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Midmore, E.K.; McCartan, S.A.; Jinks, R.L.; Cahalan, C.M.

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Edwyn K. Midmore¹, Shelagh A. McCartan², Richard L. Jinks² and
Christine M. Cahalan³

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Highlights

- Using cumulative germination data, thermal time models were developed for *Betula pendula*.
- Models indicated varying degrees of dormancy and pre-chill requirements among provenances.
- Thermal time parameters were used with climatic data to predict germination times under mild and cold winters in southern England.
- Predictions suggest that pre-chilled French seeds would germinate about six weeks later than the fastest germinating provenance.

Abstract

Climate predictions indicate that growing conditions may become unfavourable for certain tree species in parts of Britain. Guidelines suggest some planting of seed sources from regions between 2° and 5° south of those currently used as part of a climate change adaptation strategy. However, there has been little research on the benefits and risks associated with the use of planting stock from more southerly seed sources. Seeds of five provenances of the ‘relatively’ dormant *Betula pendula* were germinated over a range of temperatures both with and without a pre-chill. Subsequently, a thermal time model was used to predict the impact of migrating these provenances to southern England. Results identified geographical differences in germination response; those from higher latitude were more sensitive to pre-chill.

Keywords assisted migration; climate change; seed source; thermal time model

Addresses ¹ Forest Research Agency, Alice Holt, Surrey. Current: Dolwyddelan, Llandre, Ceredigion, Wales, SY24 5BZ; ² Forest Research, Alice Holt, Farnham, Surrey, GU10 4LH, UK; ³ School of Environment, Natural Resources and Geography, Bangor University, Deiniol Road, Bangor, Gwynedd, Wales, LL57 2UW

E-mail shelagh.mccartan@forestry.gsi.gov.uk

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1 Introduction

The effects of climate change on natural regeneration are likely to be complex and far-reaching (Fenner and Thompson 2005; Luna et al. 2012). According to the UK climate projections (UKCP09), average temperatures in southern England could increase by 4.2 °C in summer and 3.5 °C in winter by 2080 (Jenkins et al. 2009). Trees planted today could, when mature, experience climates similar to those currently prevailing in regions two or three degrees further south (Hubert and Cottrell 2007). Climate change poses several threats to the diversity, productivity and resilience of woodlands (Ray et al. 2010). A widely-discussed, and sometimes controversial, approach to addressing these issues is assisted migration; i.e. planting provenances from a different (typically more southerly) region that may be pre-adapted to future climates (McLachlan et al. 2007; Vitt et al. 2010; Pedlar et al. 2012). The levels of risk associated with assisted migration can be influenced by transfer distance (Worrell et al. 2000; Williams and Dumroese 2013).

Temperature is a key environmental factor regulating dormancy and germination of seeds (Heydecker 1977; Bewley and Black 1994; Thompson 2006). A warmer climate with milder winters could impact on the natural regeneration of tree species whose seeds require a period of pre-chilling for germination (Broadmeadow et al. 2005; Gosling et al. 2009). Geographical differences in temperature requirements for germination of various species have been shown using methods such as analysis of variation, time-course and maximum germination curve analysis (Barclay and Crawford 1984; Bevington 1986; Probert 2000; Fenner and Thompson 2005). These methods, although useful, are limited when seeking to predict the potential effects of changing seasonal temperatures on natural regeneration. Thermal time models estimate the minimum temperature at which germination occurs (T_b), and the thermal time (θ_t) required for a given percentage of germination, usually 50% (Pritchard et al. 1999; Steadman and Pritchard 2004; Jinks et al. 2006). Climatic data and thermal time parameters can be combined to investigate the effects of assisted migration on the germination of a target species.

This study aims to develop thermal time models and predict the potential impacts of assisted migration on the germination of five provenances of silver birch (*Betula pendula* Roth) in southern England.

2 Materials and methods

2.1 Seed source and quality

The term provenance refers to the geographic locality of a stand of trees from where the seed was collected (Hubert and Cundall 2006). Three provenances of *Betula pendula* were selected from Great Britain (central England [UK403], the Lake District [UK301] and north-east Scotland [UK201]) and two from continental Europe, southern Finland and eastern France (Table 1). The five seedlots were purchased from commercial suppliers. Each seedlot contained varying proportions of winged seeds (technically achenes) and inert material, principally bracts and strobile particles. Moisture content (MC) was determined following standard protocols (ISTA 2009) on a fresh weight basis (Table 2).

2.2 Germination tests

The International Seed Testing Association (ISTA 2009) recommends using weighed replicates for germination tests of *Betula pendula*. Consequently, representative 0.1 g samples (contain-

Table 1. Seed zone/region with coordinates in degrees latitude and longitude, approximate elevation and harvest year of provenances.

Seedlot	Seed zone / Region	Approx. location	Approx. elevation	Harvest yr.
Finland	<i>B. pendula</i> – Region 1 (Lahti, Southern Finland)	60° N; 25° E	90 m	2002
Scotland	UK201 (Scottish Highlands, Grantown on Spey)	57° N; 03° W	275 m	2001
England	UK301 (England Keswick, Cumberland)	55° N; 03° W	100 m	2009
England	UK403 (Central England, Nesscliffe, Shropshire)	53° N; 03° W	75 m	2010
France	BPE 901-montagne (East France – Rhône-Alpes)	47° N; 05° E	230 m	2010

Table 2. Total number of seeds tested in each provenance, pure seed moisture content and average and standard deviation of number of filled and empty seeds in a 0.1 g sample.

Provenance	Total number of seeds	Moisture content (%)	Filled seeds (Average±SD)	Empty seeds (Average±SD)
Finland	8440	9.7	108±11	43±16
UK201	10454	9.6	56±13	130±23
UK301	9001	6.5	48±11	112±20
UK403	10144	10	88±14	94±17
France	12966	7.2	79±15	156±24

ing seeds and inert matter) from each provenance were distributed across moistened filter paper (Ederol No. 187, 90 × 145 mm, D-330 g m⁻²). These were suspended above a reservoir of water within germination boxes (Gosling 1988). There were two treatments: a control without pre-chill (NPC); and a 21-day moist pre-chill (PC) at 4±1 °C. Four pseudo-replicates per treatment were incubated at seven constant temperatures (10, 13, 17, 20, 25, 30 and 35 °C) for 21 days. During incubation, germination was systematically monitored under ambient light conditions. Germination was considered successful when seedlings measured 10 mm from radicle to cotyledon and had a balanced and healthy appearance. Seedlings displaying abnormal symptoms (e.g. stunted, necrotic and damaged radicles, or deformed hypocotyls) were discarded. After incubation un-germinated seeds within each replicate were stained with 0.5% 2,3,5 tetrazolium chloride for 24 hours at 30 °C to assess viability. Seeds were cut and scored as empty or filled. The proportions of filled and empty seeds varied among provenances (Table 2), and germination capacity was therefore calculated as the percentage of normal seedlings produced from filled seeds by the end of the incubation period. This permitted direct comparison between provenances whilst accounting for potential heterogeneity of samples. Generalised linear mixed models (GLMM) were fitted to the data for germination capacity (%) with a binomial error distribution and logit link function. Replicate was defined as a random effect.

2.3 Thermal time model and predictions

The thermal time analysis used a generalised linear model (GLM) which relates time-to-germination of each provenance to a thermal time (θ_i) parameter (Jinks et al. 2006). A logit link function was used in the model, which assumes that base temperature (T_b) is constant for a seed population at

sub-optimal temperatures. The model was based on the generalisation and re-parameterisation of a calculation (Eq. 1) used to determine θ_{50} by repeat probit regression (Ellis et al. 1986).

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

where $\text{probit}(g)$ is probit units of germination, k is a constant, $(T - T_b)t_g$ is thermal time for a given proportion of germination (g) in degree-weeks, and σ is the standard deviation of the thermal time for germination. The re-parameterised equation (Eq. 2) is below:

$$\text{logit}(g) = \beta_1 + \beta_2(T \times t_g) - \beta_3 t_g \quad (2)$$

where probit was replaced by the logit function for ease of fitting. The coefficients in Eq. 2 can be related to the parameters in Eq. 1 as follows: $\beta_1 = k$; $\beta_2 = 1/\sigma$; and $\beta_3 = \beta_2 T_b$.

Then T_b is estimated directly (Eq. 3) as:

$$\frac{\beta_3}{\beta_2} = T_b \quad (3)$$

and the thermal time requirement for 50% germination (Eq. 4) as:

$$\frac{\beta_1}{\beta_2} = \theta_{50} \quad (4)$$

The model assumes a linear relationship between temperature and germination rate (Finch-Savage and Whalley 2006). Thermal time analysis was applied to cumulative germination data for temperatures 13 °C to 30 °C inclusive. Data for upper asymptotes were removed, as these false plateaux were due to dormancy, particularly in the NPC seeds. At 35 °C germination decreased significantly due to thermo-inhibition; these data were excluded from thermal time analysis. Using the thermal time parameters and climatic data, germination in southern England (50°75'N, 1°75'W) was predicted for each provenance. The climatic data were sourced from the CRUTS v3.10 database for a thirty-year period (1980–2009) (Mitchell and Jones 2005). The predictions assume that provenances received either no pre-chill (NPC, mild winter scenario) or the equivalent of a three-week pre-chill (PC, colder winter scenario). The 1st of March was used as a starting point for thermal time accumulation; heat accumulation and germination occurs when the ambient temperature exceeds predicted T_b .

3 Results

Seedlot quality varied considerably. Each 0.1 g replicate contained over 100 seeds with the average number of filled seed ranging from 48 (UK201) to 108 (Finland). The Finnish seeds had the highest purity (ratio of seed to inert matter) of 64%, while other provenances ranged between 38% and 44%.

3.1 Germination

For all provenances, maximum-germination plots (Fig. 1) show that control seeds (NPC) germinated over a narrower temperature range than pre-chilled seeds (PC). In control seeds, no germi-

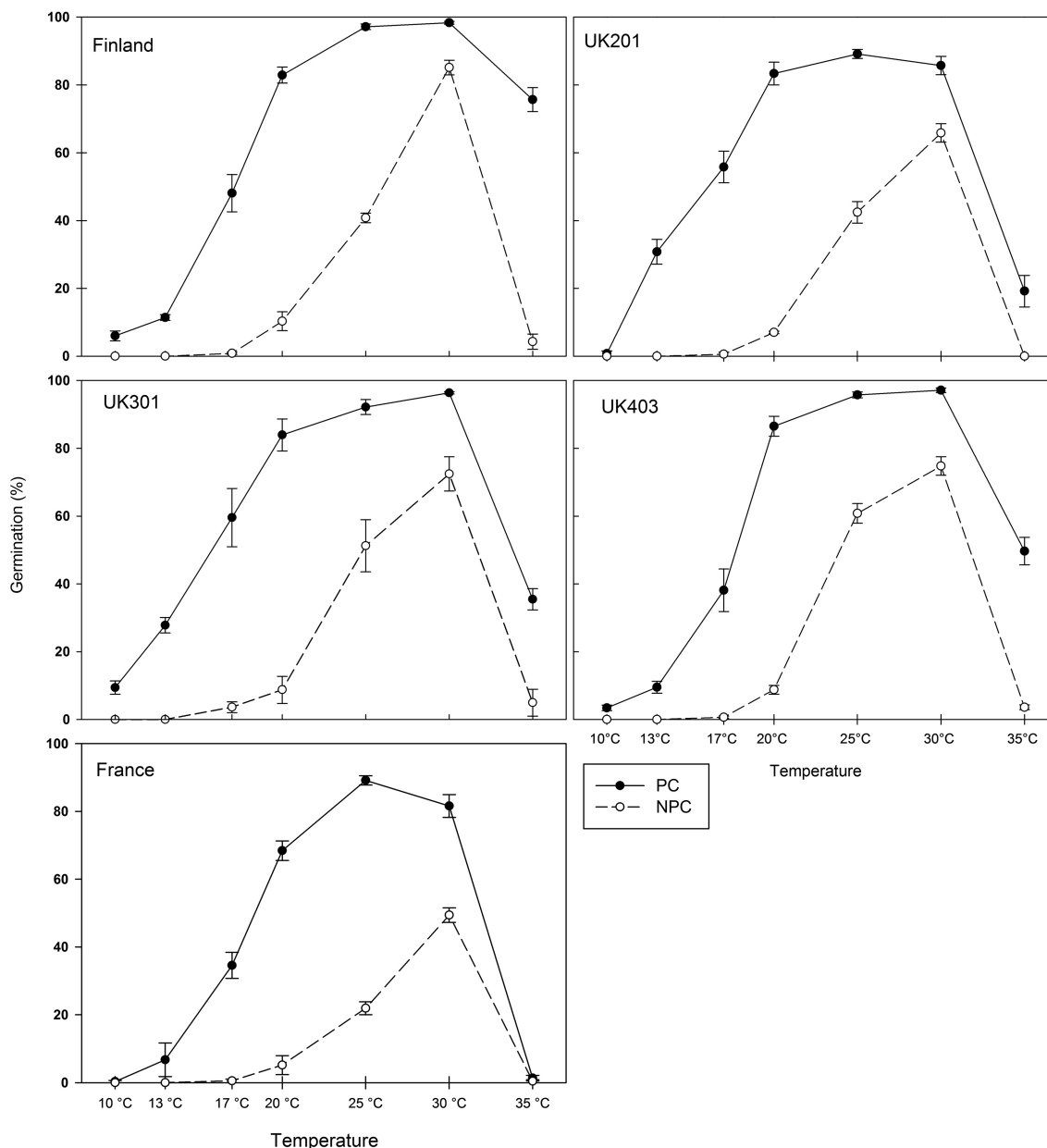


Fig. 1. Maximum germination capacity (at day 21) for five provenances of *Betula pendula* expressed as a percentage of filled seed. Closed symbols: germination following pre-chilling (PC). Open symbols: germination of control seeds (NPC). Error-bars: Standard error.

nation occurred at 10 °C or 13 °C. Above 13 °C, germination capacity increased with increasing temperature, reaching a maximum at 30 °C. Maximum germination capacity varied among provenances, with 54% of French seeds germinating compared with 91% of Finnish seeds. Following pre-chilling, germination occurred rapidly over a wider temperature range. For all provenances, germination was thermo-inhibited at 35 °C (a supra-optimal temperature), a common trait in wild species (Dürr et al. 2015). The French seeds were the most dormant while the Finnish seeds were the least dormant (Fig. 1). The GLMM analyses showed that all the main effects (temperature, pre-chilling and provenance) were significant (all $p < 0.001$). Seedlots were of different ages, and seedlot age was tested by replacing provenance with each of the co-variables seedlot age and latitude in turn. Replacing provenance with latitude resulted in a highly significant main effect of latitude

Table 3. Thermal time parameters (with standard errors) of *Betula pendula*: estimated base temperature (T_b) in °C; thermal time to 50% germination (θ_{50}) in degree-weeks for both treatments (NPC and PC); relative change in parameters after pre-chilling (PC – NPC).

Provenance	Control seeds (NPC)				Pre-chilled seeds (PC)				PC – NPC	
	T_b	S.E.	θ_{50}	S.E.	T_b	S.E.	θ_{50}	S.E.	T_b	θ_{50}
Finland	15.8	0.8	21.2	1.4	10.3	0.9	13.4	1.2	5.6	7.8
UK201	13.1	2.2	37.9	5.0	6.8	1.1	23.6	2.0	6.3	14.3
UK301	9.4	1.8	37.4	3.7	7.5	0.9	16.8	1.3	1.9	20.6
UK403	12.6	1.0	28.1	2.0	10.2	1.0	14.8	1.4	2.4	13.2
France	12.3	1.9	42.5	4.8	9.9	1.1	19.6	2.0	2.5	23.0

($p < 0.001$); there were no significant interactions between latitude, germination temperature and pre-chilling. When provenance was replaced with seedlot age, the main effect of seedlot age was not significant ($p = 0.34$), and there were no significant interactions between seedlot age and temperature or between seedlot age and pre-chilling.

3.2 Thermal time model

Table 3 shows the estimated base temperature (T_b) and the thermal time required for 50% germination (θ_{50}) for each provenance. For control seeds (NPC), T_b was highest for Finnish seeds and lowest for northern English (UK301) seeds. With the exception of UK301, T_b appeared to increase with increasing latitude. In addition, the predicted thermal time required for 50% germination (θ_{50}) for the French seeds was approximately double that of the Finnish seeds. After pre-chilling (PC), the estimated base temperature (T_b) for germination and thermal time required for 50% germination (θ_{50}) decreased in each provenance. Differences in the relative magnitude of the change in thermal time parameters indicate varying degrees of dormancy and pre-chill requirements among provenances.

3.3 Predictions

The predictions show germination of seeds from different provenances after a mild winter (NPC) compared to a colder winter (PC) in southern England (Fig. 2). Under mild conditions, seeds from northern England (UK301) reach a predicted maximum germination of 99% by mid-Aug. Seeds from central England (UK403) reach 40% germination but at a slower rate. Maximum germination for Scottish and French seeds is predicted to be 10% and 12% respectively, and practically zero (1%) for Finnish seeds. After a colder winter (equivalent to a three-week pre-chilling [PC]), all provenances are predicted to reach 100% germination by July, central English and French seeds having the slowest rate.

4 Discussion

Betula pendula is a masting species that is characterised by its wide variation in the quantity and quality of seed produced annually (Atkinson 1992). This monoecious species produces male catkins, which release vast quantities of wind-dispersed pollen in spring (Atkinson 1992). Subsequently, female catkins develop into cylindrical strobiles that disintegrate at the end of summer/autumn releasing wind and water-dispersed seeds (Suszka et al. 1996). Upon dispersal, seeds are

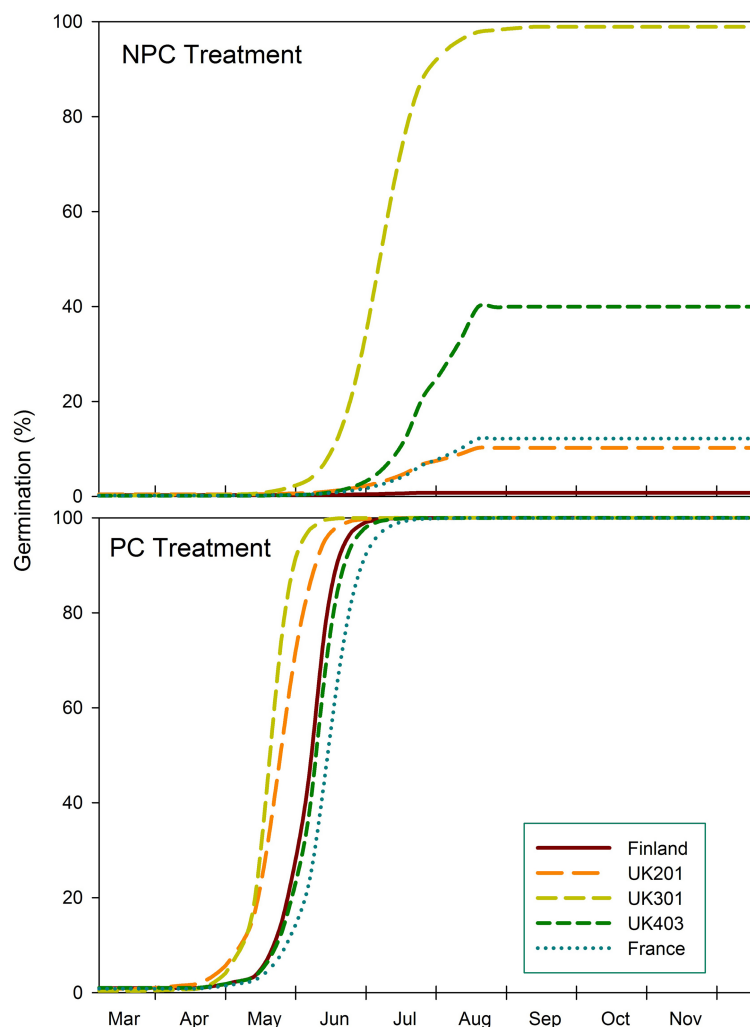


Fig. 2. Predicted germination of seeds from Finland (FIN), Scotland (UK201), north England (UK301), central England (UK403) and Eastern France (FRA) provenances under conditions that simulate a mild (NPC) and slightly colder winter (PC) in southern England.

relatively (or conditionally) dormant; this is regulated by an interaction between photoperiod and temperature (Vaartaja 1952; Black and Wareing 1954, 1955; Vanhatalo et al. 1996). Under natural conditions some seeds may germinate in autumn but seedlings are unlikely to survive (Vanhatalo et al. 1996). During winter, seeds are exposed to a moist-chilling condition resulting in a widening of the range of temperatures suitable for germination.

The beneficial effect of moist pre-chilling on germination of *Betula pendula* is well documented (Atkinson 1992; Vanhatalo et al. 1996; De Atrip and O'Reilly 2007; Tylkowski 2012). This study confirmed that a pre-chill improved the germination capacity and germination rate, and widened the thermal thresholds for germination in all provenances. Results revealed differences in degree of dormancy among the provenances (indicated by the area between the NPC and PC plots in Fig. 1) and therefore in pre-chill sensitivity, particularly at sub-optimal temperatures. In a similar study, Bevington (1986) compared North American provenances of paper birch (*Betula papyrifera*). He found that northerly seeds germinated over a wider range of temperatures and showed greater sensitivity to pre-chilling. Seeds also had consistently thinner, more translucent pericarps than their southern counterparts. Bevington (1986) proposed that the thinner pericarps of

northerly seeds could facilitate germination at lower temperatures, possibly being an adaptation to a shorter growing season. In this study, the Finnish seeds also appeared to have thinner pericarps than other provenances.

Temperature is a key environmental factor in the regulation of dormancy and germination, which in turn synchronise regeneration with seasons. This is demonstrated by the base temperature (T_b) for germination of provenances which, with the exception of UK301, appeared to increase with latitude. In addition, provenances with a lower T_b often had a higher θ_{50} . This negative correlation between T_b and the thermal time required for fifty percent germination mirrors a general trend described in a recent review (Dürr et al. 2015). In this study, the greatest effect of pre-chilling (PC – NPC) on base temperature for germination was seen in northerly provenances (Finland and Scotland). Germination, therefore, becomes constrained to a safe window when the threat of winter damage has passed. Generally, an increase in pre-chill duration results in a corresponding decrease in T_b (Pritchard et al. 1999; Necajeva and Probert 2011). In some cases, secondary dormancy can develop following excessive pre-chill duration (Bevington and Hoyle 1981). Pre-chill temperature is also important; Vanhatalo et al. (1996) found that dormancy was released at 2.4 °C and 5.5 °C but imposed at 12.4 °C. Thus, adaptations to cope with or avoid low winter temperatures become more important towards the poles where favourable growing seasons are shorter (Saikkonen et al. 2012). As near-surface temperatures decrease with increasing altitude (Blandford et al. 2008), this dynamic may contribute to the increased dormancy observed in provenances of higher altitude (UK201 and France). Indeed elevation has been shown to influence optimal pre-chill duration in certain tree species, e.g. *Sorbus aucuparia* (Barclay and Crawford 1984).

In this study, statistical analyses showed that pre-chilling, temperature and provenance significantly influenced germination capacity. Furthermore, the provenance effect was due to latitude rather than seed age. Seeds of *Betula* species are orthodox, and following a reduction in moisture content can be stored successfully without loss of germinability for several years (Clausen 1975; Suszka et al. 1996). There are even reports of unexplained increases in germinability following extended storage (Clausen 1975; Tylkowski 2012). All seedlots had high maximum germination capacity, regardless of seed age and particularly after pre-chilling. In this study, however, latitude was confounded with maternal effects. Maternal effect refers to the ecological environment of the maternal parent and its influence on the phenotype of its progeny (Donohue 2009). The impact of latitude is two-fold; firstly, it influences photoperiod, which remains constant for a specific time of the year at a specific latitude (Saikkonen et al. 2012). Thus, seeds of the more northerly provenances (Finland) were exposed to shorter photoperiods during seed development and maturation than those of the southerly provenances (France). In *Betula pendula*, relative dormancy is regulated by an interaction between photoperiod and temperature, in which light can substitute for pre-chilling (Vaartaja 1952; Black and Wareing 1954, 1955; Vanhatalo et al. 1996). Donohue (2009) reported that seeds of *Arabidopsis thaliana* matured under short photoperiods were more responsive to pre-chilling than those matured under longer photoperiods. Secondly, latitude influences the temperature during seed maturation and post-dispersal; temperature also varies among years. Kelly et al. (2003) examined amplified fragment length polymorphisms in 15 individuals of *Betula pendula* in northern England. Results showed individuals clearly grouped in relation to mean temperature of establishment year (between 8.5 and 10.4 °C). This suggests that ‘pre-prepared’ genotypes, which germinate preferentially in cool or warm years, are an important feature of the adaptive capacity of *Betula pendula* (Kelly et al. 2003).

These two examples highlight the challenges faced when selecting seed sources for assisted migration as part of a climate change adaptation strategy. Under projected climate change scenarios, seeds are likely to receive less pre-chill during milder winters, and therefore may be unable to accumulate sufficient thermal time for germination within a safe window. Some provenances

may germinate poorly and erratically and others not at all. In addition, trees are long-lived, and selected provenances therefore need to be well adapted to both present and future climates. In this study, predictions suggest that pre-chilled French seeds would germinate about six weeks later than the fastest germinating provenance (UK 301), with the risk that seedlings would suffer water stress under the present climate in southern England. Currently, the UK guidelines for *Betula pendula* recommend using seeds from British breeding programmes and avoiding seed sources from continental Europe (Forestry Commission 2015). In Finland, the recommended transfer distance is 150 km north or south to avoid potential damage by both late spring and early autumn frosts (Vakkari 2009).

5 Conclusion

Using thermal time models, germination parameters (base temperature and thermal time) were derived for five provenances of *Betula pendula* (Finland to France). The models showed that there were significant differences in the degree of dormancy and pre-chill sensitivity of the provenances. These differences were due to latitude, suggesting local adaptation to different regions. Thermal time models provide a useful means of predicting the germination capacity and germination rate of seeds under different climate change scenarios, and therefore for assessing the potential risks associated with assisted migration.

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