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Research paper

Endodormancy release in Norway spruce grafts representing trees of different ages

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Studies addressing endodormancy release in adult trees are usually carried out using twigs detached from the trees in the experiments. Potential problems caused by cutting the root–shoot connection when detaching the twigs can be avoided by using grafts as the experimental material. We studied the effects of chilling on the endodormancy release in Norway spruce (*Picea abies* (L.) Karst.) grafts where twigs of 16-, 32- and 80-year-old trees were used as the scions. The grafts were first exposed to chilling in natural conditions and then samples of them were transferred at intervals to a regrowth test in forcing conditions in a greenhouse. The bud burst percentage, BB%, in the forcing conditions generally increased from zero to near 100% with increasing previous chilling accumulation from mid-October until mid-November, indicating that endodormancy was released in almost all of the grafts by mid-November. The days to bud burst, DBB, decreased in the forcing conditions with successively later transfers until the next spring. Neither BB% nor DBB was dependent on the age of the scion. However, in the early phase of ecodormancy release, the microscopic internal development of the buds was more advanced in the grafts representing the 16-year-old than in those representing the 32- or 80-year-old trees. In conclusion, our findings suggest that no major change in the environmental regulation of endodormancy release in Norway spruce takes place when the trees get older. Taken together with earlier findings with Norway spruce seedlings, our results suggest that regardless of the seedling or tree age, the chilling requirement of endodormancy release is met in late autumn. The implications of our findings for Norway spruce phenology under climatic warming and the limitations of our novel method of using grafts as a proxy of trees of different ages are discussed.

Keywords: bud burst percentage, chilling, days to bud burst, ecodormancy, endodormancy, forcing, graft, primordial shoot ratio, quiescence, rest, scion, tree age.

Introduction

Boreal and temperate tree species are adapted to seasonal climatic variation with their annual cycle of development. In late summer and early autumn, short photoperiods cause in many tree species growth cessation, bud set and dormancy induction (Wareing 1956, Vaartaja 1959, Ekberg et al. 1979, Junttila 2007). However, there are also several interactions with air temperature (Koski and Selkäinaho 1982, Koski and Sievänen 1985, Partanen and Beuker 1999, Partanen 2004, Tanino et al. 2010), and in some species, low temperatures alone cause growth cessation (Heide and Prestrud 2005, Heide 2011). The subsequent dormant period of the buds is traditionally described by a simplified dichotomy of concepts based on whether physiological or environmental factors prevent vegetative bud burst and subsequent growth (Doorenbos 1953, Romberger 1963, Sarvas 1972, 1974, Fuchigami

et al. 1982, Hänninen 1990, Charrier et al. 2011, 2018*a*, 2018*b*, Hänninen et al. 2019). After growth cessation the buds enter first a state of endodormancy (Lang et al. 1987) in which physiological factors inside the buds prevent bud burst and growth onset. When endodormancy is released, i.e., the growth-arresting physiological factors are removed in the buds, a state of ecodormancy (Lang et al. 1987) is reached. During ecodormancy bud burst and growth onset are prevented by unfavorable environmental conditions, typically low nongrowth-promoting air temperatures prevailing in winter. During ecodormancy microscopic development takes place in buds whenever temperature rises to a sufficiently high level, and finally ecodormancy is ended, and visible bud burst occurs as a result of sufficiently long periods with high temperatures (Sarvas 1972, 1974, Sutinen et al. 2009, 2012, Viherä-Aarnio et al. 2014). An evolutionary trade-off is expected to influence the timing of bud burst (Hänninen and Hari 1996, Leinonen and Hänninen 2002): early bud burst increases risk of damage caused by late spring frosts (reduced survival adaptation, Heide 1985), whereas a late bud burst implies shortening of growing season and restricted use of growth resources at the site (reduced capacity adaptation, Heide 1985).

In his literature review, Hänninen (2016) identified two contradictory conceptual models for endodormancy release in boreal and temperate trees. According to the 'traditional model,' chilling is the main driving force of endodormancy release and endodormancy is released during autumn. Since the classical study of Coville (1920), the traditional model has found support in many studies where endodormancy release has been studied with chilling–forcing experiments by observing occurrence and timing of bud burst in growth-promoting forcing conditions after varying durations of exposure to chilling temperatures (for reviews see Perry 1971, Fuchigami et al. 1982, Arora et al. 2003, Hänninen and Tanino 2011, Cooke et al. 2012, Hänninen 2016). However, the traditional model has been questioned since the 1990s in studies where process-based tree phenology models have been tested with long-term phenological records (Häkkinen et al. 1998, Häkkinen 1999, Hannerz 1999, Linkosalo 2000, Linkosalo et al. 2000, 2008, Fu et al. 2012) or in experiments using whole-tree chambers (Hänninen 1995, Hänninen et al. 2007). In these studies, simplified models where the accumulation of forcing units is started on a given day during late spring have repeatedly outperformed more complicated models where endodormancy and chilling requirement are explicitly addressed. This has given rise to the 'alternative model' (Hänninen 2016): rather than in autumn, endodormancy is fully released later in the following spring, and in addition to chilling, some other factors, such as photoperiod, are also regulating it.

The contradiction between the two conceptual models has caused major uncertainty in scenario studies where process-based tree phenology models are used for projecting the effects of climatic warming (Hänninen 2016). Computer simulations with process-based tree phenology models following the principles of the traditional conceptual model project endodormancy release during autumn and a premature bud burst during intermittent mild periods in winter and early spring, leading to catastrophic frost damage of trees (Hänninen 1991, 2006). Recently, this phenomenon has been called 'false springs' (Chamberlain et al. 2019, Zhu et al. 2019). In contrast, simulations with process-based tree phenology models following the principles of the alternative conceptual model project postponing endodormancy release until spring also under warming climate; thus, avoiding premature bud burst and frost damage (Linkosalo et al. 2000, Hänninen 2016).

Partanen et al. (2005) suggested that the regulation of the endodormancy release changes as the trees get older. This may partially explain the contradiction between the traditional and the alternative models of endodormancy release (Hänninen 2016). However, testing this hypothesis with a traditional chilling–forcing experiment is difficult because for practical reasons, the forcing treatments can be carried out for adult trees only with twigs detached from the trees. Even though twigs have been found to be relatively good proxies for whole trees in experiments addressing endodormancy release (Vitasse and Basler 2014, Partanen et al. 2016), the possibility of artifacts caused by cutting the physiological connection between the roots and shoots cannot be ruled out (Basler and Körner 2012).

Grafts with scions from adult trees provide an unused potential proxy for adult trees in experimental studies of endodormancy release. Unlike in experiments with detached twigs, the root–shoot connection remains intact when using grafts in the experiments. Here we studied the effects of chilling on the endodormancy release in Norway spruce (*Picea abies* (L.) Karst.) grafts representing 16-, 32- and 80-year-old trees. Based on the above discussion of the two conceptual models of endodormancy release in boreal trees, we hypothesize that endodormancy release takes place earlier in grafts representing young than in those representing old trees. We also examined whether there are differences among the grafts representing the different tree ages in the internal microscopic bud development leading to visible bud burst.

Materials and methods

Production of grafts

Two-year-old Norway spruce seedlings were used as stocks in the grafting. The seedlings were grown at the Finnish Forest Research Institute (currently part of the Natural Resources Institute Finland, Luke) in Suonenjoki (62°39′ N, 27°03′ E) in 2004–05, using seeds collected from the seed orchard number 177 Sairila in Hartola (61°34′N, 26°05′E) including

Table 1. Characteristics of the Norway spruce trees used for grafting in the study. Twigs from the trees were detached on the indicated dates and used as scions in grafts representing trees of different ages. For the sake of brevity, throughout the study, the four graft groups representing the trees of different ages and origins are referred to as their age groups.

Age (years)	Location of origin	Growing location and trial	Number of trees	Average number of twigs per tree	Time of twig collection	Age group
16	Elimäki 60°40′ N 26°30′ E	Punkaharju Progeny trial 141201	40	6	23 March 2006	16-y Elimäki
16	Juva 61°56′ N 27°58′ E	Punkaharju Progeny trial 141201	40	6	23 March 2006	16-y Juva
32	Juva 61°56′ N 27°58′ E	Punkaharju Provenance sample area 516	22	16	29 March 2006	32-y Juva
80	Elimäki 60°40′ N 26°30′ E	Punkaharju Heikinheimo provenance trial	12	42–54	5 April 2006	80-y Elimäki

76 grafted clones of Norway spruce, all of them having their origin in a restricted geographical area in the interior of southern Finland (Nikkanen et al. 1999). A seed mixture of these was used for producing the stocks. The seeds were sown between 19 and 23 April 2004 in Plantek (BCC, Landskrona, Sweden) PL81F trays (81 cells per tray, 549 cells m^{-2}, cell volume 85 cm^3). The seedlings were grown for two growing seasons using standard nursery practices applied in Finland. During their second growing season in 2005, the seedlings were subjected to a short-day (12 h) treatment between 11 July and 1 August 2005.

The grafts were produced at the Finnish Forest Research Institute (currently part of the Natural Resources Institute Finland, Luke) in Punkaharju (61°48′ N, 29°19′ E) in March to April 2006. The twigs to be used as scions in the grafts were collected from 16-, 32- and 80-year-old Norway spruce trees growing in the neighborhood of the Punkaharju Research Station (Table 1). The origin of the trees is in southern Finnish, i.e., Elimäki (60°40′ N, 26°30′ E) for the 80-year-old and Juva (61°56′ N, 27°58′ E) for the 32-year-old trees, respectively. Both provenances were represented in the 16-year-old trees. Because our purpose is to study to possible effect of tree age, for the sake of simplicity, the four graft groups will be referred to later as their age groups. The number of sampled trees varied among the age groups between 12 and 40 (Table 1). After collecting several twigs (6–54) from each of the sampled trees, the twigs from the different trees representing the same age group were pooled together. After sampling the twigs were put into plastic bags with snow and kept in −5 °C until grafting was carried out.

Grafting was done between 24 April and 10 May 2006 at the Punkaharju Research Station. Between 23 and 30 May 2006, the grafts were transplanted from the Plantek 81F trays to Plantek PL25 trays (25 cells per tray, 156 cells m^{-2}, cell volume 380 cm^3). In the second growing season in June 2007, the grafts were transplanted to Soparco, (Le Musset, Condé-sur-Huisne, France) 11 × 11 × 11 cm (1 l) plastic pots, where they remained until the end of the experiments. During the first three growing seasons 2006–08, the grafts were grown in a greenhouse under natural light conditions and average daily temperature of 17 °C (ranging from about 7 °C to about 25 °C). During the fourth growing season, the grafts were grown in outdoor natural conditions. During the first winter 2006–07, the grafts overwintered in the greenhouse, with temperature ranging between +1 and +4 °C. During the next two winters, 2007–08 and 2008–09, the grafts overwintered in outdoor natural conditions. In all, then, the grafts had been continuously in outdoor natural conditions for about 12 months at the time the first experiments were started in autumn 2009. After that, the grafts used in the later experiments were continuously in the outdoor natural conditions until the beginning of the experiment 1 or 2 years later.

Experiments

After collecting the twigs and grafting and growing the grafts, information concerning the donor tree identity (genotype) was no longer available; but within any given age group, the grafts were considered to represent the different donor trees in a random order when they were collected for the experiment. The experiment was repeated three times, starting in the autumn of each of the three consecutive years 2009–11. The last experiment ended in the spring 2012. The grafts were first exposed to chilling in natural conditions, and then a sample of them was transferred at intervals to a regrowth test in forcing conditions in a greenhouse. Both the date of a given transfer and the chilling accumulated at the time of the transfer varied among the three experiments carried out during the three consecutive years. In the first experiment starting in 2009, the transfers were made between October and December of that year; in the other two experiments starting in 2010 and 2011, the transfers were made between October of the beginning year and April of the next year (Table 2). At each transfer five grafts from each of the four age groups were sampled for bud burst observations in the forcing conditions. In both of the experiments starting in 2009 and 2010, two additional grafts were sampled in three transfers for stereo microscopic study (Table 2).

Table 2. Dates when the grafts were transferred from the outdoor natural chilling conditions to a regrowth test under forcing conditions in a greenhouse or first to preforcing conditions (darkness, +4 °C) for a cautious melting (dates in parentheses). The bold letters indicate the transfers in which stereo microscopic measurements were done in addition to visual observations.

Transfer	Year		
	2009–10	2010–11	2011–12
1	14 October	13 October	11 October
2	**28 October**	**27 October**	26 October
3	**(18 November) 25 November**	**17 November**	16 November
4	2 December	**(8 December) 15 December**	(7 December) 14 December
5	**(9 December) 16 December**	(12 January) 19 January	(11 January) 18 January
6	(16 December) 23 December	(16 February) 23 February	(15 February) 22 February
7		(22 March) 30 March	(22 March) 28 March
8		27 April	25 April

Chilling, preforcing and forcing conditions

Air temperature at the shoot level of the grafts was recorded once an hour in the outdoor natural chilling conditions by Tinytalk data loggers (Gemini Data Loggers, Chichester, UK), located inside a well-ventilated radiation shield. On the basis of the hourly temperature measurements, a chilling unit sum was calculated from 1 September to 31 December. The tabulated values of the triangular air temperature response represented by Sarvas (1974) were used: accordingly, chilling accumulation takes place in the range from −3.5 to +10.5 °C with the maximum accumulation rate of 1 chilling unit per hour from +3.4 to +3.6 (Hänninen 2016, p 74). The minimum, mean and maximum daily air temperatures and the chilling unit sum accumulation during autumn are presented in Figure 1.

Day length in the forcing conditions was 12 h (light period between 6 a.m. and 6 p.m.) and was controlled by using black curtains. When necessary the natural day length was extended using metal halide lamps (Philips HPI-T Powertone 400 W, Philips, Helmond, the Netherlands). Photosynthetically active radiation was approximately 50 μmol m^{-2} s^{-1} at the shoot level. Air temperature was +20/+15 °C (day/night) in the forcing conditions. When the outdoor temperature fell below 0 °C (Figure 1), the grafts to be transferred from outdoors to the forcing conditions were first transferred to preforcing conditions (darkness, +4 °C) for 1 week and only after that moved to the forcing conditions (Table 2). This was done in order to enable cautious thawing and avoid needle damage (Repo et al. 1984). In the analysis of the data, the day of the transfer from the preforcing to the forcing conditions was taken as the transfer day. The air temperature at the shoot level was recorded every hour both in the preforcing and the forcing conditions by using Tinytalk data loggers. In the forcing conditions, the loggers were located inside a well-ventilated radiation shield; in the preforcing conditions in darkness, no shields were applied. The grafts were watered manually with tap water as needed in the forcing conditions.

Determination of bud burst

The terminal buds of the main shoot and of the four uppermost lateral shoots of each graft were observed visually three times a week until bud burst or until the bud was visibly dead, as indicated by its dry appearance. The bud was classified as burst when new needles were visible. Bud burst percentage, BB%, was calculated for each graft for the five observed buds. Days to bud burst, DBB, was calculated for each graft as the time from the beginning of forcing to the first day when the third bud out of five had burst. Using the daily mean temperatures, a temperature sum (day degrees, d.d.) with the threshold temperature of 0 °C was calculated for each graft for the period needed for bud burst in the forcing conditions.

Microscopic analyses of the buds under forcing conditions

In three transfers in both 2009 and 2010, two extra grafts from each of the four age groups were randomized for a study of the internal microscopic bud development. After varying time in the forcing conditions, the grafts were taken into stereomicroscopic analyses (Table 3). Thus, 12 different combinations of accumulated chilling unit sum and temperature sum at the time of the microscopic analysis were created.

For the stereomicroscopic analyses, in 2009 a 2.5-cm tip from the main shoot including the terminal bud and the whorl buds was cut from each graft. In 2010, in addition to the main shoot, also the tips from four nearest lateral shoots with their terminal and whorl buds were cut for the microscopic analyses. To avoid any further development in the buds before microscopy, the shoot tips were immediately put into a test tube containing fixative solution (2% glutaraldehyde in cacodylate buffer, pH 7.0., 0.05 M; Sutinen et al. 2009). The samples were cut between 8 and 9 a.m., and the tubes were sent in a cool bag to the Joensuu Research Unit of the Finnish Forest Research Institute (currently part of the Natural Resources Institute Finland, Luke).

The terminal bud and all the whorl buds in each 2.5-cm shoot tip were cut longitudinally into two halves. For the morphological

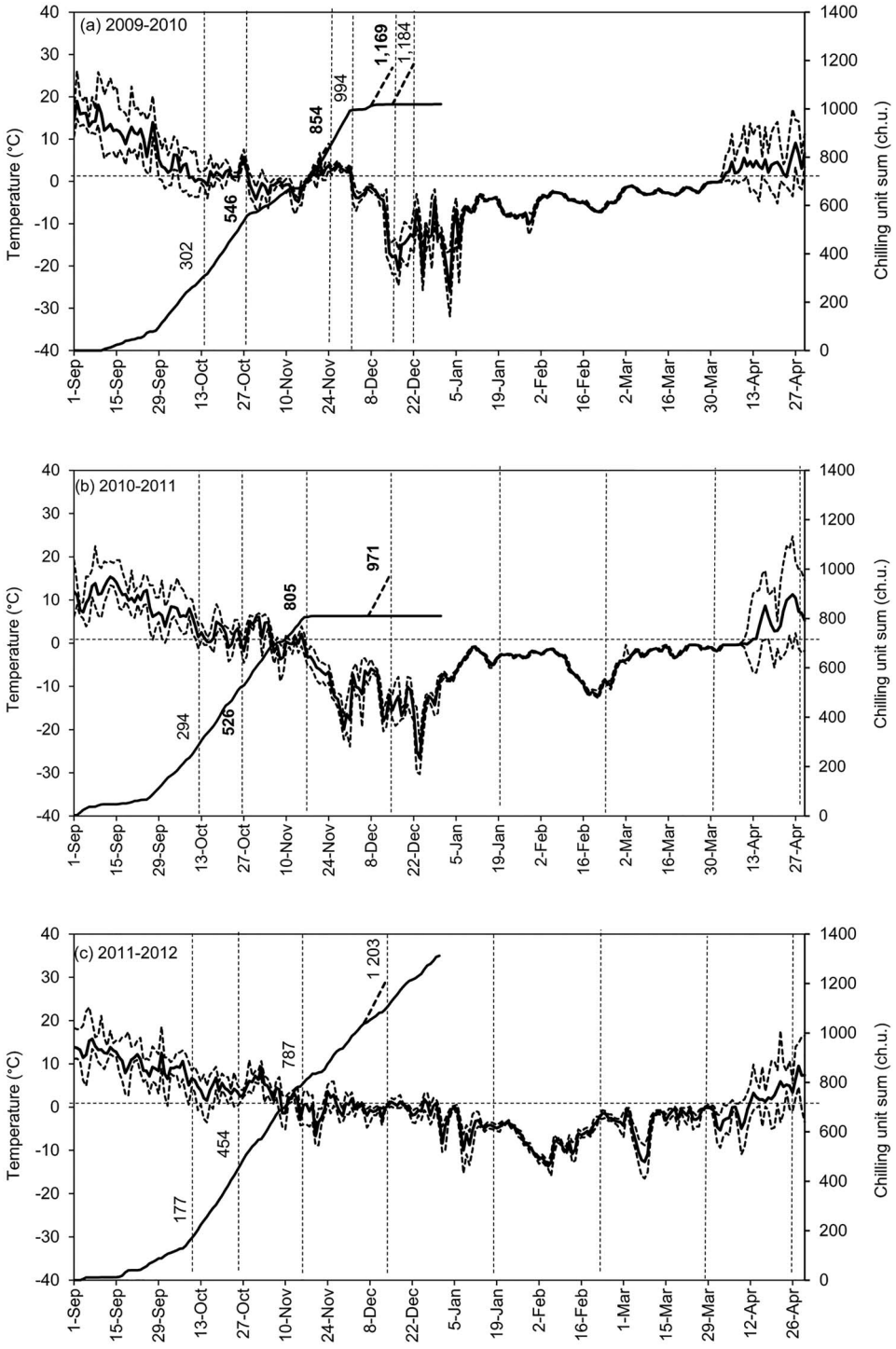

Figure 1. The daily minimum, mean and maximum air temperatures (fluctuating curves) and the daily chilling unit sum accumulation at the graft shoot level from 1 September to 31 December, based on hourly temperature measurements in the outdoor chilling conditions (solid ascending curve) at Punkaharju, Finland (61°48′ N, 29°20′ E), in 2009–2010 (a), 2010–2011 (b) and 2011–2012 (c). Dashed vertical lines indicate the transfer times from the outdoor natural chilling conditions or from the preforcing conditions (+ 4 °C) applied for melting of the grafts during winter, to the forcing conditions in the greenhouse. The figures attached to the lines indicate the corresponding chilling unit sum accumulated by each transfer. The dashed ascending lines indicate the chilling unit accumulation in the preforcing conditions. The figures in bold font in (a) and (b) indicate the transfers when stereomicroscopic studies addressing the internal bud development were also carried out. The dashed horizontal line indicates the temperature of 0 °C and the chilling unit sum of 700 ch.u.

Table 3. The observed primordial shoot ratio (PSR) under forcing conditions in a greenhouse in buds of Norway spruce grafts representing 16-, 32- and 80-year-old trees. The PSR was measured both in 2009 and 2010 in three transfers after two varying forcing times (Table 2). The results in bold on the lowermost line indicate the average PSR of the age group over all measurements. The chilling unit sum accumulated before transfer to forcing and the temperature sum accumulated in the forcing conditions until the measurement of the PSR are also shown.

Year	Transfer to forcing	Days of forcing	Chilling unit sum (ch.u.)	Temperature sum (d.d., $T \geq 0$ °C)	Primordial shoot ratio of age groups			
					16-y Elimäki	16-y Juva	32-y Juva	80-y Elimäki
2009	28 October	14	546	247	0.53	0.39	0.28	0.22
2009	28 October	23	546	407	0.56	0.70	0.45	0.30
2009	25 November	7	854	123	0.40	0.49	0.32	0.25
2009	25 November	14	854	246	0.52	0.65	0.46	0.33
2009	16 December	5	1169	86	0.56	0.32	0.38	0.43
2009	16 December	12	1169	208	0.56	0.44	0.62	0.37
2010	27 October	14	526	248	0.38	0.33	0.28	0.29
2010	27 October	23	526	408	0.30	0.39	0.32	0.28
2010	17 November	7	805	124	0.38	0.48	0.26	0.25
2010	17 November	14	805	248	0.43	0.40	0.31	0.33
2010	15 December	5	971	88	0.27	0.30	0.33	0.25
2010	15 December	12	971	211	0.43	0.61	0.34	0.35
					0.44	**0.46**	**0.36**	**0.30**

studies, the outer surface and the inner parts of the longitudinally cut buds were photographed with a digital camera (Leica CD Microsystems Camera, Heerbrugg, Switzerland) at 6× and 12× objective magnification under a stereomicroscope (Wild, Heerbrugg, Switzerland). The length of the primordial shoot and length of the whole bud were measured from digital images as described by Sutinen et al. (2009, 2012). To eliminate the effect of different bud sizes, the ratio of the primordial shoot length to that of the whole bud (from here on, primordial shoot ratio, PSR) was calculated, and the average PSR of a graft was used in the analyses of the effect of tree age on primordial shoot length (Sutinen et al. 2009, 2012, Viherä-Aarnio et al. 2014).

Statistical analyses

The experimental unit in all statistical analyses was the graft. The differences of BB% and of DBB among the four age groups of the grafts were analyzed separately for each year because the transfer dates and the chilling unit sums of different years did not correspond to each other (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Differences among BB% values were analyzed using logistic regression with a binomial response and an estimated dispersion parameter. Differences among DBB values were analyzed with two-way analyses of variance and a 'log' transformation of DBB. After the log transformation, the residual distribution was normal and homoscedastic. In both analyses the explanatory variables were the age group, the transfer time and their interaction. The differences of the primordial shoot ratios among the four age groups of grafts were analyzed using the analysis of variance of randomized block design. As the response variable, a 'logit' transformation of primordial shoot ratio was used (Warton and Hui 2011). The explanatory variable was the age group, and the 12 different combinations of the accumulated chilling unit sum and accumulated temperature sum on the corresponding 12 observation dates (Table 3) were used as the block effect. The residual variation was normal but increased with increasing predicted values. To address this, an additional weighted analysis with weights inversely proportional to the variance estimates was carried out (Weisberg 1985). The two analyses gave similar results, so that only the results of the unweighted analysis are reported. Normality and homoscedasticity of residuals were checked with Q-Q and residual plots. Statistical analyses were carried out using IBM SPSS Statistics for Windows, Version 22.0, IBM Corp., Armonk, NY, USA.

Results

The effect of the transfer time on BB% was significant ($P < 0.001$) and the pattern of BB% development over the transfers was similar in all 3 years (Figure 2). In the first transfer, BB% of the four age groups was 0–12% in 2009 (Figure 2a), 0% in 2010 (Figure 2b) and 0–4% in 2011 (Figure 2c), indicating that endodormancy was released only in a small part of the grafts. With successive later transfers with increased accumulated previous chilling, the values of BB% increased until mid-November towards 100% indicating that endodormancy was released almost in all of the grafts by mid-November (Figure 2, see Figure S1 available as Supplementary Data at *Tree Physiology* Online). For the development of BB% from December onwards, no data was available for 2009–10 (Figure 2a), whereas in the experiments in 2010–11 (Figure 2b) and 2011–12 (Figure 2c), BB% stayed after December mainly between 80% and 100% until April. However,

in the transfer on 23 February 2011, it varied exceptionally between 48 and 72% (Figure 2b).

BB% was not dependent on the age of the tree ($P = 0.126$ in 2009; $P = 1.000$ in 2010; $P = 0.776$ in 2011). The interaction of the transfer time and the age group was significant in 2010 and 2011 ($P = 0.065$ in 2009; $P = 0.017$ in 2010; $P = 0.012$ in 2011). The interaction was significant due to the significant BB% differences ($P < 0.05$) in some transfers (transfers 2, 4 and 5 in 2009, transfers 2 and 4 in 2010, transfers 2, 3 and 4 in 2011). However, no systematic age effect was found, as the order of the BB% values of age groups varied irregularly from year to year and from transfer to transfer (see the crossing lines in Figure 2).

The effect of the transfer time on DBB was significant ($P < 0.001$), and the pattern of DBB development over the transfers was similar in all 3 years as DBB decreased in every year continuously with successively later transfers with increased accumulated previous chilling (Figure 3, see Figure S2 available as Supplementary Data at *Tree Physiology* Online). DBB was not dependent on the age of the tree ($P = 0.077$ in 2009; $P = 0.920$ in 2010; $P = 0.688$ in 2011). The interaction of the transfer time and the age group was not significant in any of the 3 years (in all years $P > 0.326$).

Primordial shoot ratio, PSR, depended significantly on the age of the scion ($P < 0.001$). The average PSR values of the two oldest age groups of grafts, 0.30 and 0.36, representing 80- and 32-year-old trees, respectively, were both significantly lower than either of the two younger age groups representing the 16-year-old trees (0.44 and 0.46 for Elimäki and Juva origins, respectively) (in all comparisons $P < 0.021$) (Table 3). The average PSR values of the two oldest age groups did not differ from each other ($P = 0.064$), and similarly the values of the two youngest age groups did not differ from each other ($P = 0.658$).

Discussion

Endodormancy release in Norway spruce

In all 3 years of the present study, BB% was in mid-October at or near zero indicating that all, or most, of the buds were in endodormancy at that time. BB% generally increased with accumulated chilling, indicating that endodormancy was released (Figure 2, see Figure S1 available as Supplementary Data at *Tree Physiology* Online). With some exceptions, BB% exceeded 80% in a time window from mid-November to December. From January to April, BB% varied in general between 80 and 100%. In the transfer of 23 February 2011, however, BB% was exceptionally low. This may have been due to the stress caused by the exceptionally low air temperature (<−20 °C) at the time the grafts were transferred from below the snow to the open air.

Similarly to BB%, DBB was not dependent on the age of the tree, as it decreased with accumulated chilling similarly in all of the age groups (Figure 3, see Figure S2 available as Supplementary Data at *Tree Physiology* Online). This inverse relation of chilling and forcing on vegetative budburst has been found in several earlier studies, not only with spruce species (Nienstaedt 1967, Worrall and Mergen 1967, Viherä-Aarnio et al. 2014) but also with other tree species (Cannell and Smith 1983, Myking and Heide 1995). This decrease is usually interpreted to be a manifestation of the gradual effect of chilling on endodormancy release. Accordingly, with increased chilling the rate of internal microscopic development of the bud is increased so that the time required for bud burst in the forcing conditions is decreased until the DBB curve levels off when the chilling requirement is met (Hänninen 2016 and references therein).

In all, contrary to our hypothesis, our BB% and DBB observations did not show any differences in the timing of endodormancy release among grafts representing trees of varying ages. Furthermore, based on the bud burst percentage in the regrowth test the time of endodormancy release was in late autumn, in most cases in November (Figure 2, see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Similar results have been previously found for 2-year-old seedlings of Norway spruce (Nienstaedt 1967, Hänninen and Pelkonen 1988, 1989, Hänninen 1990). With the exception of the study of Nienstaedt (1967), similar central Finnish Norway spruce provenances as examined in the present study with grafts were addressed in the earlier studies with seedlings. Taken together, these findings suggest that no major change takes place in the environmental regulation of endodormancy release in Norway spruce when the trees get older. Rather, both small seedlings and 80-year-old trees appear to follow the traditional conceptual model of endodormancy release (Hänninen 2016, p. 94): chilling is the main driving force of endodormancy release, and the chilling requirement is met by mid-November (however, see also Basler and Körner 2012).

The findings support the traditional conceptual model (Hänninen 2016) and also suggest that as the growth-arresting physiological conditions are removed during autumn, the trees run a high risk of premature bud burst during the mild periods projected to occur frequently under climatic warming in winter and early spring, with a high risk of damage occurring during subsequent periods of frost (Hänninen 1991, 2006). However, for two reasons this projection may not be realized. First, Basler and Körner (2012) found that in Norway spruce photoperiods shorter than the one used in the forcing conditions of the present study (12 h) delay endodormancy release and bud burst. Second, it should be noted that the computer simulations implying the projection of increased frost damage are based on the prevailing dichotomy of concepts stating categorically that either physiological (endodormancy) or environmental (ecodormancy) factors prevent during dormancy the vegetative bud burst and subsequent growth (Doorenbos

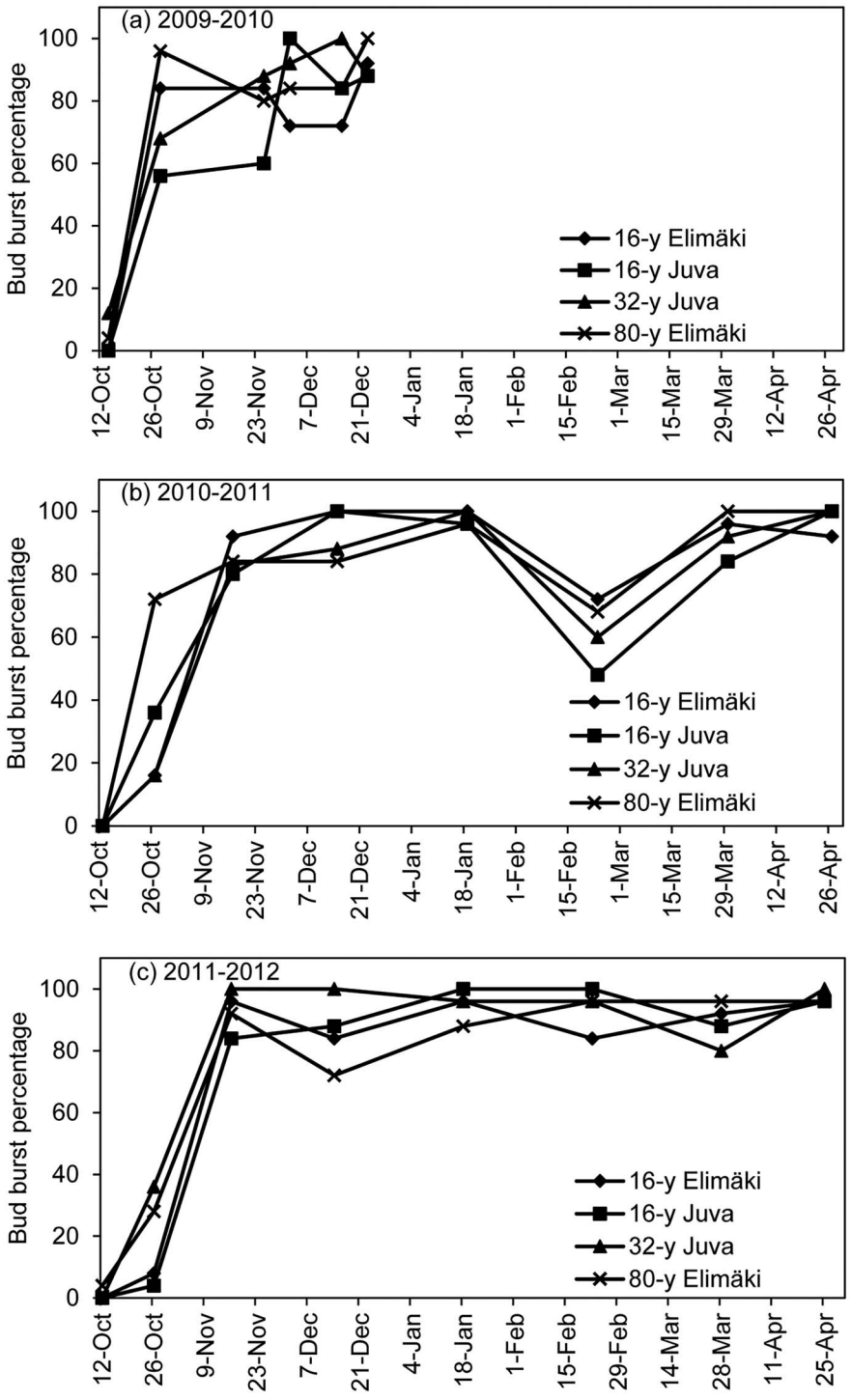

Figure 2. Average bud burst percentage, BB%, of the five uppermost buds in Norway spruce grafts representing 16-, 32- and 80-year-old trees of southern Finnish origin (Table 1) in the 2009–10 (a), 2010–11 (b) and 2011–12 (c) chilling–forcing experiments. The horizontal axes indicate the date when the grafts were transferred from outdoor natural chilling conditions (or from the preforcing conditions of +4 °C) into a regrowth test in forcing conditions in greenhouse (Table 2, Figure 1). Standard errors of mean BB% varied in 2009–10 between 0.0 and 13.2% (a), in 2010–11 between 0.0 and 11.1% (b) and in 2011–12 between 0.0 and 9.7% (c).

1953, Romberger 1963, Sarvas 1972, 1974). The dichotomy is a simplification because it does not address the interactions of physiological and environmental factors in regulating bud burst (Vegis 1964, Cooke et al. 2012, Junttila and Hänninen 2012, Lundell et al. 2020). As shown by Hänninen (2016, p. 315–316), addressing the interactions in computer simulations may considerably alter the projections for premature bud burst and increased incidence of frost damage under climatic warming.

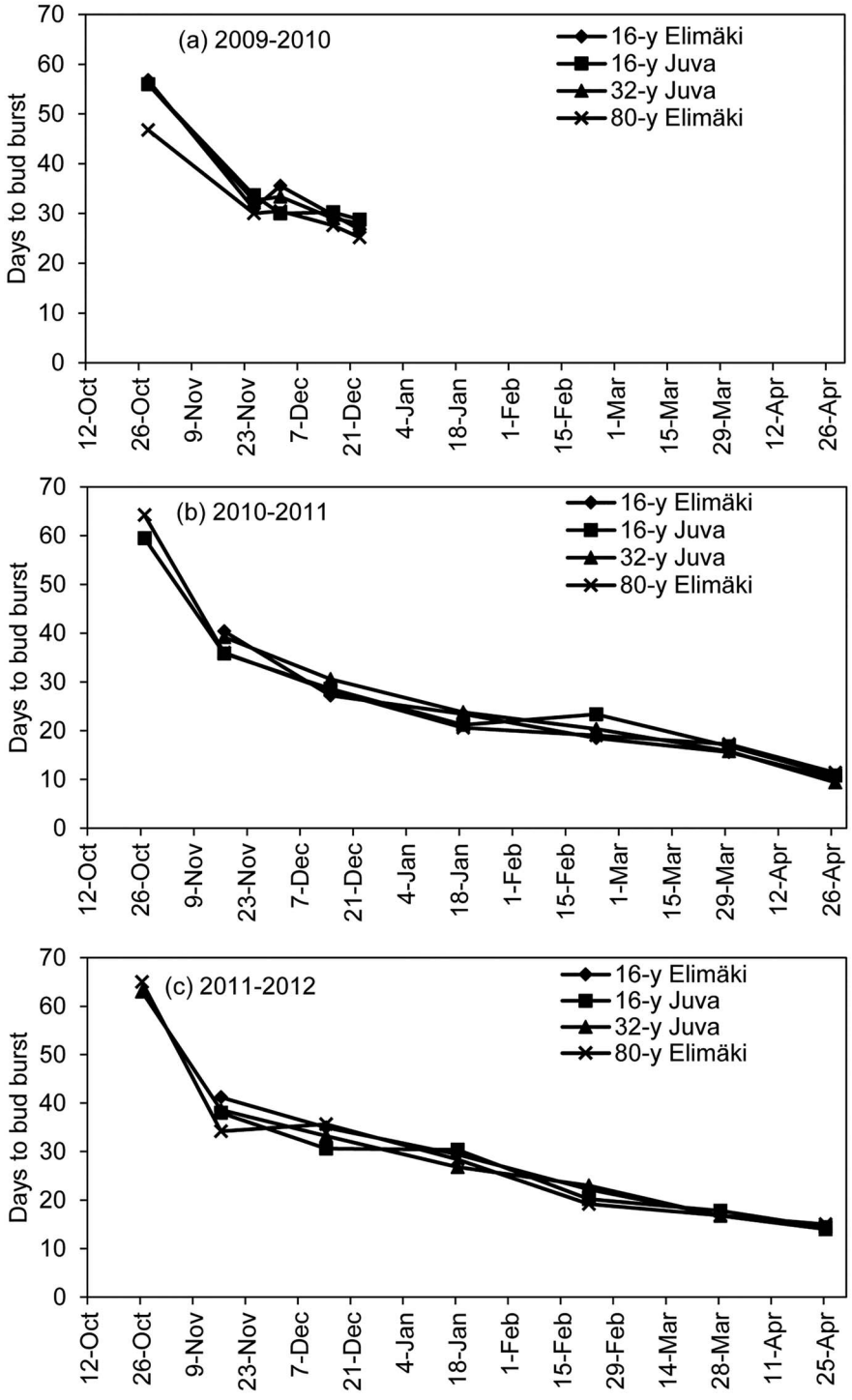

Figure 3. Average days to bud burst from the beginning of forcing, DBB, of the five uppermost buds in Norway spruce grafts representing 16-, 32- and 80-year-old trees of southern Finnish origin (Table 1) in the 2009–10 (a), 2010–11 (b) and 2011–12 (c) chilling–forcing experiments. The horizontal axes indicate the date when the grafts were transferred from outdoor natural chilling conditions (or from the preforcing conditions of +4 °C) into a regrowth test in forcing conditions in greenhouse (Table 2, Figure 1). Standard errors of mean DBB varied in 2009–10 between 2.9 and 3.7 days (a), in 2010–11 between 1.9 and 3.0 days (b) and in 2011–12 between 2.0 and 4.4 days (c).

Unfortunately, the experimental data available so far do not facilitate addressing the interactions in the computer models for any given tree species, so further experimental studies are called for.

The PSR of grafts representing 80- and 32-year-old trees was lower than that representing the 16-year-old trees. The observed PSR values in our experiment (Table 3) are in accordance with the values observed in Viherä-Aarnio et al.'s (2014) study.

They studied microscopically the internal development of buds in detached twigs of 17-year-old Norway spruce trees in an experiment otherwise similar to the present one. They found that at the beginning of the internal bud development, PSR was 0.3, increasing to 1.0 towards bud burst. They also found that the higher the accumulated chilling unit sum before starting forcing, the lower was the temperature sum that was required to initiate primordial shoot growth in the forcing conditions and the stronger was the effect of the further temperature sum accumulation on the internal microscopic development during ecodormancy release. However, in the present study, the shoot tips were taken for microscopy in an early phase of the ecodormancy release, as shown by the relatively low values of the primordial shoot ratio (PSR <0.6 in 44 out of the 48 observations, Table 3). We did not observe any differences in the timing of bud burst among the grafts representing trees of different ages. Based on this, it is obvious that the differences we observed among the graft age groups in their PSR values would have vanished if the forcing had been extended also for the microscopic observations so that the internal microscopic development of the buds had approached the bud burst stage. However, further experiments with longer forcing times are needed to confirm this.

Differences in spring phenology between seedlings and mature trees have been documented in several earlier studies (Ununger et al. 1988, Partanen et al. 2001, Vitasse 2013). It should be noted that these earlier findings are not necessary contradictory to our conclusion stating that no age-related differences were found in endodormancy release in Norway spruce. This is because any observed difference in the phenological timing in spring bud burst may be caused also by different environmental responses during spring that are not related to the endodormancy release taking place earlier (Hänninen 2016). Furthermore, in natural conditions differences in endodormancy release are not always reflected as corresponding differences in phenological timing of bud burst. This is because ontogenetic development towards bud burst takes place after endodormancy release only in sufficiently high temperatures. It is possible, then, that due to low air temperatures generally prevailing in natural conditions during winter, no ontogenetic development towards bud burst takes place after endodormancy release in a tree having an early endodormancy release, before endodormancy is released also in another tree having a late endodormancy release. In this case there would be no difference in the time of start of ontogenetic development towards bud burst between these two trees. However, this may change in the future when winters are projected to warm considerably (Hänninen 1991, 2006). In all, even though endodormancy release and spring bud burst are two different phenomena, these considerations emphasize the central role of understanding the environmental regulation of endodormancy release when projecting the effect of climatic warming on spring bud burst (Chuine et al. 2016).

Methodological limitations

Grafting is an ancient horticultural technique that has been widely utilized for propagating improved cultivars. The reason for using grafts in horticulture is the general empirical finding that the scion maintains the horticultural traits of the mature donor tree (Mudge et al. 2009). More recently grafting has been used also for breeding in forestry (Jayawickrama et al. 1991, 1997). In the present study, the use of grafts with scions representing trees of different ages was introduced for studying the endodormancy release in trees of different ages. With this method the potential problems caused by cutting the root–shoot connection involved in the use of detached twigs are avoided. However, rather than the real trees of different ages, also the grafts are a proxy of them. When using grafts as the proxy, it is possible that any effect of the rootstock on endodormancy and its release could hamper inferences made on the basis of differences in the age of the donor trees of the scions. We used 2-year-old rootstock, so if the rootstock has a major influence in the endodormancy and its release, then our main conclusion about the similar endodormancy release in seedlings and trees of different ages would be undermined. Based on some earlier studies addressing various aspects of tree ecophysiology, growth, and reproduction, such an effect of rootstock cannot be ruled out (Sorgona et al. 2007, Huang et al. 2009, Kumari et al. 2015, Gautier et al. 2019), but in other studies, the effect of scion has dominated (Melchior 1987, Jayawickrama et al. 1991, 1997, Day et al. 2001, Mencuccini et al. 2007). Most relevantly to our study, Melchior (1984) did not find any effect of the age of the rootstock in the timing of bud burst in Norway spruce grafts, thus providing support for our conclusion.

Bonhomme et al. (2013) studied the localization of chilling perception in *Prunus persica*. Their results show that rather than being transferred from one axis to the next, the effect of chilling is highly localized in tree tissue. While providing support for using both detached twigs and grafts as proxies of naturally growing trees in studies addressing the effects of chilling in endodormancy release, the findings of Bonhomme et al. (2013) do not exclude the possible artifacts caused by interrupting the root–shoot connection when using detached twigs, nor those caused by the rootstock while using grafts, as proxies of naturally growing trees.

Another potential source of error is the fact that when producing the grafts in the present study they were kept in artificial greenhouse conditions for 3 years. It is possible that long-term acclimation and even epigenetic changes occurred in the grafts during that time. However, the risk of these potential effects causing differences between the grafts and the naturally growing donor trees is reduced by the fact that before starting

the experiments, the grafts were kept in natural conditions for about 12 (experiment in 2009–10), 24 (experiment in 2010–11) or 36 months (experiment in 2011–12).

Our purpose was not to examine the differences among tree provenances. However, it was necessary to include the two provenances studied because neither of them included all of the three age classes studied. In this way the effects of age and provenance are confounded in our study so that they cannot be analyzed separately. In order to avoid any confusing effect of provenance, we selected two provenances representing as close geographical origins as possible: both Elimäki and Juva represent interior southeastern Finnish provenances. So, as our purpose was to study the effects of tree age, we maximized its variation and minimized the potentially confusing geographical variation of the provenances.

Conclusions

To our knowledge, this is the first study where grafts with scions from trees of different ages were used as a proxy for adult trees in studies of endodormancy release in boreal trees. We studied the endodormancy release with the grafts using observations at the whole-tree level and the anatomical level. The results are needed in studies carried out at the ecosystem level, especially when assessing the ecological effects of the ongoing climate change. A premature bud burst during mild periods in winter and early spring would expose trees to severe damage during subsequent periods of frost, and that would have dramatic influences on ecosystem dynamics. This hypothesis was presented decades ago but no definite conclusions concerning it are yet possible. Our results suggest that in Norway spruce, the risk of increased frost damage in a warming climate change cannot be ruled out.

Taken together with earlier findings with seedlings, our experimental findings suggest that no major change in the environmental regulation of endodormancy release takes place when the Norway spruce trees get older. In all age classes, chilling appears to be the main driving force of endodormancy release, and the chilling requirement appears to be met in the autumn. However, due to the methodological uncertainties and limitations involved in the present and in the earlier studies, more research on the interactions of physiological and environmental factors in regulating the endodormancy release, the internal microscopic bud development and finally the visible bud burst is needed.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

Authors' contributions

The study was designed by J.P., H.H., R.H. and S.S. The experiments were carried out by J.P. and S.S. The data were analyzed by J.P., with R.H. carrying out the statistical analyses. R.Z. contributed in writing the discussion addressing the possible limitations caused by using grafts as a proxy of trees of different ages. All authors contributed to the inferring the conclusions and writing the manuscript.

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