

# Testing prescribed fire as a tool to promote Scots pine *Pinus sylvestris* regeneration

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**Abstract** Techniques for encouraging natural tree regeneration are of increasing interest to managers of Scots pine *Pinus sylvestris* forests. We tested prescribed fire at a management scale, with deer present or excluded, as a means of increasing rates of Scots pine forest expansion on heathland. At a semi-natural pinewood in Scotland, ten experimental blocks were established, within range of pine seed-fall. Each block comprised four, 100 m<sup>2</sup> plots. Two plots at each site were burnt and two fenced, allowing the effects of burning on pine regeneration to be measured at two levels of deer abundance. We monitored pine seedlings, seed-fall, deer dung and vegetation for 5 years following treatment. Differences in seedling detection rates between treatments were quantified using dummy seedlings, and analyses corrected accordingly. Mean new pine seedling establishment was 9.8 times higher on burnt ground than unburnt ground (confidence intervals 3.2–30). Differences were even more pronounced in a year of high seed-fall, and following fires with low rates of spread. Establishment rates varied strongly between experimental blocks. Exclusion of deer increased establishment rates, but only in the first 2 years after fire. There was evidence that both seedling survival, and cumulative recruitment of older (over 12 months) seedlings, were improved by prescribed

burning. Our results support the use of prescribed fire as a tool to promote increased Scots pine seedling establishment. This technique is likely to give strong fine-scale variation in seedling densities, and so would most suit areas where a variable spatial pattern of regeneration is sought, for landscape or naturalness reasons.

**Keywords** Burning · Deer Cervidae · Heather *Calluna vulgaris* · Seedling establishment

## Introduction

Of the native Scots pine, *Pinus sylvestris* forests of boreal Eurasia, those of Scotland are among the most severely reduced by human impacts (Angelstam et al. 1995), with perhaps just 1% of the post-glacial maximum extent remaining (Tipping 1994). The surviving fragments are of considerable conservation importance, being protected under both UK and European legislation (Mason et al. 2004). Many are predominantly made up of old trees, with few young saplings (Summers et al. 1999; Edwards and Mason 2006). UK government policy aims to more than double the area of native pinewood, with the emphasis on natural regeneration (Anon 1995). In addition to 19,759 ha of ancient native Scots pine forest, Scotland has ca. 101,000 ha of planted Scots pine (Mason et al. 2004), much of it both old and of conservation interest (e.g. Summers et al. 2008). In forests used for timber production, UK government policy, as elsewhere in the boreal and temperate zones (Swanson and Franklin 1992; Fries et al. 1997; Puettmann and Ammer 2007), increasingly promotes forest management that more closely approximates the processes of natural forests, such as restocking by natural tree regeneration (Malcolm et al. 2001).

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Scots pine woodlands in western Europe often adjoin heathlands dominated by heather *Calluna vulgaris* (Ericaceae), with podzolic and shallow peat soils being common under both habitats (Carlisle and Brown 1968, Gimingham 1972). Such soils are considered highly suitable for natural regeneration of conifers (Nixon and Worrell 1999). In the last 100–200 years, overgrazing by deer and livestock has been the main factor preventing pinewood regeneration in Scotland (Steven and Carlisle 1959) and reduction in large herbivore numbers can produce substantial areas of new trees (Sykes and Horrill 1985; Beaumont et al. 1995; Edwards and Mason 2006). However, even with low grazing pressure, the establishment rate of new Scots pine seedlings is low wherever heathland vegetation remains dominant (McVean 1963; Miles and Kinnaird 1979). Similar issues have been noted elsewhere for a range of conifer and ericaceous species (Zackrisson et al. 1997; Mallik 2003). This, combined with the short distance of Scots pine seed dispersal (Nixon and Worrell 1999), results in low rates of forest spread. Where forests are fragmented, speeding up regeneration would increase the size and connectivity of forests, and hence their resilience to large-scale disturbances (wildfire, storms) and climate change (Hannah et al. 2002). It would also contribute to increases in forest area, being sought under regional (Anon 2006) and Europe-wide (Anon 2003) policy, also driven in part by concerns over climate change.

Prescribed fire has a long history of use as a tool to promote Scots pine regeneration in Fennoscandia (Yli-Vakkuri 1961; Parviainen 1996; Östlund et al. 1997). Profuse Scots pine regeneration after fire has often been observed in Scotland (Steven and Carlisle 1959; Sykes and Horrill 1981). Using prescribed fire to promote Scots pine regeneration under Scottish conditions has been advocated for many years (Steven and Carlisle 1959; McVean 1963; Miles and Kinnaird 1979; French et al. 1996; Mason et al. 2004) but rarely attempted. Early trials in Scotland gave poor results (Henman 1961; Edwards 1980). However, replication was limited in these trials, and there were difficulties in applying satisfactory burning treatments. These partly reflect the lack of a skills base in the use of prescribed fire within woodland in the UK (Bruce and Servant 2003; Dugan 2004), which is in contrast to the situation in Fennoscandia and North America (Parviainen 1996; Brown et al. 2004). The poor results from these trials, and a long history of destructive anthropogenic fires (Steven and Carlisle 1959), led to scepticism (Cameron 1995) or opposition (Booth 1984) to the use of prescribed fire for Scots pine regeneration in the UK. In recent years, however, the importance of natural fires in influencing boreal forest biodiversity and structure has been increasingly recognised (Zackrisson 1977; Johnson 1992; Sannikov and Goldammer 1996; Granström 2001). Consequently, giving an appropriate place to the use of fire within

ecological forest management has been increasingly emphasised (Attiwill 1994; Anglestam 1998; Kuuluvainen 2002; Brown et al. 2004). Understanding how natural disturbances like fire can be used as a model for forest regeneration management is a particular research need (Puettmann and Ammer 2007).

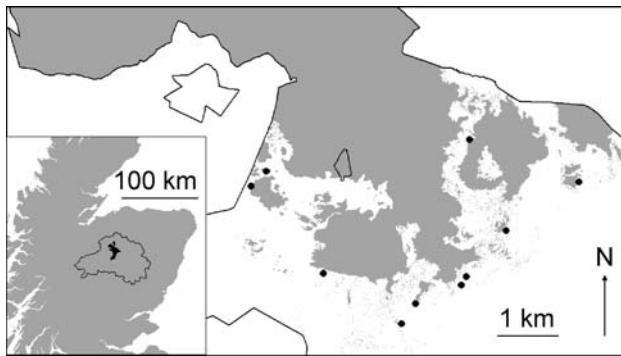
In an earlier, small-scale experiment (Hancock et al. 2005), which involved sowing Scots pine seeds in micro-exclosures, we showed that prescribed fire gave a 3.5-fold increase in Scots pine seedling establishment rates on heathland. Here, we develop this approach with another experiment on heathland, at a more realistic management scale, on study areas open to herbivores, with seed input from natural seed-fall. The current experiment aimed, at two levels of deer abundance, to: (1) quantify establishment of new Scots pine seedlings, in each of the first five seasons after burning; (2) estimate differences in seedling survival between burnt and unburnt areas; and (3) measure cumulative recruitment, 5 years after burning, of established (over 12-months old) seedlings.

## Methods

### Study area and experimental sites

The study took place at Abernethy Forest Nature Reserve (Summers et al. 2008), within the Cairngorms National Park, in the central highlands of Scotland (Fig. 1). The reserve holds the largest fragment of ancient semi-natural pinewood in the UK (2,039 ha: Anon 1994). Forest expansion to the natural tree-line is a major aim at the site (Amphlett 2003). Study plots were at altitudes of 380–440 m, on shallow peat soils (mean depth 29 cm, SE 3.1) over sand, gravel or rock. At the nearest weather station (Aviemore: 3°50' W, 57°12' N, altitude 228 m, 10–16 km west of the experimental sites) during 1994–2003, mean annual rainfall was 1,060 mm, and mean temperatures in January and July were 2.4 and 13.9°C, respectively.

The study took place at ten experimental blocks, considered typical of areas suitable for prescribed burning for tree regeneration. Block locations (1) comprised principally *Calluna vulgaris*–*Vaccinium myrtillus* heath (H12: Rodwell 1991); (2) held few Scots pine seedlings; and (3) were within 50 m of cone-bearing Scots pine trees. They were accessible for machinery needed to carry out management. The area meeting these criteria was not mapped, making random selection of sites impractical, so sites were selected during a series of visits involving reserve management and scientific staff. Deer densities across the forested and potentially forested area of the reserve were estimated in 2003, based on 65 km of dung transects (unpublished data). Estimates were 4.7 km<sup>-2</sup> for red deer *Cervus elaphus*



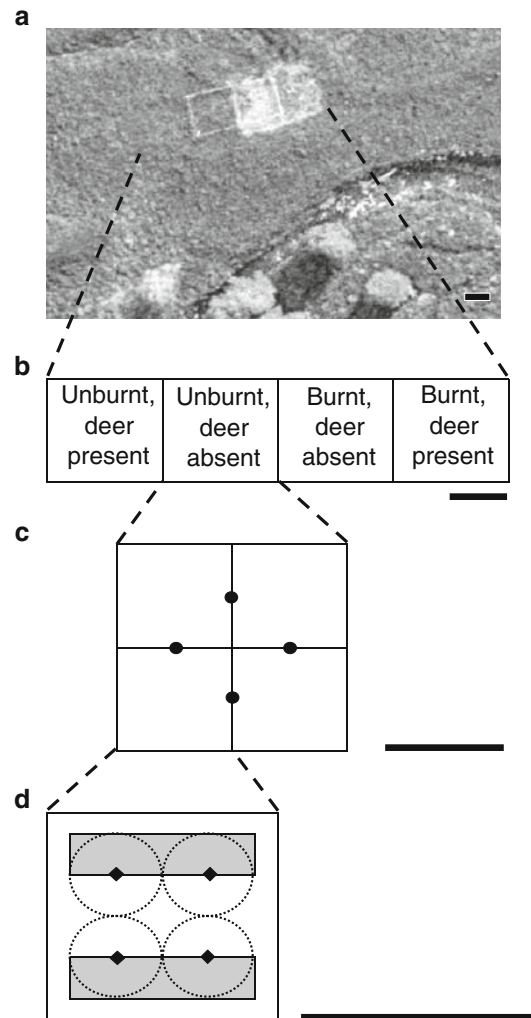
**Fig. 1** The study area and experimental sites. Main map: central part of Abernethy reserve (black boundary), forested area and scattered trees (grey stipple), and the ten experimental blocks (black circles). Inset part of Scotland (grey stipple), with Cairngorms National Park (black boundary) and Abernethy reserve (black)

(95% confidence intervals 3.6–6.2), and  $8.7 \text{ km}^{-2}$  for roe deer *Capreolus capreolus* (6.3–12). These equate to approximately  $650 \text{ kg km}^{-2}$  (500–900) deer biomass. Other animals present at the site, likely to be important to pine seedling establishment and survival, include slugs *Arion ater*, bank voles *Clethrionomys glareolus* and mountain hares *Lepus timidus*.

Each block consisted of four adjacent  $10 \text{ m} \times 10 \text{ m}$  plots, within which there were four  $5 \text{ m} \times 5 \text{ m}$  quadrats (Fig. 2). In early spring 2002, two adjacent plots at each block were burned. Later that year, one burnt and unburnt plot at each block were fenced to exclude deer, such that a factorial design was created, with one plot at each block in each of the following four treatments: ‘unburnt, deer present’, ‘unburnt, deer absent’, ‘burnt, deer present’, and ‘burnt, deer absent’. The locations of the different treatments were randomised, with the constraint that the two burnt plots, and the two fenced plots, had to be adjacent to facilitate management.

#### Fire management and characterisation

Heather-burning in the UK is restricted by law to October–April (Anon 2001), and typically takes place in early spring. The prescribed burning technique used here varied according to the weather conditions (Dugan 2004). In cool, moist conditions, the area to be burnt was ignited at the upwind edge and the fire allowed to run across the area (‘head-fire’ burns). In dry, warm conditions with some wind, the area was ignited in a series of 1–3 m strips, starting from the downwind edge (‘strip ignition’ burns: Supplementary Figure 1). In very dry conditions with a light wind, the area was ignited along the downwind edge and the fire allowed to creep back into the wind across the area (‘backing fire’ burns). In all cases, the edges of the burnt area were defended by applying water.



**Fig. 2** The layout of an experimental block. **a** Air photograph of a block, showing nearby seed trees (bottom of photograph). The burnt area (pale vegetation) and fence can be seen. **b** Schematic diagram of a block. **c** One plot, showing the seed trap locations (black dots) and four quadrats. **d** One quadrat, showing the seedling/dung search strips (grey shading), sample points (diamonds) and cover score areas (dotted circles). A 5 m scale bar is given in each figure

Prescribed fires encompassed a range of fire characteristics, which in turn might influence ecological outcomes (Schimmel and Granström 1996). Therefore, we characterised experimental fires by measuring heat output per unit area, fireline intensity (Byram 1959), fire rate of spread, ‘depth of burn’ (Schimmel and Granström 1996), and a related measure, flame duration at a point. Fire characteristics were measured at the quadrat scale, and averaged by plot.

Heat output was calculated from the biomass burnt, of live heather shoots (the main fuel), their moisture content on burn days, and published data on the heat of combustion of heather; see Hancock et al. (2005) for details of the calculations involved. Non-destructive estimates of heather biomass were made before fires, using a graduated 2 m

stick, marked with 10 cm bands ('FuelRule': Davies et al. 2008). Briefly, this method is based on regression equations, developed and tested in similar vegetation, which relate measures of visual obstruction of the FuelRule, to vegetation biomass measured using destructive sampling (Davies et al. 2008). A similar approach was used to develop regression equations relating burnt heather stem density and size, to post-burn biomass (Davies 2006). This work allows the same measures to be taken elsewhere, in similar vegetation, and used to estimate biomass non-destructively. To take these measures, the FuelRule was pushed into the moss/litter layer at four sampling points per quadrat (Fig. 2d), until the resistance of the soil/humus was felt. Then, from a standing position, and holding the FuelRule vertically at arm's length, the percentage of the FuelRule visible of each of the 10 cm bands was recorded (termed the 'stick visibility scores'). After fires, the basal diameters and lengths of the five nearest burnt heather stems to each point were measured, and stem density estimated within a 0.25 m<sup>2</sup> area. These measures allowed pre- and post-fire biomass to be calculated (Davies et al. 2008, eqn. 2; Davies 2006, eqns. 8 and 9). Their difference gave an estimate of the biomass burnt. Fuel moisture was determined by taking a small sample (wet weight 2.3–7.2 g) of live heather shoots just before each fire, from several plants near the area to be burned. These were placed in an air-tight aluminium container. Later, they were weighed before and after oven-drying for 48 h at 80°C. Moss/litter moisture was determined in a similar way for two small (12–25 g) samples per fire.

Fireline intensity was estimated from visual estimates of flame length (Byram 1959). To assist these estimates, 2 m steel 'fire poles', marked with 25 cm painted bands, were fixed at quadrat centres before fires (Supplementary Figure 1). During fires, the time during which flames touched each fire pole was estimated and one to four photographs were taken per quadrat. Up to three flame length and fire front (flame depth) measures (Johnson 1992) were taken from each photograph, and averaged by quadrat. Rate of spread was estimated as the fire front depth divided by flame duration at the fire pole. Depth of burn was measured by marking the surface of the moss/litter layer before fires with a small metal rod at each sample point (Fig. 2d), then measuring any drop in depth immediately after the fire. A hand-held weather meter, held 2 m above ground, was used to record ambient air temperature (once per fire) and wind speed (mean of ten 3 s average readings per fire).

#### Measuring seed-fall, seedling establishment and deer usage

In late April each year, shortly before the main period of Scots pine seed-fall in the area (Summers and Proctor 2005), four seed traps were placed within each plot, outside

the areas used for other recording (Fig. 2c, Supplementary Figure 2). Each trap consisted of a 35 cm top diameter plastic container, with a muslin liner. The lip of each trap was 30 cm above the moss/litter surface, thus traps measured seed fall into a 0.96 m<sup>2</sup> vegetation canopy gap, 30 cm above ground. Seeds were removed and counted in July and September, and tested for viability by cutting them open to see if an endosperm was present. Viable seeds found in all traps at each plot were totalled for each year.

To measure pine seedling establishment, and quantify deer usage, standard searches were carried out in two 1 m × 4 m 'search strips' in each quadrat (Fig. 2d), in May and September each year. These involved stooping over the strip from its outer edges, for around 5 min in every case, looking for pine seedlings and deer dung. At each seedling, the following measurements were taken: (1) whether paired needles were absent or present, allowing the seedling to be classed as 'year-one' (probably within 12 months of germination, Carlisle and Brown 1968) and '12-months-plus', respectively; (2) height above the surface of the moss/litter layer; (3) vegetation structure from stick visibility scores (see above); and (4) the coordinates of the seedling within the strip. Coordinates were approximate because measuring tapes could not be set completely straight in the long vegetation and rough microtopography that was typical of the plots.

For deer dung counts, groups of pellets separated by more than 10 cm were treated as distinct groups. For each group, the number of pellets was counted and the diameter of a typical pellet measured. During spring counts, dung was cleared from search strips. Conversely, there was no clearance in the autumn counts, so that the next spring count would be roughly comparable with the first spring count. Given approximate degradation times at the site (Laing et al. 2003), the spring count measures dung accumulation over approximately 1 year, but with more of the winter dung present, while the autumn count primarily measures summer dung deposition.

It was expected that the detection rate of both seedlings and deer dung would vary between treatments, due (for example) to large differences in vegetation structure between burnt and unburnt areas. We therefore quantified detection rate in two trials, using dummy seedling and dummy dung groups, placed at random locations in the search areas before standard searches (Supplementary Material). The trial results were used to model seedling detection rate as a function of 'ground-level vegetation openness' (see below) and seedling size class ('small': less than 5 cm, or 'large': 5–15 cm). This allowed us to estimate detection rate for each seedling size class, for all plots and years, based on vegetation openness data. Estimated detection rate was later included in seedling analyses as a covariate, to statistically control for variation in detection rate.



## Vegetation recording and block characteristics

Vegetation structure was quantified in September each year using the same measuring stick used for heather biomass measurement (above). At four points per quadrat (Fig. 2d), we recorded stick visibility scores (above) and the maximum height within 5 cm of the stick for moss/litter. These measures, and interpolation, were used to produce a ‘ground-level vegetation openness’ score, which was the visibility score of a 10 cm band of the measuring stick, centred 5 cm above the surface of the moss/litter layer. At each point, the top cover of live vegetation other than moss was measured within a 2 m diameter circle (Fig. 2d). Moss/litter height, ‘ground-level vegetation openness’ and live vegetation cover were, respectively, taken as measures of substrate depth, light levels, and vegetation competition as experienced by establishing seedlings, all of which are considered important factors affecting Scots pine seedling establishment (Yli-Vakkuri 1961; McVean 1963; Carlisle and Brown 1968; Jäderlund et al. 1998; Wennström et al. 1999; Oleskog and Sahlén 2000).

Pine seedling establishment was expected to vary between blocks due to differences e.g. in microclimate (Vaartaja 1950; Tegelman 1998; Vickers and Palmer 2000), so we measured altitude, slope, peat depth, frost frequency, aspect and shade/shelter. Slope angle (in degrees) was measured using a clinometer. Peat depth was measured with a metal probe, pushed into the soil at each plot centre, and an average taken for the block. Relative frost frequency between blocks was estimated by placing temperature loggers, recording maximum hourly temperature, at each plot centre in one winter (2005/2006) during the main period of frosts (mid-November to mid-March). Frost frequency was taken as the proportion of days with at least 1 h below 0°C, averaged for the four plots at each block. Aspect in relation to south was measured by firstly, taking the down-slope bearing at each quadrat centre, then finding the southerly component of each bearing, as the cosine of the angle between the bearing and a line pointing due south, and finally averaging these components across the whole block. Shelter in relation to direct sun, and prevailing south-westerly winds, was determined at each plot centre, by using a clinometer to measure the angle between the horizontal and the lowest point of open sky, in a southerly, south-easterly and south-westerly direction. The mean of these values was then taken for each block, with high values indicating more sheltered, shaded blocks.

## Methods of analysis

Analysis of pine seedling data aimed to test three null hypotheses, namely that the following did not vary with treatment: (1) annual ‘year-one’ seedling establishment, (2)

seedling survival and (3) cumulative ‘12-months-plus’ seedling recruitment after 5 years. We tested the effect of each treatment factor (burning, deer presence/absence) and their interaction, within one full model for each response variable. In all cases a Generalised Linear Model (GLM) was fitted, using the GENMOD procedure in SAS (SAS Inst. 2000). This approach is analogous to ANOVA but allows analysis where the dependent variable, as in our case, does not have a normal distribution.

The GLM framework also allowed variation in continuous, ‘nuisance’ variables to be ‘statistically controlled’, by their inclusion as covariates. Two such variables were seedling detection rate, and seed-fall: variation in either of these could obscure treatment effects. Therefore, measures of both were incorporated into analyses as covariates. Our measure of seed-fall was the total count of viable seeds at each plot in each year. Seedling detection rate was estimated for all plots and years, using a model based on data from the two dummy seedling trials (Supplementary Material).

For the year-one seedling establishment model, the response variable was the count of seedlings under 12 months old, on the autumn count at each plot in each year. In 2 years, 2002 and 2004, no such new seedlings were found in unburnt vegetation, making year-wise estimation of burn effects impossible. So we grouped the first 4 years as two pairs of years, giving a categorical time-period variable with three levels: 2002–2003, 2004–2005 and 2006. Data from each year were treated as independent. This was considered acceptable as each seedling identified as ‘year-one’ could only be counted once on successive autumn surveys. We then modelled year-one seedling count in a GLM, estimating the effects of the two treatment factors, time-period, and their first-order interactions, after accounting for variation linked to seed-fall, detection and block (Supplementary Material: equation 1).

To investigate the effects of fire characteristics on seedling establishment, we fitted a ‘burn-only model’, similar to above, but for the data from the burn plots only (Supplementary Material: equation 1a). Based on previous studies (Schimmel and Granström 1996; Hancock et al. 2005) we hypothesised that fires that had higher heat output, greater fireline intensity, more moss/litter consumption, longer flame durations at a point, and/or slower rates of spread, would be followed by higher seedling establishment. We therefore plotted the residuals of the burn-only model against these variables to see if the pattern fitted our expectation.

For the seedling survival model, data were collated at the scale of individual seedlings, for all seedling surveys other than the first (when seedling locations were not recorded) and last (for which there was no data on subsequent survival). For each seedling record, data were examined for

the subsequent survey, to see if a seedling was located at a similar location (within an estimated measurement error of 15 cm). Where this was the case, the seedling was assumed to have survived between the two surveys. Only at five search strip surveys, out of 216 included in analysis, did seedling densities exceed 1 m<sup>-2</sup>, so the potential for re-located seedlings to be wrongly attributed was considered low. Re-location, or not, was used as a binary response variable in this analysis. We modelled this in a GLM that estimated the effects of the two treatment factors, time period and age class, after compensating for the effects of block, differing detection rates between treatment, and the length of time between consecutive surveys (Supplementary Material: equation 2). Data were too sparse to allow fitting of an interaction term between the two treatment factors, hence analysis is based on an assumption that any such interaction is negligible. For both this and the recruitment analysis (below), we only included seedlings smaller than 15 cm, in order to exclude a few older seedlings surviving from before the start of the experiment.

For the model of cumulative recruitment over 5 years, the response variable was the number of ‘12-months-plus’ seedlings recorded on the final survey (autumn 2006). This count was modelled in a GLM that estimated the effects of the two treatment factors, and their interaction, after compensating for the block effect and differences in detection rate and seed-fall (Supplementary Material: equation 3).

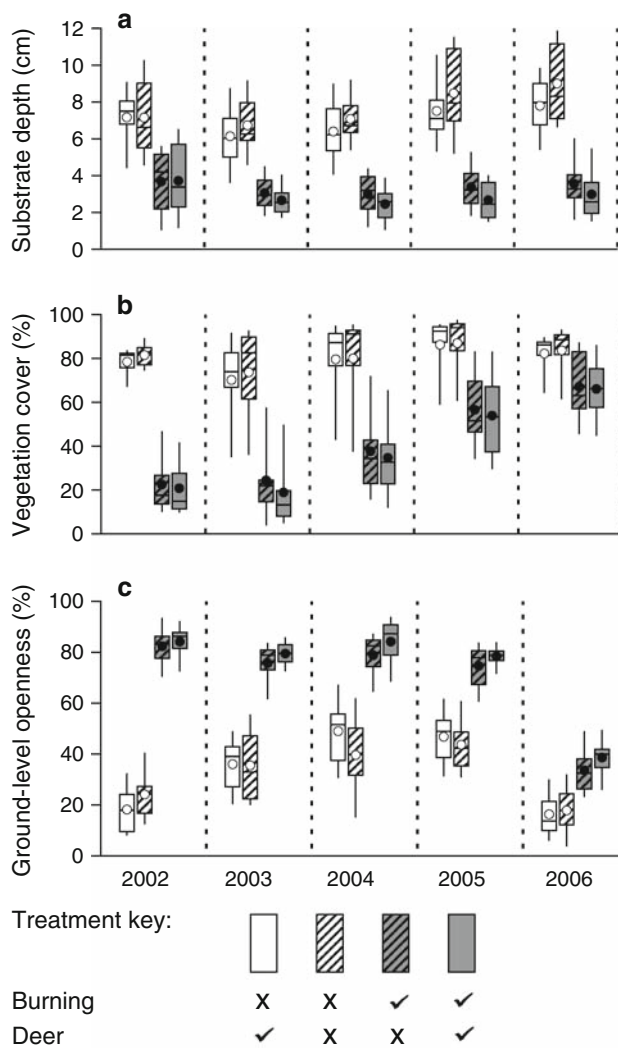
**Results**

Fire characteristics, vegetation changes, and seed-fall

Fires were generally of low intensity, with average flame lengths of 0.7 m, but variable, encompassing a 2- to 20-fold range of fireline intensities, duration of heating, and rate of spread (Table 1). On average, about 1.2 cm of the moss/litter layer was consumed during fires, or about 15% of the

initial depth. After fires, there was a further reduction in moss/litter depth in burnt plots, owing to die-back and weathering: by the second year after fires, moss/litter depths in burnt areas were less than half those in unburnt areas, and remained low for the rest of the study (Fig. 3a). The moss/litter layer was slightly deeper where deer were excluded.

The top cover of live vegetation other than moss was reduced after fires to about 20% in burnt plots, compared to 80% in unburnt plots (Fig. 3b). Subsequently, there was a steady increase in live vegetation cover in burnt plots,



**Fig. 3** Vegetation characteristics at experimental plots. Measurements were made each autumn, starting in the autumn after spring fires. **a** Depth of substrate (moss/litter layer). **b** Vegetation cover (top cover of all live vegetation, other than moss). **c** Ground-level openness (visibility of measuring stick, 5 cm above the moss/litter surface—see text for details). Box plots show upper and lower quartiles (box), median (central line), and 5th and 95th centiles (whiskers). Means are shown as dots (white unburnt, black burnt). White boxes unburnt, deer present; striped boxes unburnt, deer absent; grey striped boxes burnt, deer absent; grey boxes burnt, deer present

which reached around 66% after 5 years. In unburnt vegetation, an unusual natural heather die-back episode in early 2003 (Hancock 2008), resulted in lower means and higher variance in vegetation cover in that year, with some recovery in the following years. There were only minor differences in vegetation cover between plots with and without deer.

Ground-level vegetation openness (Fig. 3c) was about four times higher in burnt plots than unburnt plots in the first season after burning, and remained twice as high, 5 years after burning. Temporary increases in openness in unburnt vegetation followed natural heather die-back in 2003. Deer presence was associated with slightly higher openness in burnt areas.

As expected, seed fall varied markedly between years. Previous studies at this site implied a regular peak in seed fall, every 3 years (Summers and Proctor 2005). However, only the second of the two expected high seed years (2003, 2006) occurred at our experimental areas. Thus, during the study period, there were four low seed-fall years, and one high year (2006), when mean seed-fall was 13 times greater than that of other years (Fig. 4).

Seedling detection trials

In the 2003 seedling detection trial, using only small dummy seedlings, detection was about 50% higher in plots with deer present, than those with deer absent, and about 40% higher in burnt plots, than unburnt ones (averaging the effect of one treatment factor across both levels of the other). In the 2005 trial, which included larger seedlings, the difference between burnt and unburnt plots was more pronounced, but differences between plots with and without deer, less so. In this trial, the detection rate of dummy seedlings in burnt plots was nearly double that of unburnt ones.

The best approximating model of seedling detection, based on data from both trials, included height class and ground-level vegetation openness (Table 2). Detection rate was higher both for taller seedlings, and in more open

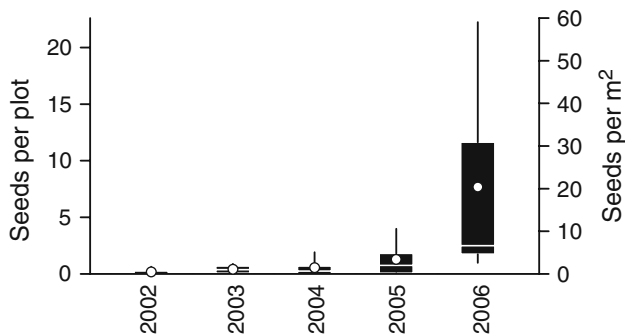


Fig. 4 Viable Scots pine seed-fall at experimental sites, by year, across all treatments. Key to box plots as Fig. 3

Table 2 Model of seedling detection as a function of height class and vegetation openness

Term	df	$\chi^2$	P
Significance tests			
Height class	1	18.6	<0.0001
Vegetation openness	1	3.7	0.056
Variable	Estimate	Standard error	
Parameter estimates			
Height class			
0–4 cm	–0.92	0.19	
5–15 cm	0.46	0.26	
Vegetation openness	0.0084	0.0044	

This was the best approximating model (Burnham and Anderson 2002) of the five different models fitted, including all possible combinations of height class, vegetation openness, and their interaction

Model deviance was 246, and residual degrees of freedom 197. Parameter estimates relate to the logit-transformed probability of detection. For categorical variables, estimates are least squares means

vegetation, but there was no interaction between these effects. Estimated detection rate across all plots and years, averaged 0.28 (range 0.23–0.34) and 0.55 (0.50–0.61) for small (less than 5 cm high) and large (5–15 cm high) seedlings, respectively.

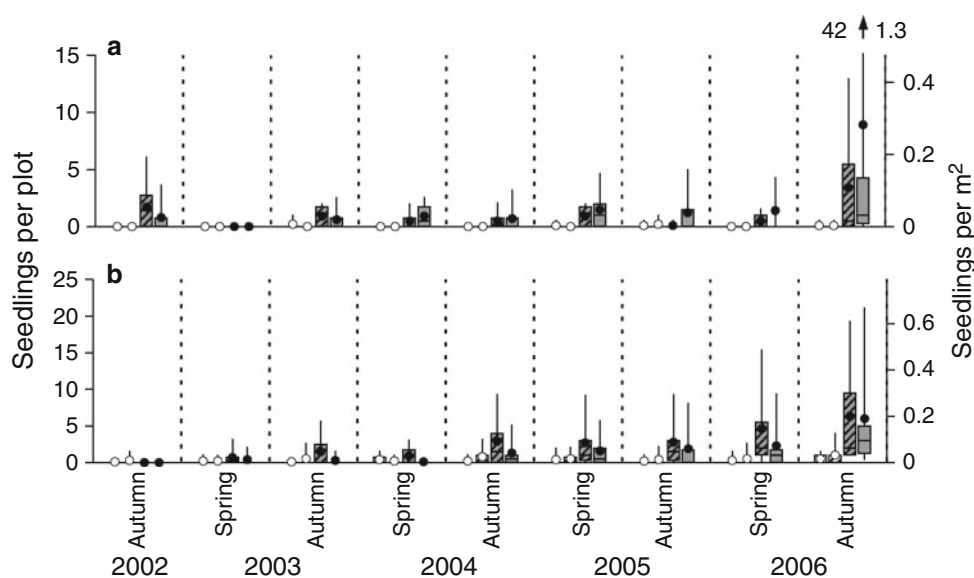
Deer dung counts

Interpretation of deer dung counts was complicated by the gradual appearance of old dung, revealed as dead moss/litter in the burnt plots disintegrated, in the four seasons following burning. This was hard to tell from weathered, more recent dung. However, by the fifth season after burning, this process had ceased; thereafter, little dung of any kind was found. Lumping the two counts in the fifth season after burning, a total of ten and nine deer dung groups were found in (unfenced) unburnt and burnt vegetation, respectively. The dung detection trial suggested only small differences in detection rate between treatments, with the mean detection rate in (unfenced) unburnt and burnt plots being 0.37 and 0.48, respectively (s.e. 0.11). Together, these results imply approximately 1.7 times greater use of unburnt than burnt vegetation by deer. However, the sample sizes were small.

Year-one pine seedling establishment

Small numbers of ‘year-one’ pine seedlings were found at each survey in the first 4 years, with counts usually higher in burnt plots (Fig. 5a). In 2006 (the year of high seed-fall), large numbers of young seedlings were found in burnt areas, but these were mostly concentrated into three of the ten blocks.

**Fig. 5** Scots pine seedlings recorded at experimental plots. **a** Year-one seedlings, **b** older seedlings. The 95th centile for young seedlings in the burn treatment in autumn 2006 is outside the plotted range; the values (per plot and per  $m^2$ ) are shown. Burning and fencing took place 6 and 2 months, respectively, before the first seedling survey in autumn 2002. The main period of seed fall and seedling establishment was between the spring and autumn surveys each year. Key as Fig. 3



The model of year-one seedling establishment in relation to treatment emphasised the strong effect of burning (Table 3, Fig. 6). At mean seed-fall and seedling detection, and across all years, year-one seedling establishment in burnt plots was 9.8 times greater than that in unburnt plots (95% confidence intervals 3.2–30). The effect of deer-exclusion varied with time: in the first 2 years, year-one seedling establishment within fences was 1.8 times higher than outside (confidence intervals 0.7–4.7), but in later periods, establishment was similar inside and outside fences. The effect of burning also varied between time periods, with a relatively much higher establishment rate on burnt plots in the high seed-fall year (2006). In this year, establishment on burnt ground was estimated as 65 times (95% confidence limits 15–280) higher than unburnt ground. This compares with more modest figures of 4.5 (0.6–32) and 3.2 (0.7–15) for 2002–2003 and 2004–2005, respectively.

There were big differences between blocks, even after accounting for differences in seed-fall (Table 3). At one block, no year-one seedlings were found, while another held 49% of all that were located. Fitted block means formed an approximate geometric series, particularly among the ‘best’ seven blocks: when ranked, each mean was about twice the value of the next highest. Block means were not significantly correlated with topographical measures (altitude, slope, peat depth, shelter from south and aspect), or frost frequency.

The ‘burn-only’ model showed two patterns consistent with our hypothesised relationships (“Methods”): higher residuals (more seedlings) where rates of spread were low, and duration of heating high. These two fire variables were strongly inversely correlated ( $r_s = -0.60$ ,  $P < 0.0001$ ). Fitting rate of spread as an additional covariate in the burn-only model gave a greater reduction in model deviance than

duration of heating. The modelled effect suggested that the number of seedlings establishing would decline by 27% for each increase in rate of spread of  $0.01 \text{ ms}^{-1}$ , and would be 20 times higher after the slowest fires recorded ( $0.004 \text{ ms}^{-1}$ ), than after the fastest ( $0.099 \text{ ms}^{-1}$ ). Fires with low rates of spread occurred on later dates ( $r_s = -0.38$ ,  $P = 0.0002$ ), and consumed a greater proportion of the moss/litter layer ( $r_s = -0.70$ ,  $P < 0.0001$ ). Fire rate of spread was partly related to ignition strategy: head-fires (“Methods”) had rates of spread that were 3.3 and 3.5 times greater than those associated with strip ignition, and backing fires, respectively. The typical ignition strategy shifted from head-fire (eight fires), to strip ignition (eight fires), to backing fire (one fire), as conditions became warmer, calmer and drier: mean ambient temperatures during fires with these three styles of ignition were 7.3, 9.4, and  $11.2^\circ\text{C}$ ; mean wind speeds were 3.5, 3.2, and  $3.1 \text{ ms}^{-1}$ , and mean moss/litter moisture contents were 75, 60 and 33%. However, there was a range of conditions over which both head-fires and strip ignition were used (temperature:  $6.2\text{--}11^\circ\text{C}$ ; wind:  $2.3\text{--}4.1 \text{ ms}^{-1}$ ; moss/litter moisture: 58–77%), implying a choice of ignition strategies in some weather conditions.

#### Pine seedling survival and cumulative recruitment after 5 years

Data on survival, or strictly speaking, probability of relocation, was available for 342 seedlings. Four seedlings were found in the ‘unburnt, deer present’ treatment (none relocated), 11 in ‘unburnt, deer absent’ (3, or 27%, relocated), 185 in ‘burnt, deer absent’ (91, or 49%, relocated), and 142 in ‘burnt, deer present’ (58, or 41%, relocated). As none of the seedlings in the ‘unburnt, deer present’ treat-



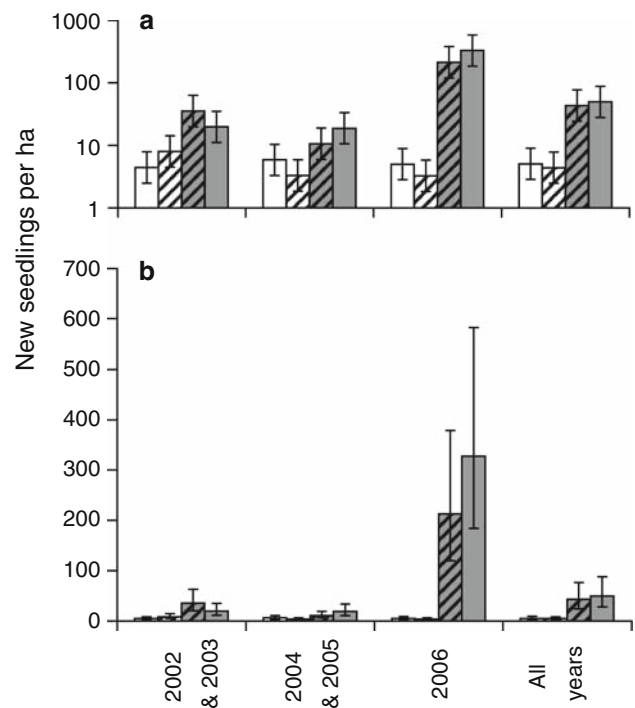
**Table 3** Model of new seedling establishment in relation to treatment (Supplementary Material: equation 1)

Term	<i>df</i>	$\chi^2$	<i>P</i>
Significance tests			
Compensatory variables			
Seed-fall	1	57.82	<0.0001
Detection	1	4.06	0.044
Block	8	341.34	<0.0001
Treatment variables			
Burning	1	18.52	<0.0001
Deer presence/absence	1	0.11	0.74
Period	2	3.64	0.16
Burning*deer	1	0.00	1.00
Burning*period	2	9.77	0.0076
Deer*period	2	7.47	0.024
Variable	Estimate	Standard error	
Parameter estimates, for treatment terms (except interactions)			
Burning			
Unburnt	-7.67	0.49	
Burnt	-5.39	0.37	
Deer			
Present	-6.46	0.38	
Absent	-6.60	0.39	
Period			
2002–2003	-6.70	0.47	
2004–2005	-7.16	0.47	
2006	-5.74	0.58	

Parameter estimates give  $\log_e$ -transformed estimates of new seedlings establishing per  $\text{m}^2$  per year, at mean values of compensatory variables. Model deviance was 149, and residual degrees of freedom 160. Parameter estimates for categorical variables are least squares means

ment were re-located, it was impossible to estimate survival for this treatment alone, so only the two main effects ‘burn’ and ‘deer’ were fitted in the model, not their interaction. Analysis therefore involved the assumption that the effects of burning on survival did not vary between areas with and without deer, and vice versa. Similarly, at three blocks, all seedlings were either re-located or not re-located, meaning that the variance of the block mean could not be calculated. Therefore, we excluded these blocks from analysis, which was based on 330 seedlings found at the remaining seven blocks (Table 4).

Analysis suggested no strong effect of deer presence/absence but an effect of burning that was close to statistical significance ( $P = 0.065$ ). The odds of seedling survival (re-location) between consecutive surveys were 3.6 times greater in burnt areas than unburnt areas, but 95% confidence intervals were wide and spanned one (0.85–15). Analysis suggested stronger effects on seedling survival of



**Fig. 6** New Scots pine seedling establishment by year and treatment: results of modelling analysis, on a log scale (a) and back-transformed (b). Bars show estimates of likely numbers of new, ‘year-one’ seedlings to be observed, under a scenario where detection rate and seed-fall are uniform across treatments and years, at their mean values of 0.28 and  $5.4 \text{ m}^{-2}$  respectively. Key as Fig. 3

block and survey period, which had highly significant effects in the model, implying strong spatial and temporal variation in survival. Mean survival estimates for different blocks and surveys encompassed a 3.9- and 7.5-fold range of survival probabilities respectively. Block estimates were correlated with peat depth ( $r_s = 0.93$ ,  $P = 0.0025$ ), suggesting better survival, irrespective of treatment, where peat was deeper. Mean winter survival (following three autumn surveys) averaged 36% (range 15–53%), about twice as high as mean summer survival (following four spring surveys), which averaged 18% (7–34%).

Numbers of older (‘12-months-plus’) seedlings gradually accumulated over the study period (Fig. 5b), mainly in the burnt plots, but were highly variable between blocks. By the end of the study period, mean densities of detected older seedlings in burnt plots (Supplementary Figure 4) were about  $2,000 \text{ ha}^{-1}$ , in plots both with and without deer present. In unburnt vegetation, mean densities of detected seedlings were much lower, being about  $160 \text{ ha}^{-1}$  in plots with deer and  $320 \text{ ha}^{-1}$  in plots with no deer.

Recruitment of ‘12-months-plus’ seedlings, after 5 years, was strongly affected by burning (Table 5, Fig. 7), being 36 times higher on burnt ground, than unburnt (95% confidence limits 5.8–220), at mean seed-fall and

**Table 4** Model of seedling survival, or, strictly, re-location probability, in relation to treatment (Supplementary Material: equation 2)

Term	<i>df</i>	$\chi^2$	<i>P</i>
Significance tests			
Compensatory variables			
Seedling age class ('year-one', or '12-months-plus')	1	0.68	0.41
Number of days between surveys	1	0.73	0.39
Detectability when first found	1	0.05	0.83
Block	6	19.12	0.004
Survey number	6	24.84	0.0004
Treatment variables			
Deer presence/absence	1	0.35	0.55
Burning	1	3.40	0.065
Variable	Estimate	Standard error	
Parameter estimates, for treatment terms			
Burning			
Unburnt	−1.88	0.85	
Burnt	−0.59	0.36	
Deer			
Present	−1.32	0.58	
Absent	−1.15	0.54	

Parameter estimates give logit-transformed estimates of relocation probability between two surveys, at mean values of compensatory variables

Model deviance was 396, and residual degrees of freedom 312. Parameter estimates for categorical variables are least squares means

detection. A marginally non-significant interaction term suggested that the effect of burning may differ between plots with and without deer, with a greater difference between burnt and unburnt areas where deer were present. There was, again, large (22-fold) variation in block means but these were not significantly correlated with any of the topographical or microclimate variables investigated. As in the year-one seedling establishment analysis, the block means formed an approximately geometric series when ranked, with each being about 1.5 times that of the next highest.

## Discussion

### Effects of fire on pine seedling recruitment

We found strong evidence that prescribed burning of heather moorland on peat soils is an effective tool to increase the rate of Scots pine seedling establishment. Previous work at Abernethy (Hancock et al. 2005), but using a different approach (sowing of seeds in micro-enclosures), found a smaller difference between burnt and

**Table 5** Model of 5-year cumulative recruitment of seedlings over 1 year old, in relation to treatment (Supplementary Material: equation 3)

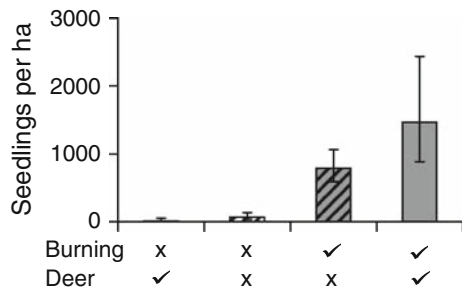
Term	<i>df</i>	<i>F</i>	<i>P</i>
Significance tests			
Compensatory variables			
Seed-fall	1, 25	2.78	0.11
Detection	1, 25	1.26	0.27
Block	9, 25	6.09	0.0002
Treatment variables			
Burning	1, 25	29.07	<0.0001
Deer presence/absence	1, 25	0.63	0.43
Burning × Deer	1, 25	3.25	0.084
Variable	Estimate	Standard error	
Parameter estimates, for treatment terms (except interactions)			
Burning			
Unburnt	−5.80	0.78	
Burnt	−2.23	0.35	
Deer			
Present	−4.27	0.65	
Absent	−3.76	0.36	

Parameter estimates give estimates of  $\log_e$ -transformed seedling numbers per  $m^2$ , at mean values of compensatory variables

Model deviance was 38, and residual degrees of freedom 25. Significance tests were scaled using deviance/degrees of freedom. Parameter estimates are least squares means

unburnt areas. However, this earlier study did suggest that seed losses to, for example, voles and insects would have been higher in unburnt vegetation, had this not been prevented by micro-enclosures. This might explain the larger difference found in the current study, where such losses were not artificially reduced. Lehto (1956) found higher seed losses in unburnt vegetation, and attributed most losses to insects and fungi. Nystrand and Granström (2000) found that pine seedlings were often eaten by slugs, which were strongly moisture limited. Therefore, slugs may have greater relative impacts on seedlings in the moister environment of unburnt vegetation. The prospects for elevated seedling densities on burnt areas in the longer-term would appear good, with evidence that both seedling survival, and cumulative year-five recruitment, were higher in burnt areas.

There are few comparable experimental studies. In Scotland, Edwards (1980) found that seedling densities at the end of the first season after prescribed burning were only 40% higher, at four burnt, 10 m × 10 m plots, than those at six controls. Early experimental work on natural regeneration at Scottish pinewoods, including fire, by the UK Forestry Commission, was reviewed by Henman (1961). In these trials, seedling densities at the three 0.04 ha burnt



**Fig. 7** Mean cumulative recruitment after 5 years, of Scots pine seedlings at least 1 year old, by treatment. Vertical bars show estimates of likely numbers of '12-months-plus' seedlings to be observed after 5 years (four recruitment seasons), under a scenario where detection rate and seed-fall are uniform across treatments, at their mean values of 0.55 and 1.6 m<sup>-2</sup> year<sup>-1</sup>, respectively

plots were less than half those of controls, after 21–29 years. The poor results from prescribed burning in these studies could reflect chance block effects, to which the studies were vulnerable given limited replication, or difficulties with carrying out satisfactory prescribed burning, as suggested in the study reports.

Among the studies in mainland Europe, that of Lehto (1956) includes the largest number of sites. He tabulates results for Scots pine recruitment at 0.25 ha plots in a range of Scots pine stands managed for tree regeneration in Finland. The ground vegetation treatments included prescribed fire ( $n = 23$ ), and 37 controls. Mean Scots pine seedling densities in *Calluna*-type vegetation, up to 60 years after fires, were 6.8 times higher in prescribed fire areas than in untreated areas. Interpretation of these results is complicated by the fact that different management approaches were commonly used on different kinds of sites and over different time periods. Hille and Den Ouden (2004) tested prescribed fire for Scots pine regeneration in northern Germany, using hand-sowing and micro-exlosures. They found that counts of year-one seedlings on burnt areas were about 7–11 times greater than controls. Our study also found approximately order of magnitude increases in establishment and early recruitment, but in a different region and soil type. Thus, our results are more similar to these mainland European studies, than those of earlier studies in Scotland.

Positive effects of prescribed fire on seedling establishment have often been found for other pine species, e.g. Shelton and Wittwer (1991) reviewed seven trials of prescribed fire and regeneration for *Pinus taeda* and *P. echinata*. They found seedling densities to be 2.4–5.1 times higher after prescribed fire than those of unburnt areas.

Just as in our earlier study (Hancock et al. 2005), we found slow-moving fires to produce substantially better conditions for seedling establishment than fires of average speed. Fires with low rates of spread tended to result in a

greater proportion of moss/litter being consumed. Therefore, our results were consistent with the model of Schimmel and Granström (1996), which predicts that fires resulting in a greater 'depth of burn' will be more favourable to species, like Scots pine, which colonise fire sites via seed dispersal.

#### Effects of deer-exclusion on seedling recruitment

In contrast to the strong positive effect of burning on pine seedling establishment, there was no strong, consistent effect of deer-exclusion, which appeared to vary according to time period, or whether the ground had been burnt or not. Deer-exclusion had a more positive effect on seedling establishment in the early years of the study, than later on. Contrary to expectations, there was some evidence that the positive effect of burning on seedling recruitment was reduced by deer-exclusion. In some circumstances, herbivores may have positive effects on pine seedlings, by reducing the abundance of competing vegetation, which might outweigh other, negative, impacts (Richardson and Bond 1991; Hester et al. 2000). However, the situation could change in future years as vegetation and seedlings grow in burnt areas, perhaps increasing the likelihood of seedling browsing by deer.

#### For how long after a fire is seedling recruitment enhanced?

Establishment of year-one seedlings on burnt ground remained substantially higher than on unburnt ground at the end of our study period, five growing seasons after the fires, suggesting that the recruitment 'window' remained open. Consequently, the total eventual recruitment of pine into the burnt patches has the potential to be higher than levels reported here.

Yli-Vakkuri (1961) suggested that the suitability of burnt ground (not peat soils) for seedling establishment reached a peak, 3–5 years after burning. In the first 2 years, he suggested that the temperature and moisture regime of freshly burnt ground was too inhospitable. Dimpleby (1953), studying natural pine regeneration after heathland fire in England, also suggested that initial seedling establishment peaks at roughly 3–5 years after a fire, then declines because of the increasing cover of heather. Conversely, Lampainen et al. (2004) found that seedling recruitment of Scots pine, after a 1969 wildfire, was spread over many years. In our 5 year study, the difference in year-one seedling establishment between burnt and unburnt ground was most pronounced in year five. This could reflect increasing relative suitability of burnt ground with time since burn, or, alternatively, the weather conditions and/or high seed-fall of that particular year.

### The variability of seedling density—a good or bad thing?

We found considerable variation in seedling density between our 10 m × 40 m blocks, even after accounting for the high between-block variation in seed fall. For example, recruitment after 5 years (corrected for seed-fall differences) varied 22-fold between different blocks. Some of these differences may have been due to different fire characteristics at different blocks. These reflect weather conditions and ignition strategy on the burn day, and also block characteristics like soil and topography. Similarly, the subsequent establishment and survival of seedlings may be related to block characteristics. For example, greater survival on blocks on deeper peat could reflect reduced risk of seedling water stress. There was some evidence that summer losses were generally greater than winter ones in this study. However, much variation between blocks remained unexplained, making absolute seedling densities, at the level of an individual 10 m × 10 m plot, hard to predict. Some of this variation could be caused by spatial variation in seed and seedling consumers, such as rodents, beetles and slugs (McVean 1963; Nystrand and Granström 2000; Worthy et al. 2006), which we did not measure. Such consumers can have a powerful influence on seedling recruitment, in a manner that is strongly spatially variable, but not strongly linked to forest site types (Nystrand and Granström 2000).

Studies with a strong silvicultural focus have emphasised the need to develop techniques of natural regeneration that provide high densities and even stocking rates between different areas (Béland et al. 2000; Wennström et al. 1999). However, where multi-objective forests are desired, or nature conservation objectives are paramount, such as at Abernethy, a forest with a more patchy tree distribution may be preferred. Ultimately, this is likely to be associated with a more variable forest floor light and humidity environment and hence a wider range of invertebrate (Atlegrim and Sjöberg 2003) and plant (Vellak and Paal 1999; Parlane et al. 2006) communities. In Scotland, the flagship pine-wood species, capercaillie *Tetrao urogallus*, is associated with semi-natural stands showing a range of features including a more clumped tree distribution (Picozzi et al. 1992), perhaps because such woods hold a more patchy mosaic of understorey shrubs, or the combination of both open-crowned trees with large branches, and denser patches. During establishment, herbivores may accentuate patchiness by having greater impacts where seedlings are at low density (Gill 1992; Hester et al. 2000).

Studies of natural forests emphasise their heterogeneity, especially in the early and late seral stages, which is poorly replicated in plantation forests (Swanson and Franklin 1992; Peterken 1996). Regeneration following fire in Scots pine forests is often clumped and variable in structure

(Kuuluvainen and Rouvinen 2000, Lampainen et al. 2004). Similar patterns have been found, at spatial scales similar to that of our blocks, for natural regeneration of other tree species (Bonnicksen and Stone 1980; Askew 1983; Ward and Parker 1989; Fröhlich and Quedneau 1995), and for Scots pine following other types of disturbance (Burdon et al. 1994). Natural regeneration using prescribed fire could help create high spatial variation in forest habitats, driven by variation in stand density. This heterogeneity, as well as being a valuable feature of more natural woodlands, is increasingly sought in multi-use productive forests (Malcolm et al. 2001; Puettmann and Ammer 2007).

### Conclusions: management implications and future work

This study provides strong evidence of the efficacy of prescribed burning as a management tool favouring Scots pine regeneration. Our results are particularly applicable to heather-dominated habitats on shallow peat soils. High spatial variation in seedling densities is likely to result when using this technique. It is therefore more appropriate where a patchy, rather than evenly spaced, pattern of regenerating forest is desired, for example where landscape or 'naturalness' considerations are prioritised rather than mainly silvicultural ones. For optimum results, for example when using the technique further from seed trees, managers should aim to produce slow-moving fires. These are more likely to be created by strip-ignition or back-burning, than head-fires. Except in the most marginal (cool, moist) conditions, strip burning can often be used instead of head-fires, although it is more time-consuming.

The approach we have used here with prescribed burning and natural seed-fall, would be less effective at locations distant (e.g. more than 100 m) from seed trees, due to low seed-fall (Nixon and Worrell 1999). Where there is a desire to establish forest in such areas, planting would be the typical approach. However, the results of this and our earlier study suggest that prescribed burning, combined with manual sowing of locally collected seed, would also be worth considering. Early small-scale Scottish trials of just such an approach gave promising results in some circumstances (McVean 1963). While this technique would be slower than planting in leading to established stands (Kardell 1986, Ackzell 1993), it can be cheaper (Kardell 1986, Wennström et al. 1999). Considering the sowing of conifers with only manual site preparation, Tirén (1974) estimated that the use of prescribed fire could halve establishment costs. Comparing costs and results of direct sowing on burnt ground, with those of planting, for Scots pine and perhaps other species e.g. birch *Betula* spp., would be a worthwhile subject for a future management trial.



Five years after fires, pine seedling recruitment at our experimental sites was still many times higher in burnt vegetation than unburnt. McVean (1963), who sowed pine seeds into post-fire heather stands, found a phase of increased establishment after the first few years. Lehto (1956) found elevated densities of small seedlings at some prescribed fire plots even 30 years after fires. Therefore, the current experimental areas should be re-visited, ideally annually for the duration of the recruitment window, and occasionally thereafter. This will allow measurement, under the different treatments, of the longer-term phasing of recruitment and eventual densities of established seedlings.

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