the summer or early autumn when the cones are fully formed but before they are detached by storms or animals. The upper two-thirds of the crown is observed using binoculars from a single viewpoint in a sub-sample of representative trees. This is standard methodology and straight forward to do in practice (Innes, 1990). The upper two thirds are chosen for assessment as the lower third tends to bear less seed bearing cones and more of the pollen bearing cones (Faulkner, 1962). The sample of trees is considered to represent cone production of that species within the stand or local area in the year of observation. For larches and lodgepole pines, which retain some of their cones for several years after the seeds are shed, it is best to carry out the assessment when the cones are still green to ensure that only the current year cones are counted (April to May for larches, August to September for pines). Good light and still conditions are needed to make these assessments, and to reduce bias it is best if the same person makes the assessment in the same stands at the same time each year.

Table 7a–c Typical quantities of cones indicated by different classes of indices used in three different methods of cone abundance assessment.

a. Descriptive (Nixon and Worrell, 1999)

Absent	Light	Moderate	Heavy
No cones on any trees	A few cones (<50) on about one tree in every 50	A significant number of cones (50–100) visible on about 25–50% of the trees	Very many cones (>100) on some (5–10%) trees, a significant number of cones on many others and at least a few cones on nearly every other tree

b. Coning index score (Broome and Poulsom, 2006; Broome and Deioanni, unpublished)

	0	1	2	3
Cone density per square metre of canopy				
Scots pine	0.3	1.4	8.0	12.7
Lodgepole pine	0.0	3.4	11.3	30.3
Japanese larch	0.0	7.6	26.3	93.9
Hybrid larch	0.0	7.6	26.3	93.9
Norway spruce	0.1	0.3	4.2	14.5
Sitka spruce	0.0	0.8	2.4	14.5

c. Fallen cone count/cone line (Gurnell *et al.*, 2009; Bryce, Cartmel and Quine, 2005)

	Low production	Medium production	High production
Cumulative number of cones per square metre below canopy over 6 months of maximum cone fall			
Scots pine	1.0–5.0	7.0–9.5	21.0–33.0
Japanese larch	0.0	5.6	44.0
Norway spruce	0.0–0.6	2.2	8.0

In the descriptive method the stand can be assigned to one of four cone abundance classes based on cone numbers and the proportion of trees bearing these (Table 7a).

In the cone index method each tree is given a score within a defined scale (e.g. 0–3, 0–5 or 0–10) that describes the abundance of cones seen from none to abundant. An average score can be obtained for the stand by weighting the scores by the number of trees assigned to each score. A measure of cone density can be linked to the index (Table 7b gives examples of cone densities for a four-class cone index method).

Fallen cone count/cone-line method

The fallen cone count method is based on the assumption that most of the fully developed cones produced in one year will fall from the tree over the autumn, spring and summer after shedding seed and before the maturation of the cones of the following year. During this period, the total number of cones and cone cores are periodically (e.g. weekly or monthly) counted in a set assessment area which has been previously cleared of cones. The assessment areas are usually 1 × 50 m transects spread throughout the woodland (hence the name cone-line method). An average density of cones per square metre can be calculated and related to the number of trees under which the cone count was made. These figures can then be assigned to production classes (Table 7c). This is the method used in feeding sign surveys for squirrels as it can also be used to provide information on squirrel numbers. The fallen cone count method is best employed for the assessment of spruces, which generally shed all their cones annually, but it does not work well for larches (which retain their cones for 3–5 years) or interior provenances of lodgepole pines (6–8 years or more cone retention).

Conclusions and recommendations

Production of conifer seed makes an important contribution to the dynamics of ecosystems, and as well as providing the prospect of natural regeneration the seed provides a food resource for a number of key woodland species. Seed production can vary considerably as a result of tree species, tree age, woodland management and climate. A range of techniques, from forest design to stand management, are available to managers wishing to encourage seed production. Discussion of the questions listed in the introduction to the Research Note and information from relevant studies, both published and unpublished, will, we hope, provide useful guidance to people involved in woodland management to help them make appropriate decisions.

The main conclusions reached on each of the discussion points are listed below:

- Crossbills and red squirrels are examples of species particularly dependent on conifer seed as a food resource. Studies indicate that fluctuations in seed production do affect population trends in these species, though in different ways. Other studies indicate that the populations of both seed-eating species and their predators can be affected by fluctuations in conifer seed production.

- For most species that feed on conifer seed preferences are generally a trade-off between ease of access to the seed and its energy value. However, some species (e.g. the common and parrot crossbills) are adapted to feeding on particular conifers.

- Areas with a variety of conifer species and trees of different ages are most likely to provide a continuity of seed supply. Ages of onset of coning, whether a species cones regularly or has 'mast' years, and the time of year when seeds are shed from the cones are all factors to bear in mind when making decisions about what species to plant, fell or encourage.

- The number of seeds produced by conifers would appear to be maximised by thinning to encourage the growth of crowns as well as by other management interventions such as root pruning or partial stem girdling. However, to maximise the amount of energy available to seed-eating species it is important to consider energy production per seed as well as the number of seeds per tree or area.

- The numbers of cones produced is often but not always closely reflected in the number of filled seeds produced but some species seem to have more variation than others. Also the relationship can be affected by climatic conditions and weak regional trends in seed yield per cone have been noted in some species.

- As direct assessment of seed production is difficult cone production is often used as a proxy. Three main methods are used. Descriptive and cone index methods use visual assessment of the cones while they are still on the tree, while the cone-line method is a way of counting and assessing fallen cones.

This Research Note has synthesised knowledge on the conifer species typically grown in Britain and their cone and seed production under climatic conditions experienced in the last six or seven decades. With the challenges to forestry posed by climate change and increased threat of pests and diseases, a greater range of conifer species are being considered for planting. Further research is needed to understand how seed production in Britain's current range of conifer species may change under future climate projections, and to provide information on the seed production potential of the emerging conifer species which may be more widely planted in the future.

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