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Effects of temperature on dormancy release in Norway spruce and Scots pine seedlings

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TIIVISTELMÄ: LÄMPÖTILAN VAIKUTUS KUUSEN- JA MÄNNYNTAIMIEN DORMANSSIN PURKAUTUMISEEN

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Models concerning the effects of temperature on dormancy release in woody plants were tested using two-year old seedlings of Scots pine (*Pinus sylvestris* (L.) and Norway spruce (*Picea abies* (L.) Karst). Chilling experiments suggest that the rest period has a distinct end point. Before the attainment of this end point high temperatures do not promote bud development towards dormancy release, and after it further chilling does not affect the subsequent bud development. A new hypothesis of dormancy release is suggested on the basis of a comparison between present and earlier findings. No differences in the proportion of growth commencing seedlings were detected between the forcing temperatures of 17°C and 22°C. The rest break of 50 percent of Norway spruce and Scots pine seedlings required six and eight weeks of chilling, respectively. Great variation in the chilling requirement was found, especially for Scots pine.

Lämpötilan vaikutusta puiden dormanssin purkautumisessa kuvaavia malleja testattiin kaksivuotiailla kuusen- ja männyntaimilla. Kylmäkäsittelykokeiden tulokset viittasivat siihen, että taimien lepovaiheella on suhteellisen selvärajainen loppupiste. Korkeat lämpötilat eivät aiheuta silmun kehitystä ennen loppupisteen saavuttamista, minkä jälkeen tapahtuva lisäaltistus matalille lämpötiloille ei vaikuta myöhempään silmunkehitykseen. Vertailemalla tuloksia aikaisempien tutkimusten tuloksiin esitettiin uusi hypoteesi dormanssin purkautumiselle. Kasvun aloittavien taimien osuudessa ei havaittu eroja hyötämislämpötilojen 17°C ja 22°C välillä. Lepotila purkautui puolella taimista kuusella kuuden, ja männyllä kahdeksan viikon mittaisen kylmäkäsittelyn aikana. Lepotilan purkautumisen kylmäkäsittelyvaatimus vaihteli erityisesti männyllä suuresti.

Keywords: annual cycle of development, bud burst, chilling requirement, rest period, simulation models
ODC 161.41+181.22+174.7 *Picea abies* +174.7 *Pinus sylvestris* +181.525

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1. Introduction

A pronounced rest period is characteristic for buds of northern woody plants during autumn and early winter. During the rest period, the buds remain in a state of dormancy regardless of the prevailing environmental factors (Romberger 1963, pp. 73–76). Rest is

Table 1. Models of dormancy release considered in the study. According to Hänninen (1987).

Symbol	Concept	Explanation	Reference
Model type I	A sequential model of dormancy release	Dormancy release is simulated by the accumulation of a chilling unit sum, and a subsequential accumulation of a forcing unit sum	Sarvas 1972, 1974, Richardson et al. 1974
Model type II	A parallel model of dormancy release	Dormancy release is simulated by a parallel accumulation of a chilling unit sum and forcing unit sum. Accumulated chilling unit sum affects the rate of accumulation of the forcing unit sum	Landsberg 1974
	Model of post rest	In a late phase of rest, dormancy is released in high temperatures, but not in low temperatures	Vegis 1964

broken, i.e. the growth competence of the buds is resumed, by prolonged exposure to chilling temperatures (eg. Doorenbos 1953, Romberger 1963, pp. 157–161, Flint 1974). Rest break usually takes place relatively early during autumn or winter. After that high temperatures are required for dormancy release, i.e. for growth initiation (Perry 1971, Sarvas 1974). Thus, dormancy is not released until the temperature rises during next spring.

The dormancy release of the buds has given rise to various models (Table 1). Vegis (1964) published a conceptual model of post rest, and mathematical simulation models of dormancy release have been published by Sarvas (1972, 1974), Landsberg (1974), and Richardson et al. (1974). When examining the models Hänninen (1987) found that they are in some respects contradictory to each other.

In the sequential model (type I) (Sarvas 1972, 1974, Richardson et al. 1974) the rest period is assumed to have a strict end point. According to this, 1) the bud has to be exposed to a critical duration of chilling, specific to the genotype, before it is possible to bring about growth initiation in subsequent warm conditions; and 2) after the critical amount of chilling has been met, further chilling does not affect the subsequent bud development. On the contrary in the parallel simulation model (type II) (Landsberg 1974), the effect of chilling in breaking the rest is assumed to be gradual. Thus, no strict end point of the rest period, or critical amount of chilling required for breaking rest are assumed. According to the model of post rest (Vegis 1964), dormancy release takes place in a late phase of rest at high temperatures, but not at low temperatures (Hänninen 1987).

Hänninen (1987) deduced contrasting implications of these models. With these implications it is possible to test the models using various types of chilling experiments. The purpose of this study is to 1) test the models examined by Hänninen (1987), using two-year-old seedlings of Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.), and 2) to examine the chilling requirement for breaking rest of the seedlings.

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2. Materials and methods

2.1 Experimental design and implications of the models

The treatment of each treatment group consisted of two parts: 1) a chilling period in a chilling chamber, and 2) a subsequent forcing period in warm conditions. The duration of the chilling period was varied between 0 and 10 weeks among the groups. For each of the six durations of chilling, two treatment groups were established which were subsequently forced in either 17°C or 22°C. In total 12 treatment groups of 15 seedlings each were established for both species.

In the forcing conditions, a regrowth test was carried out by determining the values of two variables for each treatment group (Hänninen 1987): 1) dormancy release ratio (DRR) which is the proportion of the seedlings for which dormancy was released, out of the total number of surviving seedlings in the group; and 2) mean days to bud burst ($\overline{DBB}$) which is the mean number of days, counted from the date of transfer to the forcing conditions, to the date of growth commencement. Testing of the models takes place by plotting the values of DRR and $\overline{DBB}$ against duration of chilling. Model type I implies an increasing DRR-curve (Fig. 1a), and a constant $\overline{DBB}$-value (Fig. 1b), while model type II implies a constant value of unity for DRR (Fig. 1c), and an exponentially declining $\overline{DBB}$-curve (Fig. 1d). According to the model of post rest, the DRR-curve starts to rise in a high forcing temperature at a shorter duration of chilling, than in a low forcing temperature (Fig. 1e).

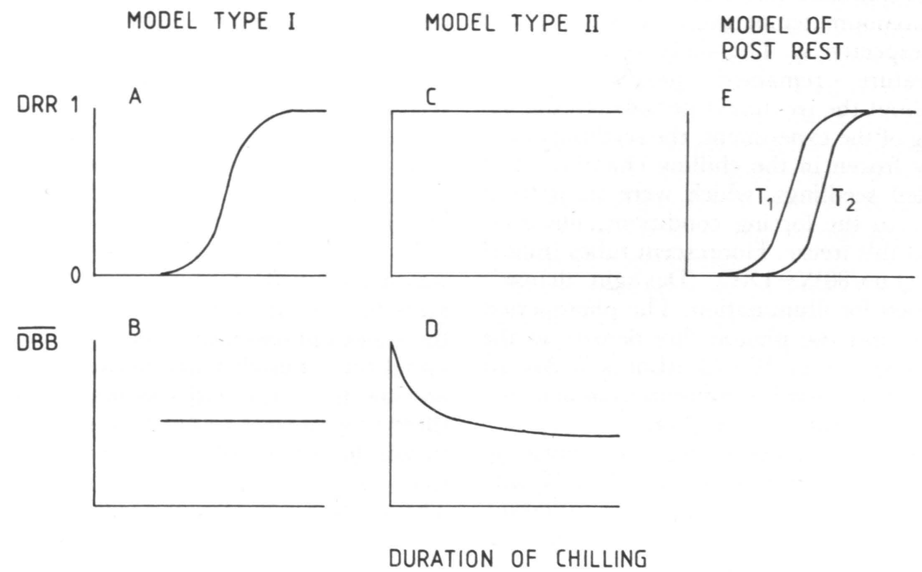

Fig. 1. Implications of the three models concerning the values of dormancy release ratio (DRR), and mean days to bud burst ($\overline{DBB}$), as a function of duration of previous chilling. DRR gives the proportion of the seedlings which began to grow, of all seedlings of the treatment group. $\overline{DBB}$ gives the mean number of days required for height growth starting, counted from the beginning of the forcing period. T_1 refers to a high, and T_2 to a low forcing temperature. According to Hänninen (1987).

2.2 Raising of the seedlings and growing conditions

The seedlings were grown at the Suonenjoki commercial nursery (62°40'N, 27°00'E, altitude 130 m asl) in Central Finland using seeds of local origin. Seeds of Scots pine were sown on May 30, 1984 in a mixture of peat and sand in plastic containers, model 'Enso'. Seeds of Norway spruce were sown on May 16, 1984 in peat in paper pots. At the time of sampling, the Norway spruce seedlings were transplanted to 'Enso'-containers.

Seedlings of Scots pine were transferred outdoors on Aug. 13, 1984, and those of Norway spruce on Sept. 3, 1984. At the end of their second growing season, on Sept. 11, 1985, the seedlings were transferred to the Botanical Garden of University of Joensuu (62°36'N, 29°43'E, 81m asl), where experimental treatments were initiated on Sept. 13. The duration of the experiment was 186 days.

In total, three growing conditions were used. Temperature was monitored in the growing conditions by thermographs.

The chilling treatments were given in a growth chamber. The daily minimum, mean and maximum temperatures were 0, 1 and 7°C, respectively. The daily course of the temperature remained nearly constant throughout the treatment periods. In the beginning of the experiment, the seedlings were slightly frozen in the chilling chamber. The unchilled seedlings, which were transferred directly to the forcing conditions, however, avoided this freeze. Fluorescent tubes (model Airam L65/80W−1XC, 'Daylight deluxe') were used for illumination. The photoperiod was 8h, and the photon flux density at the plant height was 10−20 $\mu Em^{-2}s^{-1}$. An air circulator was used to minimize temperature gradients within the chamber.

Forcing took place in the greenhouse, in two growing conditions, nominally 17°C and 22°C. Because of incoming solar radiation, daily maximum temperatures rose above the intended values during the first and last weeks of the experiment. During the first month of the experiment, no artificial light was supplied, natural daylength decreased during that time from about 13.2 to 10 hours. After that, the same kind of fluorescent tubes as in the chilling chamber, were used to supplement natural light and to increase the length of the photoperiod to 12h. Photon flux density was 5−35 $\mu Em^{-2}s^{-1}$ at plant height after sunset. During daytime more light reached the growing places, during sunny weather the photon flux density was 40−80 $\mu Em^{-2}s^{-1}$.

During chilling, no watering of the seedlings took place. Otherwise, the seedlings were watered regularly to keep the growing substrate near water saturation.

2.3 Determination of the starting day of height growth

The starting day of height growth of Norway spruce seedlings was determined by visual inspection of the terminal bud. The inspection was carried out two or three times a week. At each inspection the growth status of the bud was recorded using one of the following three characters: 0 = dormant; + = swelling, but no new needles visible; 1 = new needles visible. The starting day of each seedling was determined as the median day between the last "+"-sign and the first "1"-sign. If the new needles did not appear, then the seedling was considered not to be growing.

In the case of Scots pine, the starting day was determined by measuring terminal bud growth. A small needle was pushed through the shoot approximately 5mm below the terminal bud. The distance between the needle and the tip of the bud was measured two or three times a week to the nearest 0.5mm. The values for days without a measured value were determined with linear interpolation. The starting day of each seedling was determined as the day, when the growth attained was ten per cent of the total growth for the year. Additionally, if the total growth was less than 5mm, then the seedling was considered not to be growing.

3. Results and discussion

Few seedlings of Norway spruce survived after the 8- and 10-week chilling treatments, thus reducing the final sample size. This may explain the unexpected decline in the DRR-values corresponding to forcing in 22°C, after 10 weeks of chilling (Fig. 2a). In that group three seedlings survived, only one of which exhibited terminal bud growth. In Scots pine the dormancy release ratio increased almost linearly after four weeks of chilling in both forcing temperatures (Fig. 3a).

With the exception of the outlier discussed above, the DRR-patterns conform well with model type I (Fig. 1a), and disagree with model type II (Fig. 1c).

The DBB-curves generally declined with increasing chilling (Figs. 2b,3b). This result is in a better agreement with model type II (Fig. 1d) than with model type I (Fig. 1b). The reliability of the DBB-curves is, however, low due to the small final sample size and large variation (Figs. 2b,3b).

In conclusion: our preliminary data are not in a strict agreement with either of the models. The data conform, however, more closely with model type I than with model type II. This is because 1) no dormancy release at all took place after short durations of chilling, and 2) the DBB-curves supporting model type II are less reliable than the DRR-curves supporting model type I.

One possible reason for the decline of the DBB-curves is, that after rest break, bud development towards dormancy release may already begin in chilling conditions. In the terms of the models this means, that forcing units are accumulated also in the chilling conditions (cf. Sarvas 1974, p. 43). This was not assumed, when the implication presented in Fig. 1b was inferred (Hänninen 1987). According to this new assumption, 1) an increasing DRR-curve, and 2) a slightly declining DBB-curve is expected. Our data are in agreement with this modified model type I (Figs. 2,3).

Most previous studies have yielded exponentially declining DBB-curves (Fig. 1d), thus supporting model type II (eg. Landsberg 1974, Ritchie 1984, Cannell et al. 1985). This has also been the case with Scots pine (Hoffman and Lyr 1967), and Norway spruce (Worrall and Mergen 1967, Nienstaedt 1967). The exponentially declining DBB-curve is normally interpreted to reflect the gradually changing rest status of the buds. Our data suggest, that no such gradual progression exists in the populations we were studying. On the contrary, our data support the model of a strict end point of the rest period. According to that model, high temperatures do not promote bud development before that point, and further chilling thereafter does not substantially affect the rate of the subsequent bud development.

Hänninen and Pelkonen (1988) carried out a chilling experiment with forcing in 12°C, with the same seedling populations which were used in the present study. The growth status of the seedlings was checked twice: 120 and 240 days after the beginning of the experiment. At the first check, only seedlings chilled at least for ten (Scots pine), or six (Norway spruce) weeks had started to grow. On the contrary at the second check, a large part of even the unchilled seedlings had resumed growth. Thus, these data implicate a deeply declining DBB-curve, even though the exact form of the curve is not known due to the scarcity of observations.

In comparison with the present results the data of Hänninen and Pelkonen (1988) suggest that 12°C has a slight chilling effect on the seedlings (cf. Sarvas 1974, p. 29, Campbell and Sugano 1975, 1979). According to that, the critical chilling unit sum of the end point of the rest period is attained in the forcing conditions of 12°C, if it was not attained during the previous chilling period. The amount of "chilling" required in the forcing conditions diminishes, as the duration of the previous chilling period increases. As a result, the value of DBB declines with increasing chilling. During a chilling period longer than a specific minimum, the rest break takes place already in the chilling conditions, and the value of DBB will no longer

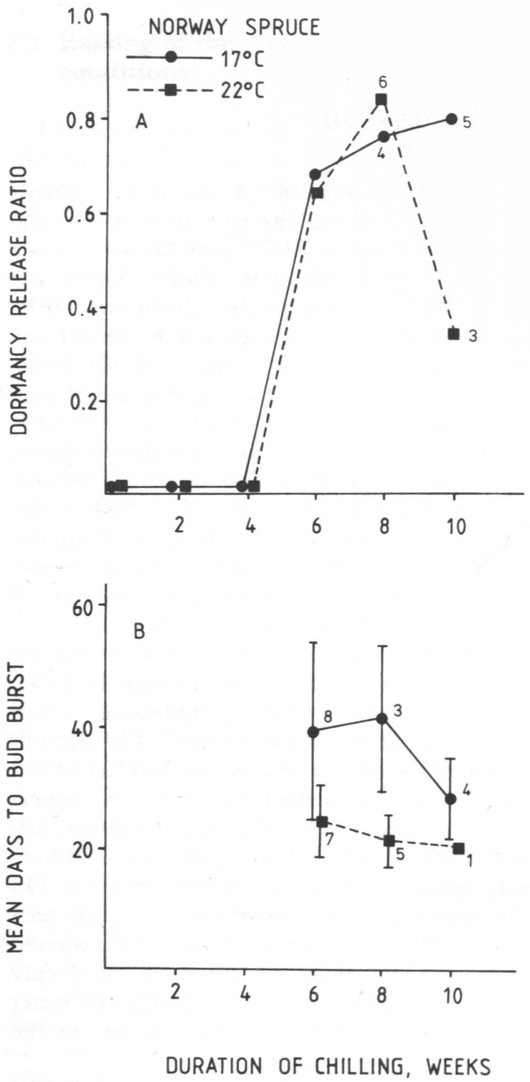

Fig. 2. a. Dormancy release ratio (DRR), and b. mean days to bud burst ($\overline{DBB}$±S.D.) for two year old Norway spruce seedlings in two forcing temperatures, as a function of duration of previous chilling. Original sample size = 15, final sample sizes below 10 as indicated by figures. Final sample size for DRR is the number of seedlings surviving until the end of the experiment, and for $\overline{DBB}$ the number of growth commencing seedlings.

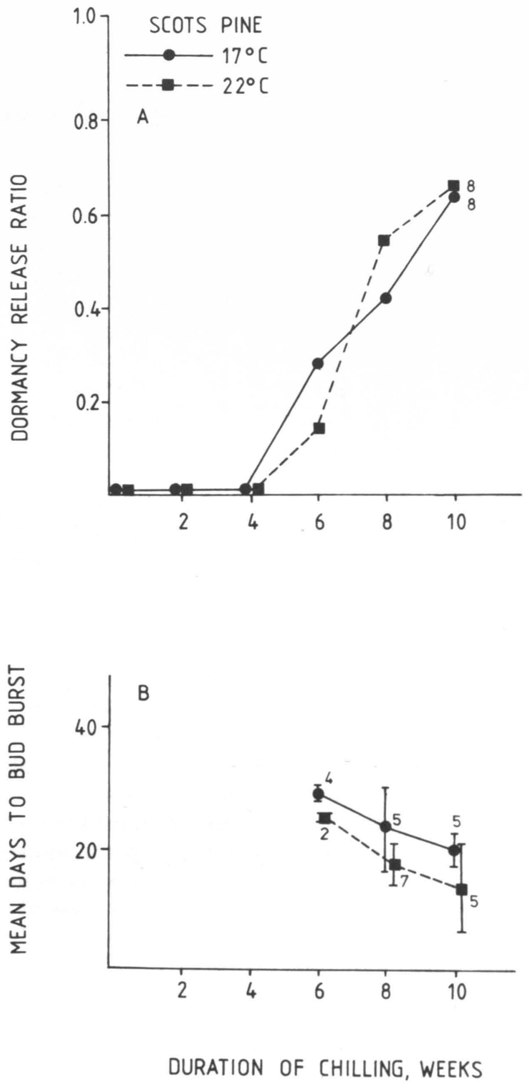

Fig. 3. a. Dormancy release ratio (DRR), and b. mean days to bud burst ($\overline{DBB}$±S.D.) for two year old Scots pine seedlings in two forcing temperatures as a function of duration of previous chilling. Original sample size = 15, final sample sizes below 10 as indicated by figures.

decline with increasing chilling. Thus in all, an exponentially declining $\overline{DBB}$-curve (Fig. 1d) results, when the seedlings are forced in 12°C.

On the basis of the above reasoning, the following hypothesis is put forward: 1) dormancy release takes place according to model type I in all cases: a critical chilling unit sum must be accumulated, before dormancy can subsequently be released in high temperatures; and 2) the upper limit for chilling temperatures varies among species, and populations of a given species (cf. Sarvas 1974, p. 29, Fuchigami et al. 1982). In this way also the previous results with exponentially declining $\overline{DBB}$-curves can be explained with model type I. According to this explanation the upper limit for chilling temperatures was higher in the previous studies, than in the present one.

In the case of Scots pine seedlings forced in 12°C, the DRR-curve first dropped from about 0.7 at zero weeks of chilling to zero at four weeks of chilling (Hänninen and Pelkonen 1988). This result was explained by assuming 1) a slight chilling effect of 12°C, and 2) a change in the temperature response of rest break of the seedlings. The DRR-curve started again to rise at ten weeks of chilling. In the present study, the DRR-curves at higher forcing temperatures had allready begun to rise at six weeks of chilling. This difference is in agreement with the model of post rest (Fig. 1e). According to that, 12°C is a "low" forcing temperature, and 17°C and 22°C "high" forcing temperatures, with respect to the post rest model (Vegis 1964, Hänninen 1987). In any case, these findings suggest that temperatures slightly above 10°C have very complicated effects on dormancy release of the seedlings.

Dormancy was released for 50 per cent of the Scots pine and Norway spruce seedlings after about eight and six weeks of chilling at approximately +1°C, respectively. Thus, the chilling requirement of Norway spruce seems to be smaller than that of Scots pine. The results indicate large variation in the chilling requirement for both species, but especially for Scots pine (Figs. 2a,3a).

The differences between the DRR- and $\overline{DBB}$-curves found and those found in earlier studies (Hoffman and Lyr 1967, Worrall and Mergen 1967, Nienstaedt 1967) makes any comparison between chilling requirement values cumbersome. In many cases in the previous studies, even the unchilled plants began to grow, though only after prolonged forcing. Thus in this respect, the amount of chilling required for subsequent dormancy release was greater in our study than in the previous ones. However, if the levelling point of the $\overline{DBB}$-curve is taken as an indicator of rest break (Lamb 1948, Worrall and Mergen 1967) in the previous studies, and its value is compared to the duration of chilling corresponding to the value of 0.5 of DRR in our results, then there appears to be no striking differences among the values of chilling requirement obtained in the studies.

The study problem and experimental design of this study were developed with the aid of previously published models. Facilitation of experimental work is not, however, the only way of using the models. If a thoroughly tested quantitative model is available, it can be used for attacking various practical problems in horticulture and forestry (Campbell 1974, Campbell and Sugano 1979, Cannell and Smith 1983, 1986, Cannell 1985, Cannell et al. 1985).

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