

Direct seeding of ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.): The effects of sowing date, pre-emergent herbicides, cultivation, and protection on seedling emergence and survival

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Abstract

Direct seeding is an alternative method to conventional planting for woodland establishment that has several potential advantages. This study reports the effects of sowing date, pre-emergent herbicides, and cultivation and protection on the emergence and survival of direct-sown ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) on three sites in southern England situated on former pasture and arable land, and on a windblown site in beech (*Fagus sylvatica* L.) woodland. Few seedlings emerged at the woodland site probably due to excessive seed predation by small mammals. At the other sites, the effects of sowing date on emergence reflected seasonal variation in soil moisture content and temperature. Periods of soil waterlogging in seed beds during winter resulted in greatly reduced seedling emergence of early sown seeds, and seedling emergence of both species ceased once the daily maximum soil temperature exceeded 25 °C, which was in late April in this study. Analysis of the thermal time requirements for complete emergence of both species under the recorded soil-temperature regime suggested that the latest sowing date that would allow emergence before soil temperatures were too high was the beginning of March. Ash seedlings were particularly vulnerable to freezing injury after spring frosts that occurred during the seedling emergence period in one experiment. This study also confirmed earlier work identifying the potential of the herbicides napropamide, pendimethalin, and isoxaben for use on direct seeded ash and sycamore, and the results show the importance of adequate vegetation management for maintaining seedling survival and growth. For winter sowing, protecting seed beds with fleece was found to enhance seedling establishment, but reduced subsequent seedling survival after the protection was removed. Compared with cultivated soil, direct-drilling tree seed between the stubble of preceding cereal crop had no effect on seedling emergence, and increased seedling survival.

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1. Introduction

There has been a revival of interest in Great Britain in using direct seeding to establish broadleaved woodlands, particularly on farmland (Watson, 1996; Willoughby et al., 1996, 2004a), and on amenity sites (La Dell, 1988). Although direct seeding is a potentially cheaper method of woodland establishment than conventional planting, it is often considered to be less reliable. This is mainly because seed germination and seedling establishment are precarious stages in the life cycle of plants (Harper, 1977), and mortality at each stage can be caused by a range of

factors that can vary from place-to-place and year-to-year. A review of direct seeding experiments carried out in Great Britain (Stevens et al., 1990) concluded that conventional planting practices using transplants were more reliable than direct seeding for establishing plantations in lowland Britain. Nevertheless, Willoughby et al. (2004b) have reported some success with direct seeding in establishing sessile oak (*Quercus petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) in trials on reclaimed or former-agricultural land, but less success with Scots pine (*Pinus sylvestris* L.). A recent Danish study on afforestation of farmland has also found encouraging results with direct-seeded oak (*Quercus robur* L.), beech (*Fagus sylvatica* L.), wild cherry (*Prunus avium* (L.) L.) and hawthorn (*Crataegus monogyna* Jacq.) (Löf et al., 2004).

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Seedling establishment is greatly influenced by soil moisture availability and temperature. Several recent studies on direct seeding have focussed on improving the micro-environment for germination by site preparation (Oleskog et al., 2000; Oleskog and Sahlén, 2000; Ammer et al., 2002; de Chantal et al., 2003), and on the benefits of using invigorated seed (Winsa and Sahlén, 2001). Because soil moisture and temperature vary seasonally, the choice of sowing date has an important affect on seedling emergence (Jinks and Jones, 1996; de Chantal et al., 2003). Ideally, sowing should be timed so that seedling emergence coincides with a period of favourable soil temperatures and adequate soil water potentials in spring. Sowing early, when temperatures are below the minimum for germination, delays emergence and so increases the risk of pre-emergence losses of seed to predation and attack by pathogens. The latest safe sowing dates are defined by the occurrence of high temperatures, which may induce secondary dormancy in certain species (Jensen, 2001), and low soil water potentials that increase the risks of desiccation injury and mortality in seeds and newly emerged seedlings. The timing and extent of these limitations will vary with climate and location, but a greater understanding of the factors that limit emergence of tree seedlings should help in defining sites and situations where direct seeding is likely to be successful.

Biotic factors such as pathogens, predation by granivores and herbivores, and competing vegetation also strongly affect the success of direct seeding. Pre-germination destruction of seed by predators can be severe and several potential control measures have been investigated (Sullivan, 1979b; Nolte and Barnett, 2000; Nilson and Hjältén, 2003). Adequate vegetation control can increase subsequent seedling survival and growth, especially with direct seeding on agricultural land (Löf et al., 2004; Willoughby et al., 2004a). Control measures currently rely on the use of herbicides and suitable compounds must provide adequate weed control without adversely affecting tree seedling emergence and survival (Willoughby, 1996). Screening trials using pot-grown seedlings have identified napropamide, pendimethalin and isoxaben as three potentially safe pre-emergent herbicides for use in direct seeding, but tolerance of young seedlings to these compounds requires confirmation in field trials (Willoughby et al., 2003).

In this study, we report the results of two experiments that investigated the effects of sowing date and pre-emergence herbicides on the emergence and survival of ash (*F. excelsior*) and sycamore (*A. pseudoplatanus*) sown on three sites in southern England (throughout, the term ‘seedling emergence’ refers to the appearance of cotyledons above the soil surface in

the field, whereas ‘germination’ refers to radicle emergence and is used for laboratory results). In the first experiment, which was set up on a former pasture site with a moisture retentive soil, we examined the effects of sowing on four occasions from late winter to late spring (i.e. into progressively warmer seedbeds), and results are interpreted in terms of fulfilling any residual chilling requirement for dormancy breakage, the accumulation of thermal time for germination, and the occurrence of early seedling mortality. We also tested the tolerance of emerged seedlings to three pre-emergent herbicides. The second experiment compared the effects of sowing date and herbicides on emergence and survival at three contrasting sites: the moisture retentive site used in the first experiment, a former arable field on a freely draining sandy soil, and a windblown area within a beech (*F. sylvatica*) plantation. In addition, the effects on emergence of a site-specific protection or cultivation treatment was tested at each site, and the effects on seedling survival of an additional herbicide treatment applied in the second year after sowing was tested at one of the test sites where first year emergence was high.

2. Materials and methods

2.1. Site details

A summary of the details of each site is shown in Table 1. The site at Alice Holt was a permanent pasture, and the areas for sowing in Experiments 1 and 2 were prepared by spraying off vegetation that included perennial weeds the preceding summer with up to two applications of herbicide, comprising either 1.8 kg a.i. ha⁻¹ glyphosate (as Roundup ProBiactive, 360 g l⁻¹ glyphosate; Monsanto (UK) Ltd., The Maris Centre, Hauxton Road, Trumpington, Cambridge, UK) with the addition of the adjuvant Mixture B (500 g l⁻¹ nonyl phenol ethylene oxide condensate and 500 g l⁻¹ primary alcohol ethylene oxide condensate; Amega Sciences, Lanchester Way, Royal Oak Industrial Estate, Daventry, Northants, UK) at 2.0% of final spray volume; or 1.0 kg a.i. ha⁻¹ paraquat (as Gramoxone 100, 200 g l⁻¹ paraquat; Syngenta Crop Protection UK Ltd., Whittlesford, Cambridge, UK). Both experimental areas were then ploughed and cultivated to create a tilth suitable for sowing. At Wishangar, weeds growing amongst the stubble of the preceding cereal crop were treated with herbicide, but only the cultivated plots in the Cultivation treatment (see below) were rotovated to create seedbeds. After herbicide treatment of weeds at Blackwood, the ground was scarified to create strips of exposed mineral soil for

Table 1
Details of the three sites used for Experiments 1 and 2

Site name	Latitude and longitude	Elevation (m)	Mean annual rainfall (mm)	Soil description and U.K. Soil Survey Classification (Avery, 1980)	Previous site history
Alice Holt	51°10'26"N; 0°50'57"W	110	705	Podzolic gleyed clay over gravel (714d)	Arable grassland
Wishangar	51°9'6"N; 0°47'59"W	60	705	Well-drained argillic brown sand (554a)	Cereal crop (wheat)
Blackwood	51°10'53"N; 1°14'22"W	110	700	Shallow well-drained silty soil over chalk (343h)	Windblown beech plantation

sowing. The area between the scarified lines contained branch debris and stumps of the windblown trees.

2.2. Experiment 1

2.2.1. Treatments

This experiment was carried out at Alice Holt (Table 1) and investigated the effects of sowing ash and sycamore on four dates in 1997: 24 February, 17 March, 21 April, and 19 May. At each date, seed viability and germination capacity (the percentage of seeds capable of completing germination) was determined over a range of temperatures in laboratory tests. After each sowing, plots were treated with one of five herbicide treatments:

1. untreated, no herbicide application;
2. 0.99 kg a.i. ha⁻¹ napropamide (as Devrinol, 450 g l⁻¹ napropamide; United Phosphorus Ltd., Birchwood Park, Warrington, Cheshire, UK);
3. 2.97 kg a.i. ha⁻¹ napropamide;
4. 2.0 kg a.i. ha⁻¹ pendimethalin (as Stomp 400SC, 400 g l⁻¹ pendimethalin; BASF plc, P.O. Box 4, Earl Road, Cheadle Hulme, Cheadle, Cheshire);
5. 0.3 kg a.i. ha⁻¹ isoxaben (as Flexidor 125, 125 g l⁻¹ isoxaben; Dow AgroSciences, Latchmore Court, Brand Street, Hitchin, Hertfordshire, UK).

2.2.2. Seed pretreatment and laboratory tests

Ash seed (Forestry Commission identity number 95(30)) was pre-treated using standard methods (Suszka et al., 1996) and had received 14 weeks of warm pre-treatment (15–20 °C), followed by 13, 16, 21 and 25 weeks of moist chilling at 3 °C by each sowing date, respectively. Freshly collected sycamore seed (Forestry Commission identity number 96(40)) was stored at 40% moisture content at 3 °C until required for sowing. At each date, the viability of the pre-treating seed was estimated using cut-tests on samples of 50 seeds to determine the sowing rate. Further samples of 50 seeds of each species were sown onto peat-sand compost in seed trays and tested over 42 days for germination at constant temperatures of 5, 10, 15, 20 and 25 °C. At the end of each test, ungerminated seeds were dissected and categorised as either fresh or dead. The final viability was

calculated as the percentage of seeds that had germinated or remained fresh at the end of the test; fresh, ungerminated seeds were assumed to be dormant.

2.2.3. Sowing

The design of the field experiment consisted of 2 species (S) × 4 sowing dates (D) × 5 herbicide treatments (H), replicated in 2 blocks giving a total of 80 plots; plots were arranged in a randomised complete block design. The equivalent of 100 viable seeds, determined from the cut-test results, were sown in each plot. Before each sowing, plots were hand-forked to prepare a tilth suitable for sowing; any existing weeds were removed during this operation. In each plot, seeds were sown in five 1-m drills 15 cm apart at a depth of 1–2 cm; adjacent plots were separated by a 1-m buffer zone. The appropriate herbicide treatments were sprayed on within 24-h of sowing using an Oxford Precision Sprayer fitted with an Allman No. 00 fan nozzle, at a pressure of 50 kPa and in a spray volume of 300 l ha⁻¹, giving a flow rate of 510 ml/min.

At the time of the first sowing, a total of 10 thermistors (five per block) were buried horizontally at 2-cm depth in the buffer zones between plots; these areas were maintained weed-free throughout. Two shielded probes were suspended 30 cm above the ground to record local air temperature. Temperatures were recorded at 10-min intervals using a DL2 logger (Delta-T Devices Ltd., Cambridge, UK), and averaged for each hour.

Once seedling emergence had commenced, weekly counts were made of live and dead tree seedlings. A seedling was considered emerged when the cotyledons had lifted above the soil surface, and dead if the shoot was brown and shrivelled.

2.3. Experiment 2

2.3.1. Treatments

At Alice Holt and Wishangar, the treatment factors investigated were two species (ash and sycamore), sowing date (winter and spring), pre-emergent herbicides (untreated, napropamide and pendimethalin), and a site-specific protection or cultivation treatment (Table 2). At Alice Holt, where emergence was high, an additional application of herbicide was made in the second year after sowing to compare the effects of applying vegetation control for 1 and 2 years. Because of space

Table 2
Treatments applied to the three sites in Experiment 2

Site	Species	Sowing dates	Herbicide treatments	Other treatments
Alice Holt	Ash	17 February 1998	Untreated	Protection: unprotected and plots covered with horticultural fleece
	Sycamore	24 March 1998	Napropamide (2.97 kg a.i. ha ⁻¹); Pendimethalin (2.0 kg a.i. ha ⁻¹)	
Wishangar	Ash	8 December 1997	Untreated	Cultivation: cultivated and uncultivated plots with seed drilled into stubble
	Sycamore	30 March 1998	Napropamide (2.97 kg a.i. ha ⁻¹); Pendimethalin (2.0 kg a.i. ha ⁻¹)	
Blackwood	Ash	10 December 1997 26 March 1998	Untreated After December sowing: napropamide (2.97 kg a.i. ha ⁻¹); after March sowing date: pendimethalin (2.0 kg a.i. ha ⁻¹)	Protection: unprotected and plots covered with light brash cut from <i>Thuja plicata</i> D. Don

See text for a detailed explanation.

constraints, a smaller experiment was set out at Blackwood using just ash and a single herbicide compound at each date, together with a protection treatment (Table 2). It was originally intended to synchronise sowing dates across the three sites, but saturated soil conditions delayed the date of first sowing at Alice Holt.

2.3.2. Seed

Ash seed (Forestry Commission identification number 95(30)) had received 14 weeks of warm pre-treatment followed by 4 (Wishangar and Blackwood) or 13 (Alice Holt) weeks of chilling by the first sowing date, and 17–18 weeks of chilling by the second date. Sycamore was again a freshly collected seed lot (Forestry Commission identification number 97(40)) that was stored at 3 °C. Viability of both species at each sowing date was estimated from cut-tests as described for Experiment 1.

2.3.3. Alice Holt

At Alice Holt, a split plot design was used comprising of 2 sowing dates (D) × 2 protection (P) treatments as main plots, and 2 species (S) × 3 herbicide (H) treatments as sub-plots, replicated twice in two blocks, giving a total of 48 sub-plots. Because of significant seedling mortality caused by frost at the same site in Experiment 1, the protection treatment was included to compare uncovered plots with plots covered with spun polypropylene fleece as a means of protecting seedlings. Sub-plot size was 12 m² and each was separated by a 1-m buffer zone.

At each date, sufficient seeds were broadcast-sown to achieve a rate of 100 viable seeds per square metre, and the herbicide treatments were applied within 5 days of each sowing. The fleece was laid over the protected plots after herbicide application, and was removed once emergence in a plot was judged to be nearly complete to prevent excessive shoot-distortion of emerged seedlings. The second herbicide application was made in spring 1999; this treatment was distributed in a balanced manner across half of the plots that had received napropamide or pendimethalin in the first year. The application was applied in March 1999 and consisted of a tank mix of 2.5 kg a.i. ha⁻¹ atrazine (as Atlas Atrazine, 500 g l⁻¹ atrazine; Nufarm UK Ltd., Crabtree Manorway North, Belvedere, Kent, UK) with 2.5 kg a.i. ha⁻¹ cyanazine (as Fortrol, 500 g l⁻¹ cyanazine; Makhteshim-Agan (UK) Ltd., Unit 16, Thatcham Business Village, Colthrop Way, Thatcham, Berkshire, UK).

Seedling numbers were counted in three 1-m² assessment areas laid out in each sub-plot on four occasions: May 1998 (when emergence was assumed to have finished), August 1998, May 1999, and November 1999. Seedling heights were assessed on up to 20 randomly selected seedlings per assessment plot during August 1998 and November 1999.

2.3.4. Wishangar

A split plot design was again used consisting of 2 sowing dates (D) × 2 cultivation (C) treatments as main plots, and 2 species (S) × 3 herbicide (H) treatments as sub-plots,

replicated twice in two blocks. The cultivation treatment (plots either cultivated or uncultivated) at Wishangar was applied to test for any effects of direct-drilling tree seed into the stubble remaining from the previous cereal crop. Seeds were sown into three drills per sub-plot spaced 0.5 m apart at a rate of 100 viable seeds per square metre; sub-plots were 6 m long, and separated by a 1 m buffer zone. Seedling numbers were counted in three 1-m² assessment plots in each sub-plot, but only in May and October 1998, after which the field was returned to agriculture.

2.3.5. Blackwood

A randomised complete block design was used for this smaller experiment using only ash at Blackwood, comprising 2 sowing dates (D) × 2 herbicide (H) × 2 protection (P) treatments, replicated in four blocks. The herbicide treatment consisted of plots receiving either no herbicide, or a single herbicide treatment of 2.97 kg a.i. ha⁻¹ napropamide after the December sowing, or 2.0 kg a.i. ha⁻¹ pendimethalin after the March sowing. The protection treatment was applied to test if a light covering (15–30 cm depth) of pruned branches from a nearby crop of western red cedar (*Thuja plicata* D. Don.) could improve seedling establishment and survival on the shallow well-drained soil at this site.

Each treatment plot consisted of three scarified lines and sufficient seeds were sown as single drills down each line to achieve 20 viable seeds per metre. The total number of viable seeds sown per plot was 1200.

2.4. Statistical and data analyses

2.4.1. Field emergence and seedling survival data

Statistical analyses of the significance of treatment factors and their interactions on seedling emergence and survival at each site were carried out using Genstat (Payne et al., 1993) using either generalised linear models (GLM) or the generalised linear mixed model procedure (GLMM) as appropriate. In a generalised linear model, the deviance has the same role as sums of squares in a regression analysis or analysis of variance, and the significance of adding models terms was assessed by analysis of deviance using corresponding probabilities from the *F*-distribution. For mixed models (GLMM), the significance of adding terms was assessed by Wald tests using χ^2 probabilities. Differences between means were tested using pairwise *t*-tests done on the scale of the linear predictor; for convenience, untransformed means of percentages are presented in Section 3. Seedling emergence and survival data were analysed using GLMM with treatment factors as fixed effects, and block and plot factors as random effects. There were, however, highly significant effects of blocks on seedling emergence in both experiments. Consequently, for emergence data only, blocks were treated as a treatment factor representing different locations within a site and were included as fixed effects in GLMMs in Experiment 2, and in a GLM in Experiment 1.

In Experiment 2 at Alice Holt, where seedling numbers were assessed on three further occasions after the first emergence

assessment, seedling survival was analysed for each of the three corresponding periods (Period 1: first summer after emergence; Period 2: the following winter/spring; and Period 3: the second summer) as the percentage survival of all seedlings that were present at the start of each period. In some assessment plots, seedling numbers apparently increased over certain periods, indicating further recruitment of seedlings, and this invalidates modelling with the binomial error distribution. Consequently, seedling counts at the end of a period were analysed using the Poisson error distribution and log link function, with the logarithm of seedling counts at the start of the period set as an offset in the GLMM. Seedling heights were analysed using GLMM to estimate treatment effects.

2.4.2. Laboratory germination data and thermal time estimation

In the laboratory tests, differences in viability and germination between species, sowing dates and temperatures were investigated using generalised linear models (GLM) with binomial error distribution. To investigate the relationship between seedling emergence in the field in Experiment 1 and thermal time, the laboratory germination data were used to estimate the base temperature T_b , which is the temperature at which the germination rate falls to zero and is assumed to be constant for a given seed lot at suboptimal temperatures. There were too few test temperatures for accurately estimating T_b from linear regressions of the rate of germination for each fifth or tenth-percentile against temperature, which is a frequently used estimation method (Garcia-Huidobro et al., 1982; Covell et al., 1986). Values of T_b can also be estimated iteratively using repeat probit regressions, varying T_b until the best fit is obtained (Ellis et al., 1986). In this study, the equation (Eq. (1)) that describes the distribution of thermal time requirement within a seed population was generalised and re-paramaterised (Eq. (2)) to allow direct estimation of T_b .

$$\text{probit}(g) = k + \frac{(T - T_b)t_g}{\sigma} \quad (1)$$

where $\text{probit}(g)$ is the germination in probit units, $(T - T_b)t_g$ the accumulated thermal time (degree-days) for a particular germination percentage g , σ the standard deviation of thermal time for germination, and k is a constant.

$$\text{cdf}(g) = \beta_1 + \beta_2(Tt) - \beta_3t \quad (2)$$

where cdf is an appropriate cumulative density function, such as the probit link function for the normal distribution, for a particular germination percentage g ; $\beta_1 = k$; $\beta_2 = 1/\sigma$; and $\beta_3 = \beta_2 T_b$.

After fitting this model, T_b can be estimated directly as:

$$T_b = \frac{\beta_3}{\beta_2}$$

For sycamore, both the probit and complementary log–log link function were fitted to laboratory germination data obtained at sub-optimal temperatures ($\leq 20^\circ\text{C}$) using the GLM procedures of Genstat (Payne et al., 1993); the complementary log–log link function gave the best fit, indicating a skewed distribution of

thermal times for germination. Although the rate of ash germination increased with temperature up to 20°C , germination capacity decreased due to an increase in dormancy at warmer temperatures (see Section 3), with no test achieving complete germination of all viable seeds. Consequently, the underlying base temperature for ash was estimated by fitting Eq. (2) as an ordinary linear regression to cumulative germination data that was restricted to sub-maximal germination counts at each test temperature; the fitted data used in the linear regression are shown as solid symbols in Fig. 2a.

The estimated values of T_b were used to calculate cumulative thermal time for the field emergence of both species after each sowing date. The extent to which there was a common relationship between emergence and thermal time was determined graphically by plotting emergence for each sowing date against the cumulative thermal time since sowing. The analysis was restricted to emergence data from only one of the blocks in Experiment 1 because adverse soil conditions resulted in much lower emergence in the other block (see Section 3). The soil temperature data were also used to calculate the accumulation of chill units to determine the quantity of dormancy-breaking chilling that was available after each sowing date. The exact temperature response for dormancy breakage of ash and sycamore seed is unknown, but published studies on other deeply dormant species (Seeley and Damavandy, 1985; Pritchard et al., 1996) show that dormancy is broken most rapidly at temperatures between 0 and 5°C , with effectiveness decreasing at warmer temperatures. In this study, temperatures between 0 and 5°C were assumed to be equally effective at accumulating a chill unit for every hour's exposure, the rate of accumulation was proportionately decreased to zero as temperatures increased from 5 to 10°C (no soil temperatures below 0°C were recorded in this study).

3. Results

3.1. Experiment 1

3.1.1. Seed dormancy status

Mean percentage viability of both species at each sowing date is shown in Table 3. Analysis of deviance showed that viability did not differ significantly between test temperatures, but differed significantly between species ($F. pr. < 0.001$) and sowing date ($F. pr. < 0.01$), with no significant interaction between these two factors. Overall, the viability of ash (74%)

Table 3

Percentage viability of ash and sycamore seeds used in Experiment 1 at each sowing date averaged across five test temperatures determined in the laboratory

Sowing date	Ash	Sycamore
Date 1	75.7 a	72.4 a
Date 2	72.0 a	67.1 b
Date 3	73.3 a	63.0 b
Date 4	74.3 a	63.3 b

Note. Values with different letters were significantly different ($P \leq 0.05$) in pairwise t -tests done on the scale of the linear predictor.

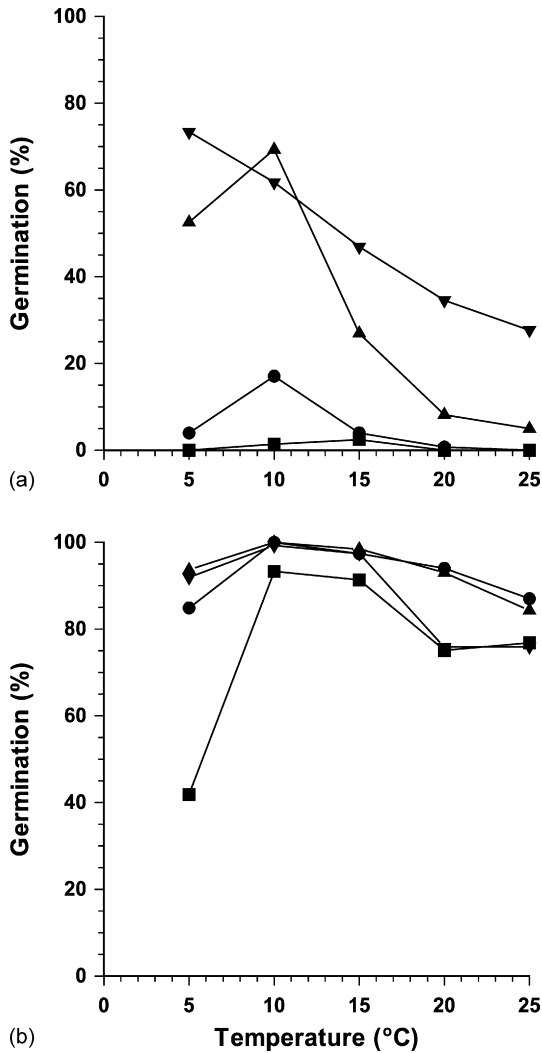


Fig. 1. The germination capacity (% of viable seeds) in Experiment 1 at each sowing date of (a) ash, and (b) sycamore after 42 days at constant temperatures of 5, 10, 15, 20, and 25 °C in laboratory tests. (■) Date 1, (●) Date 2, (▲) Date 3, and (▼) Date 4.

was higher than sycamore (66%), and average viability was about 5% higher at the first date.

In ash, there was a substantial difference in dormancy status between sowing dates. At the first date, few ash seeds germinated at any test temperature (Fig. 1a), but percentage germination progressively increased with prechill duration to between 50 and 70% of viable seed at 5 and 10 °C by the last two sowing dates. Germination capacity also increased at warmer temperatures at the third and fourth sowing dates; however, above 10 °C the germination percentages at the third and fourth sowing dates were substantially lower than at temperatures below 10 °C. In contrast, sycamore was much less dormant with nearly 90–100% germination at 10 and 15 °C on all dates (Fig. 1b). However, germination capacity at 5 °C nearly doubled after the first date, suggesting that the prechill requirement had not been fully met at the time of the first sowing. The slight decline in percentage germination of sycamore at 20 and 25 °C at the final sowing date was not

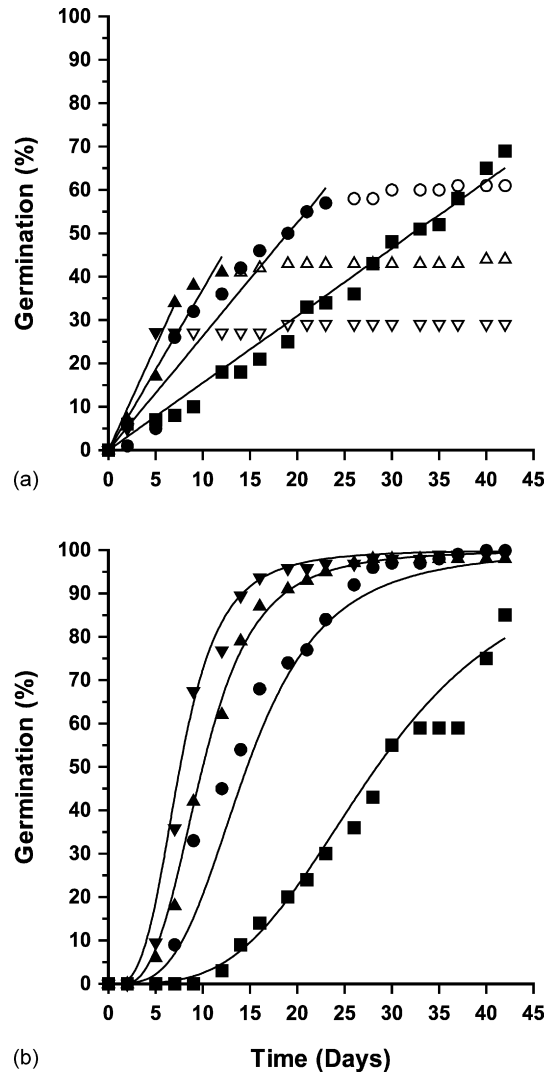


Fig. 2. Actual (points) and fitted (curves) time courses for germination (percentage of viable seeds) of (a) ash, and (b) sycamore at constant temperatures of (■) 5 °C, (●) 10 °C, (▲) 15 °C, and (▼) 20 °C in laboratory tests. In Fig. 2a, Eq. (2) was only fitted as a linear regression to data represented by the solid points (see Section 2 for further details).

significantly different from tests carried out at the previous two sowing dates.

The thermal time model gave a close fit to the time course of germination at each test temperature (Fig. 2). Estimated base temperatures were 0.12 ± 0.064 °C for ash, and 0.28 ± 0.190 °C for sycamore; these values were used to calculate cumulative thermal time from each sowing date in the field experiment (see below).

3.1.2. Soil temperatures

Mean soil temperatures remained between 5 and 10 °C until the end of March, and then increased to between 15 and 20 °C after the end of April (Fig. 3). Although there were several air frosts recorded throughout February–April, the severest occurred on 21 April and 7 May when air temperature at 30 cm above the seed beds fell to -6 and -4 °C, respectively. Minimum soil temperatures at probe-depth remained above freezing on both occasions, probably because of the large

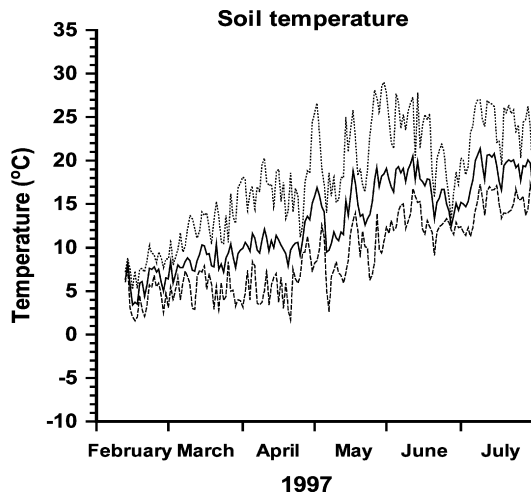


Fig. 3. Daily maximum (· · ·), average (—), and minimum (— —) soil temperatures recorded at 2 cm depth in Experiment 1.

specific heat capacity due to high soil water content. Maximum daily soil temperatures exceeded 25 °C at an increasing frequency from early May onwards.

3.1.3. Seedling emergence

Analysis of deviance showed highly significant differences in emergence between blocks and sowing dates, with a significant interaction between these two factors and species (Table 4 and Fig. 4). The difference in emergence between the two blocks was maintained across all four sowing dates and was most likely caused by local variation in soil drainage. The lower-emergence block (Block 2), which had an average of only 18% emergence overall, was placed in a wetter part of the field, and at times was so wet that standing water was present after persistent winter rain. In contrast, the average emergence in the better-drained block (Block 1) was almost double at 34%. Generally, emergence increased with each successive sowing date up to Date 3, and then decreased at the final date, and ash emergence tended to be higher than

Table 4
The analysis of deviance for seedling emergence in Experiment 1

Model term	d.f.	Deviance ratio	Approx. <i>F</i> probability
Block (B)	1	84.56	<0.001
Species (S)	1	4.23	0.062
Sowing date (D)	3	54.65	<0.001
Herbicide (H)	4	3.42	0.044
BxS	1	16.40	0.002
BxD	3	0.70	0.568
SxD	3	14.16	<0.001
BxH	4	4.15	0.024
SxH	4	2.84	0.072
DxH	12	2.08	0.110
BxSxD	3	8.73	0.002
BxSxH	4	1.10	0.402
BxDxH	12	2.67	0.051
SxDxH	12	3.30	0.024

Note. Significant effects are shown in bold.

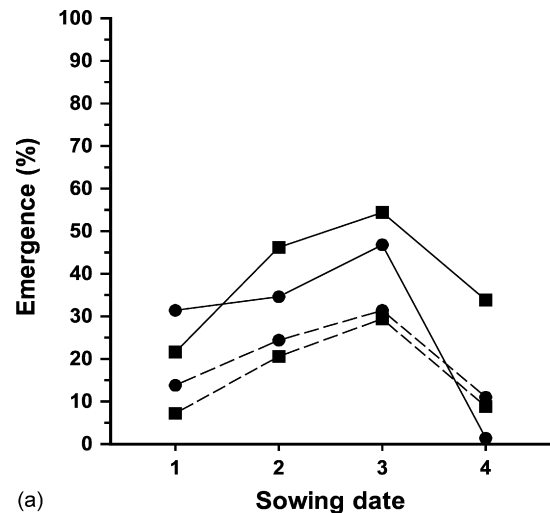


Fig. 4. Maximum percentage emergence in each block of (■) ash and (●) sycamore seeds sown on four occasions in Experiment 1. Solid lines: Block 1; dashed lines: Block 2.

sycamore in the better-drained Block 1 (Fig. 4). Highest emergence was 55% for ash sown on Date 3 in the better-drained block; lowest emergence was in sycamore sown at the final sowing date (Fig. 4). The low emergence after the final sowing date was not uniform across all herbicide treatments as there was a marginally significant interaction between species, sowing date and herbicide, and between blocks and herbicide (Table 4). In the higher-emergence block, 48% of sycamore seedlings emerged in the pendimethalin treatment from the last sowing date, compared with either the untreated control (1%) or the other herbicide treatments (average 1.5%); sycamore emergence was less than 3% for all herbicide treatments in the other block after the same date. Otherwise herbicide treatments had no significant effect on emergence of either species.

The time courses for seedling emergence and mortality are shown in Fig. 5. Apart from Date 1, the length of time between sowing and the emergence of the first seedlings was similar for both species and decreased with successive sowing dates from about 35 days for Date 2, to 16 days for Dates 3 and 4. For Date 1, however, ash began emerging nearly a month later (55 days after sowing) than sycamore, which began emerging after about 30 days.

The onset of mortality and the cessation of emergence often coincided with weather related events, particularly frost and high soil temperatures (Fig. 5). Within 3 to 4 weeks after the frost in early May, all of the ash seedlings that had emerged after the first and second sowing dates had died (Fig. 5a). In sycamore, seedling mortality also increased after this frost, but only about 40–50% of the emerged seedlings eventually died (Fig. 5b). After Date 3, where few seedlings had emerged by the time of the frost, less than 15% of seedlings of either species died. The cessation of seedling emergence usually coincided with periods of high soil temperature (Fig. 5). The maximum soil temperature recorded during any emergence period was always less than 25 °C. Apart from sycamore sown on the first date, emergence always ceased when the maximum soil

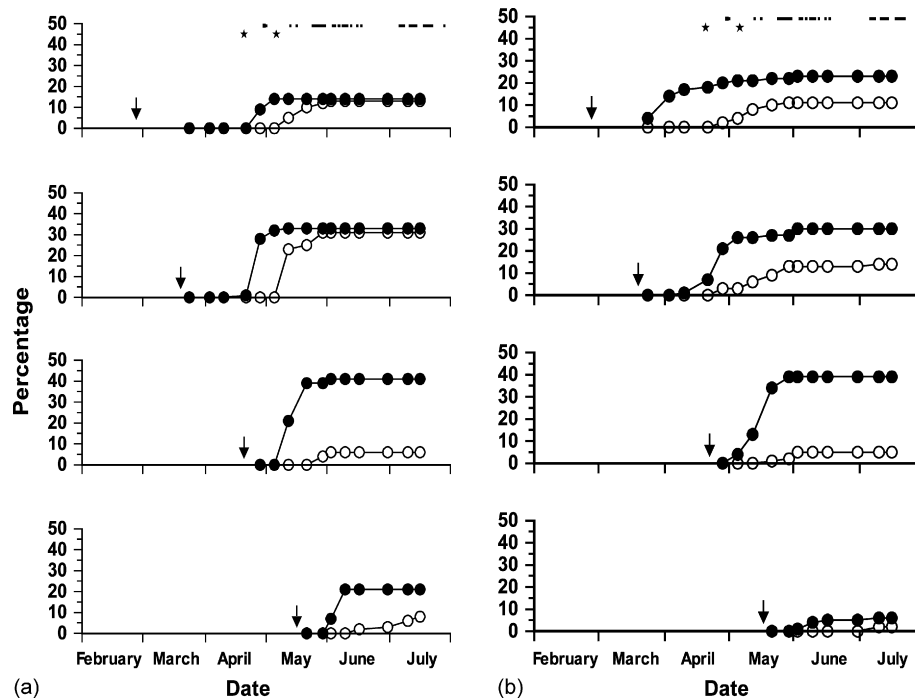


Fig. 5. Cumulative emergence (solid symbols) and death (open symbols) of seedlings over time of (a) ash, and (b) sycamore sown on four dates in Experiment 1. Each point is averaged across herbicides and blocks; emergence and death are expressed as percentages of viable seeds sown. Sowing dates are indicated by arrows; dates with air frosts are shown by *; dates when maximum soil temperatures exceeded 25 °C are marked by solid points at the top of the first graph in each figure.

temperatures exceeded 25 °C for the first time. The maximum soil temperatures recorded in the assessment interval immediately before emergence stopped were 26.6, 26.6, 25.8, and 27.7 °C for ash sown on Dates 1–4; and 26.6, 25.8, and 27.8 °C for sycamore on Dates 2–4. The earliest sown sycamore stopped germinating nearly a month before soil temperatures began to exceed 25 °C, and the maximum temperature during this emergence period was 18.8 °C.

Despite this premature termination, sycamore emergence showed a reasonable relationship with accumulated thermal time (Fig. 6b), indicating that variation in the time to start of emergence is explained by differences in soil temperature between sowing dates. Sycamore emergence required about 150 degree-days for the start of seedling emergence, but the premature termination of emergence does not allow the complete relationship to be described. The cumulative emergence of ash also tends towards a common relationship with thermal time (Fig. 6a). The threshold for the start of emergence after the last two sowing dates is similar to sycamore at around 150 degree-days, hence the similarity of the time to first emergence of both species at the later sowing dates. However, the threshold increased to between 200 and 300 degree-days for the second sowing, and was nearly 500 degree-days for the earliest sowing. This suggests that seed from the earliest sowings had different thermal responses (base temperatures) than the later sowings. Estimates of the number of chill units accumulated by seed during pre-treatment by the time of each sowing, and subsequently in the seedbed from sowing to first emergence are shown in Table 5. The threshold for dormancy breakage of ash is estimated to be around 20 chill-weeks, based on the germination tests for Date 3, which had

received nearly 21 weeks of chill at sowing. The two earlier sowings were about 7 and 4 weeks short of this threshold, respectively, at the time of sowing. Date 2 seed acquired a further two chill-weeks after sowing, bringing it closer to the threshold, whereas the chill accumulation for ash seed at Date 1 was short by about four chill-weeks.

3.2. Experiment 2

3.2.1. Blackwood

Fewer than 2% of the sown ash seed emerged. Attempts at recovering ungerminated seed were unsuccessful and it was concluded that most of the seed had been predated on this woodland site. Subsequent work in nearby sites has shown that granivores, mainly *Apodemus sylvaticus*, are active seed predators in this woodland environment (Jinks, unpublished).

3.2.2. Alice Holt

Overall emergence in this experiment was high at 68%, with highly significant effects of block and sowing date, together with a marginally significant interaction between them

Table 5

The number of chill-weeks accumulated by ash seed during pre-treatment and between sowing and the date of first emergence in Experiment 1

	Chill-weeks			
	Date 1	Date 2	Date 3	Date 4
Pre-treatment	12.6	15.6	20.6	24.6
Seed bed	3.7	2.1	0.8	0.1
Total	16.3	17.7	21.4	24.7

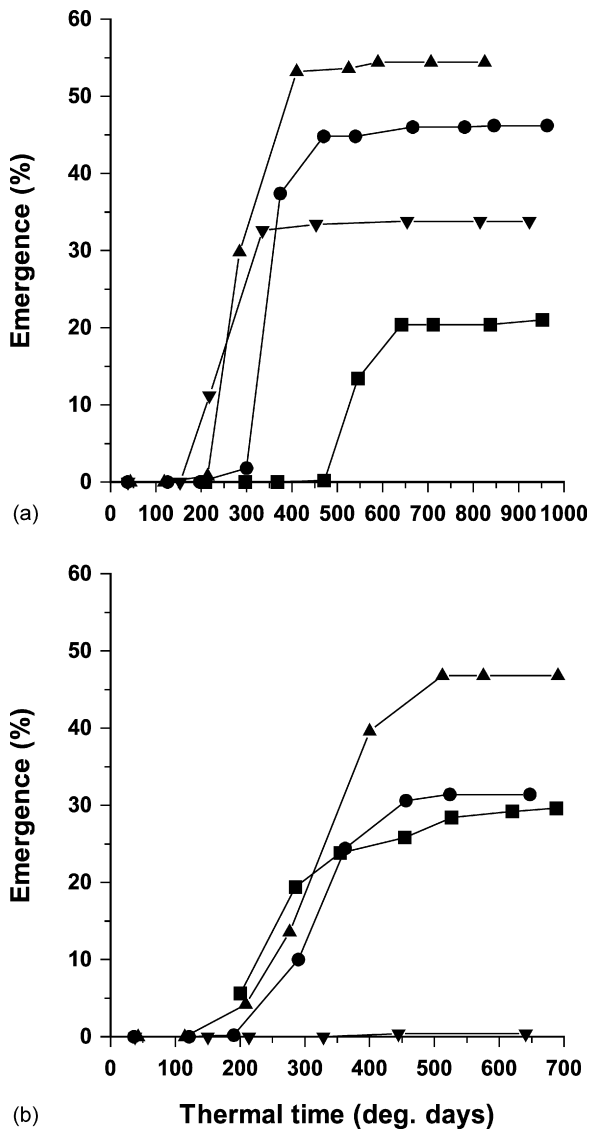


Fig. 6. Seedling emergence plotted against cumulative thermal time (degree-days) of (a) ash and (b) sycamore seedlings sown on four dates in Experiment 1. Emergence data is restricted to Block 2. (■) Date 1, (●) Date 2, (▲) Date 3, and (▼) Date 4.

Table 7

The interactions between blocks and sowing date, and protection and sowing date, on percentage seedling emergence at Alice Holt in Experiment 2

	Sowing date		Mean
	February	March	
Block			
Block 1	43.9 a	74.4 c	59.2
Block 2	67.2 b	86.2 c	76.7
Protection			
Unprotected	43.1 a	79.0 c	61.1
Fleece	68.0 b	81.7 c	74.9
Mean	55.6	80.3	Overall mean = 68.0

Note. Within each interaction, values with different letters were significantly different ($P < 0.05$) in pairwise *t*-tests done on the scale of the linear predictor.

(Table 6.) Emergence after the March sowing was just over 80% with no significant difference between the two blocks (Table 7). But emergence after sowing in February was significantly lower (44%) in Block 1, which was located in a wetter part of the field and where seed would have been exposed to waterlogging, than in the other better-drained block (67%). There were no significant differences in emergence between the two species, or the herbicide treatments. But there was a marginally significant interaction between protection and sowing date (Tables 6 and 7), due to lower emergence in unprotected plots compared with plots covered in fleece after the February sowing date. However, any advantage of fleece was offset by a marginally significant reduction in seedling survival over Period 1 (Table 6) when 64% fleeced-seedlings survived compared with 94% in plots that were not covered after sowing.

Unlike emergence, seedling survival did not differ significantly between the two blocks, but survival over Periods 1 and 2 was significantly improved by herbicide application (Tables 6 and 8). Over the first summer (Period 1) an average of 90% of the seedlings in plots treated with either herbicide survived compared with 56% in untreated plots (Table 8). Seedling height of both species by the end of the first summer was also significantly increased by herbicide application (Table 8). Over Period 2, the first winter and spring after emergence, plots that had received just the original application

Table 6

Significance of main effects and interactions of sowing date, herbicides and protection on the emergence and survival of ash and sycamore seedlings at Alice Holt in Experiment 2

Percentage emergence				Percentage survival							
Model term	d.f.	Wald/d.f.	χ^2 prob.	Model term	d.f.	Period 1 (May 1998–Aug 1998)		Period 2 (Aug 1998–May 1999)		Period 3 (May 1999–Nov 1999)	
						Wald/d.f.	χ^2 prob.	Wald/d.f.	χ^2 prob.	Wald/d.f.	χ^2 prob.
Blocks (B)	1	15.38	<0.001								
Protection (P)	1	3.97	0.046	Protection (P)	1	4.27	0.039	0.32	0.575	3.91	0.048
Species (S)	1	0.07	0.787	Species (S)	1	1.78	0.183	0.05	0.816	0.07	0.798
Herbicide (H)	2	0.39	0.675	Herbicide (H)	2	7.37	<0.001	11.95	<0.001	0.34	0.714
Sowing date (D)	1	13.12	<0.001	Sowing date (D)	1	1.04	0.309	0.76	0.384	0.83	0.362
BxD	1	4.64	0.031	PxD	1	2.94	0.086	0.16	0.692	7.07	0.008
PxD	1	4.14	0.042								

Note. Probabilities for significant effects are shown in bold; only significant higher order interactions are shown.

Table 8
The effects of herbicide treatments on percentage seedling survival and seedling height over three periods at Alice Holt in Experiment 2

First-year herbicide treatments	Period 1 (May 1998–August 1998)			Second-year herbicide treatments	Period 2 (August 1998–May 1999)		Period 3 (May 1999–November 1999)		
	Survival (%)	Height (cm)			Survival (%)	Survival (%)	Height (cm)		
		Ash	Sycamore				Ash	Sycamore	
Control	56.1 a	5.0	8.2	Control	58.9 a	96.0 a	11.3	12.4	
Napropamide	91.7 b	7.3	13.5	Single application	80.0 b	89.4 a	15.4	24.1	
Pendimethalin	88.6 b	7.3	14.2	Double application	110.7 c	87.2 a	26.7	34.7	
S.e.d.		0.82					2.30		

Note. Survival percentages within each period with different letters were significantly different in pairwise tests done on the scale of the linear predictor; values are percentages of all seedlings that were alive at the start of each period. Heights were measured at the ends of Periods 1 and 3. Significance (GLMM) of the interaction between species and herbicide was χ^2 prob. < 0.001 for height at the end of Period 1, and χ^2 prob. = 0.014 for Period 3. S.e.d. = average standard error of difference.

of pre-emergent herbicide maintained a significantly higher survival rate compared with untreated plots (Table 8). Those given a second application apparently gained seedlings, probably because the additional reduction in competition from weeds either favoured survival, or facilitated assessment, of any new seedlings that emerged in the second spring after sowing. Over Period 3, the second summer of growth, overall survival was about 90% and was unaffected by herbicide treatment, but there was a significant interaction between protection and sowing date (Table 6) due to a 15% lower survival of seedlings in the March sown \times unprotected treatment combination. The second application of herbicide significantly increased ash and sycamore heights by 2.4 and 2.8 times, respectively, compared with untreated seedlings.

3.2.3. Wishangar

Overall seedling emergence (27%) was much lower at this site (Table 10); emergence of ash (23%) was also significantly lower than sycamore (29%). There was again a highly significant difference in emergence between the blocks, and between the two sowing dates, but with no significant interaction between the two factors (Table 9). The freely drained soil at this site was never waterlogged during winter, so reasons for the block differences are less clear than at Alice Holt, but may have reflected local variation in soil moisture availability during emergence. Unlike at Alice Holt, sowing in winter (December) resulted in higher emergence than sowing in spring (March) (Table 10), again suggesting that

Table 10
The mean percentage seedling emergence at Wishangar in Experiment 2 for each Sowing date and Block

Block number	Sowing date		Mean
	December	March	
Block 1	41.3	25.4	33.4
Block 2	25.6	13.5	19.5
Mean	33.5	19.4	Overall mean = 26.5

soil water deficits and possibly higher soil temperatures on this particular soil type were more limiting at this site. Greatest emergence was 41% in seed sown in December in Block 1 (Table 10).

Unlike the Alice Holt site, subsequent survival of emerged seedlings until the following autumn was unaffected by herbicide treatment but differed significantly between ash and sycamore, with a marginally significant interaction between species, cultivation and sowing date (Tables 9 and 11). Overall survival of ash was only 12%, compared with 78% for sycamore and the lowest survival of both species occurred in cultivated plots sown in March (Table 11). Unlike survival, there was a highly significant ($P < 0.001$) effect of herbicide treatment on the height of sycamore seedlings by October (ash was not analysed because of the low survival). Untreated sycamore seedlings reached a mean height of 7.9 cm, while seedlings in plots treated with napropamide and pendimethalin reached 10.6 and 10.8 cm, respectively.

Table 9
Significance of main effects and interactions of sowing date, herbicides and cultivation on the emergence and survival of ash and sycamore seedlings at Wishangar in Experiment 2

Percentage emergence				Percentage survival			
Model terms	d.f.	Wald/d.f.	χ^2 prob.	Model terms	d.f.	Wald/d.f.	χ^2 prob.
Blocks (B)	1	36.53	<0.001				
Cultivation (C)	1	0.96	0.327	Cultivation (C)	1	0.03	0.853
Species (S)	1	4.96	0.026	Species (S)	1	110.27	<0.001
Herbicide (H)	2	0.39	0.675	Herbicide (H)	2	0.34	0.708
Sowing date (D)	1	40.63	<0.001	Sowing date (D)	1	0.11	0.737
				CxSxD	1	5.35	0.021

Note. Probabilities for significant effects are shown in bold; only the significant higher order interaction is shown.

Table 11

The interaction between species, sowing date, and cultivation on percentage seedling survival at Wishangar

Species and sowing date	Cultivation	
	Cultivated	Uncultivated
Ash		
December	10.1 a	6.0 a
March	2.1 a	16.6 b
Sycamore		
December	81.6 c	82.3 c
March	57.7 c	77.8 c

Note. Means with different letters were significantly different in pairwise *t*-tests done on the scale of the linear predictor.

4. Discussion

Results from these experiments show that seed survival, seedling emergence, and early seedling survival are all critical phases to the success of direct seeding. The particular factors that caused losses differed between each phase, with some operating on different spatial scales.

In many direct-seeding studies, outcomes are dominated by predation of seed by granivores like rodents, especially in forest and woodland situations (Sullivan, 1979a; Nilsson et al., 1996). Seeds of both ash and sycamore are susceptible to predation by small mammals (Gurnell, 1979; Tapper, 1996; Hulme and Borelli, 1999; Hulme and Hunt, 1999). Although not tested directly, seed predation may have been the reason for very low seedling emergence at the woodland site at Blackwood. However, greater emergence at the two agricultural sites, suggests that seed removal by granivores may be less significant on farmland. At Wishangar, arable farming operations may have reduced the population of small mammals since cereal harvesting in particular has been shown to increase animal predation of wood mice following removal of the cover afforded by the crop, as well as encourage emigration of mice away from harvested fields (Tew and McDonald, 1993). But seed predation may still be locally important on farmland, particularly in situations where the surrounding habitat can support populations of granivores (Löf et al., 2004). Local conditions may also reduce predation risk: the apparent lack of seed predation at Alice Holt may in part be due to rodent predation by domestic cats from nearby housing that were often seen using the field as a hunting ground.

Seed survival and seedling emergence were sensitive to extremes of soil moisture. At Alice Holt, the reduced seed survival in sections of the field with saturated soils during winter show that both ash and sycamore seeds are sensitive to low soil aeration, with ash probably being less tolerant than sycamore. There appear to be few studies showing the intolerance of tree seeds to waterlogging, although there is much field and laboratory evidence that survival of seeds of plants from terrestrial habitats is much reduced in wet soil, due to attack by pathogens and anoxia under conditions of low air-filled porosity (Thompson, 2000). In soils prone to waterlogging, the seed environment can be improved by appropriate

cultivation techniques such as raised seedbeds and installation of drains. Alternatively, direct seeding might be restricted to species such as *Alnus glutinosa* (L.) Gaertn. with seeds that require high soil water content for germination, and whose seedlings may survive short periods of flooding (McVean, 1955, 1956)

The importance of maintaining adequate soil moisture during the establishment of direct sown tree seed is clearly demonstrated by several studies on the effects of different seed bed conditions and topographies on the establishment of direct sown seed (e.g. Wright et al., 1998; Ammer et al., 2002; Nagamatsu et al., 2002; de Chantal et al., 2003). In this study, overall emergence was much less on the freely drained sandy soil at Wishangar compared with the clay soil site at Alice Holt. However, the extent to which the reduced emergence at Wishangar was due to pre-emergent losses of viable seed or failure at emergence is unknown, though it is probable that effects of soil water deficits on emergence was the more important factor. In the absence of irrigation, soils with low moisture capacities like the sandy soil at Wishangar may be unsuitable for establishing many tree species by direct sowing.

In Experiment 1, the duration of seedling emergence was strongly affected by the occurrence of high soil temperatures, with emergence ceasing once maximum daily soil temperatures at 2 cm exceeded 25 °C. Only sycamore sown on the first sowing date had completed seedling emergence before exposure to these high soil temperatures. Similar responses to high temperature have been reported for nursery emergence of *Picea sitchensis* [Bong.] Carr. (Jinks and Jones, 1996) and *P. sylvestris* (Vaartaja, 1954); in the former case, seedling emergence ceased once soil temperatures exceeded 35 °C. It is unknown to what extent the ungerminated seeds were dead, or had returned to the dormant state and would have been able to germinate after a second period of chill the following spring. In the laboratory germination tests, incubation at high temperatures had no significant effect on seed viability of either species; however, seeds were not tested at temperatures greater than 25 °C, so the upper cardinal point is unknown. In the laboratory tests on ash, dormancy increased at constant temperatures above 10 °C, suggesting that warm soil temperatures may have induced secondary dormancy in ungerminated ash seeds (Piotto, 1994). So for ash at least, a proportion of the ungerminated seed that remained after high soil temperatures may have been dormant and viable. In species like *Acer platanoides* L., which shows a similar inhibition of germination at temperatures above 10–15 °C, a proportion of ungerminated seed will germinate after a second chilling period as a consequence of further release from primary dormancy and induced secondary dormancy (Jensen, 2001). In the second experiment at Alice Holt, there was an apparent gain in seedling numbers in the second spring, which suggests that a proportion of the ungerminated seed remained viable, but dormant, and germinated after a second period of chilling. In a trial that investigated sowing tree seeds simultaneously with a cereal crop, Willoughby et al. (2004b) also found significant second year emergence from pre-treated ash, but not from sycamore sown at the same time. The apparent lack of second year

emergence in sycamore, together with its high germination capacity at temperatures as high as 25 °C, suggests that induced therm dormancy was not a significant cause of emergence cessation in warm soil. Sycamore seed is recalcitrant (Suszka et al., 1996) and so would be susceptible to desiccation injury if high soil temperatures are accompanied by low soil water potentials in the surface layers of soil.

The date at which soil temperatures begin to exceed 25 °C defines the time by which emergence should be finished. In Experiment 1, the first occurrence of maximum soil temperatures above 25 °C was in late April, with the frequency of occurrence increasing during May. Assuming a base temperature of 1 °C, and a thermal time requirement of 500 degree-days to complete emergence, backwards calculation from the date of the first occurrence of high soil temperature suggests that the latest safe sowing date in Experiment 1 would have been 3 March. Earlier sowings of fully pre-treated seeds, when soil temperatures are low, would have proportionately less benefit because of the longer time needed to accumulate thermal time. Results from Experiment 1 also showed that there can be an increased risk of insufficient dormancy breakage when a partially pre-treated dormant species like ash is sown early. Inevitably, the choice of sowing date is a compromise between sowing early enough to allow emergence to finish before the occurrence of high soil temperatures, against sowing too early, which exposes seed to pre-emergence losses. If the earliest sown ash had been fully pre-treated, its emergence would have been expected to have begun about a month earlier, and so have achieved higher emergence.

In practice, unfavourable conditions, such as saturated soils, in winter and early spring may prevent early sowing, so other possibilities can be considered to increase the chance of successful emergence when sowing is delayed. Firstly, the seedbed environment could be modified by sowing beneath the canopy of a mature stand or other nurse crop, or by applying some form of shade to delay the occurrence of inhibitory soil temperatures; however, the latter may be impractical on a large scale and the results with fleece show that covering materials may have negative effects on subsequent seedling survival. Secondly, the length of time after sowing for emergence to start could be shortened, so allowing later sowing, by supplying part of a seed lot's thermal time requirement before sowing using a suitable form of priming treatment (Heydecker, 1972). For example, improved emergence of direct sown *P. sylvestris* can be achieved by sowing invigorated seed in combination with microsite preparation (Winsa and Bergsten, 1994; Winsa and Sahlén, 2001).

Seedling survival and growth were affected by both biotic and environmental factors. Some, like late spring frost injury, occurred shortly after emergence, others like losses due to weed competition continued over longer time periods. The occurrence of late spring frosts is unpredictable and the complete killing of ash in Experiment 1 shows the vulnerability of direct sown seedlings in open field conditions to extremes of weather, unlike in a nursery where sensitive crops can be protected from freezing injury by measures like covering and irrigation. In the second experiment at Alice Holt, seedlings were not exposed to

a late frost event, so possible protective benefits of covering seedbeds with fleece were not tested. Although fleece enhanced seedling emergence when applied after the first sowing date in February, this benefit was offset by lower seedling survival after the fleece was removed. Even though more-or-less similar proportions of ash and sycamore emerged at Wishangar, subsequent survival of ash seedlings was very poor, suggesting that light freely drained soils are unsuited for direct seeding ash. While cultivation had no effect on seedling emergence, it reduced the survival of seedlings that emerged after the second sowing date, suggesting that soil disturbance might have had a negative effect on soil water relations. Potential benefits of direct-drilling tree seed without cultivation between the stubble of cereal crops needs to be confirmed for other soil types.

Napropamide, pendimethalin and isoxaben are all post-sowing pre-emergence herbicides, used to control germinating weed vegetation whilst allowing tree seed to germinate unharmed. In the experiments reported here, seedling survival and growth benefited from the vegetation control these herbicides gave, without any apparent detrimental effect on seedlings of the herbicides themselves. These results confirm the importance of adequate vegetation management for the successful establishment of direct sown trees on farmland and amenity sites (La Dell, 1988; Willoughby, 1996; Löf et al., 2004; Willoughby et al., 2004a, b). They also support earlier work (Willoughby et al., 2003) identifying the potential for napropamide, pendimethalin and isoxaben for use on direct seeded ash and sycamore.

Unlike seedling emergence, subsequent survival did not differ between blocks within sites and so was unaffected by local variation in the soil environment, demonstrating that there are patches with soil conditions that are unsuitable for seed survival and germination, but that are then suitable for subsequent seedling survival. This is an example of a discordant relationship between seed and seedling survival (Schupp, 1995). Locations with saturated soil in winter were in effect filtered out from carrying higher densities of seedlings that were more tolerant of waterlogged soil the following winter. The extent to which such conflicts arise in response to factors like soil conditions may well differ between species. Such local differences in environmental conditions, together with differential species responses, will create variation in seedling density and composition across a site, which enhances the 'natural' appearance of new woodland established by direct sowing mixtures of species compared with traditional transplanting methods. Such variation is a potential advantage for creating native woodland, but might be a disadvantage when considering direct seeding as a way of establishing more commercial crops where it is more desirable to minimise such variation.

In conclusion, the results of this study show that any one of several factors can significantly influence the successful establishment of ash and sycamore by direct seeding. Site-to-site differences were due to almost complete seed predation in the woodland habitat, and differences in soil suitability between the two agricultural sites. Seeds of both species are characterised by sensitivity to loss of viable seed when buried in waterlogged soils, slow emergence of pre-treated seed during

spring, and an inability to continue emerging once soil temperatures exceed 25 °C. These features suggest that direct seeding is more suited to regeneration on sites that are characterised by less extremes of temperature and soil conditions than occur on open agriculture fields in southern England. The development of hydrothermal threshold models of germination and emergence for species used in direct sowing would be a useful way of quantifying and predicting responses to temperature and water (Finch-Savage, 2004). Ultimate success will depend on timing emergence so that emergence and survival of seedlings is maximised. Nevertheless, sowing pre-treated seeds into prepared seedbeds during late winter will stand a good chance of success. Effective vegetation control is essential for seedling growth and survival on open fields.

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