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Effect of increased winter temperature on the onset of height growth of Scots pine: a field test of a phenological model

Heikki Hänninen, Seppo Kellomäki, Kaisa Laitinen,
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TIIVISTELMÄ: TALVIAIKAISEN ILMAN LÄMPÖTILAN KOHOAMISEN VAIKUTUS MÄNNYN PITUUSKASVUN ALKAMISEEN: FENOLOGISEN MALLIN TESTAUS KENTTÄKOKEESSA

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According to a recently presented hypothesis, the predicted climatic warming will cause height growth onset of trees during mild spells in winter and heavy frost damage during subsequent periods of frost in northern conditions. The hypothesis was based on computer simulations involving a model employing air temperature as the only environmental factor influencing height growth onset. In the present study, the model was tested in the case of eastern Finnish Scots pine (*Pinus sylvestris* L.) saplings. Four experimental saplings growing on their natural site were surrounded by transparent chambers in autumn 1990. The air temperature in the chambers was raised during the winter to present an extremely warm winter under the predicted conditions of a doubled level of atmospheric carbon dioxide. The temperature treatment hastened height growth onset by two months as compared to the control saplings, but not as much as expected on the basis of the previous simulation study. This finding suggests that 1) the model used in the simulation study needs to be developed further, either by modifying the modelled effect of air temperature or by introducing other environmental factors, and 2) the predicted climatic warming will not increase the risk of frost damage in trees as much as suggested by the previous simulation study.

Äskettäin esitetyn hypoteesin mukaan ennustettu ilmaston lämpeneminen aiheuttaa pohjoisten puiden pituuskasvun alkamisen talvella esiintyvien leutojen jaksojen aikana ja vakavia vaurioita puille kasvuunlähtöä seuraavien pakkasjaksojen aikana. Hypoteesi perustuu tietokonesimulointeihin mallilla, jonka mukaan ilman lämpötila on ainoa puiden kasvuunlähtöön vaikuttava ympäristötekijä. Mallia testattiin Itä-Suomessa luontaisella kasvupaikallaan kasvavilla nuorilla männyillä (*Pinus sylvestris* L.). Neljä koemäntyä ympäröitiin syksyllä 1990 läpinäkyvillä kammioilla. Kammioiden ilmaa lämmitettiin talvella siten, että lämmityskäsittely vastasi poikkeuksellisen lämmintä talvea tilanteessa, jossa ilmasto on lämmennyt hiilidioksidipitoisuuden kaksinkertaistumista vastaavien ennusteiden mukaisesti. Lämmityskäsittely aikaisti koemäntyjen kasvuunlähtöä kahdella kuukaudella verrattuna kontrollimäntyihin, mutta kuitenkin vähemmän kuin aikaisemman simulointitutkimuksen perusteella oli ennustettu. Tulokset viittaavat siihen, että 1) ennusteen johtamisessa käytettyä mallia joudutaan kehittämään edelleen, joko muuttaen mallitettua ilman lämpötilan vaikutusta tai

ottaen malliin mukaan toisia ympäristötekijöitä, ja 2) ilmaston lämpeneminen ei kasvata puiden pakkasvaurioriskiä niin paljon kuin aikaisemman simulointitutkimuksen perusteella oletettiin.

Keywords: bud burst, climatic change, frost damage, *Pinus sylvestris*.
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1 Introduction

The recent predictions of a global climatic warming have given rise to the question of how natural and cultivated plants would grow and develop in changing environmental conditions. In the case of trees from cool and temperate regions, the synchronization of the annual developmental cycle of the trees with the annual temperature cycle of the growing site is crucial to their survival and growth. Cannell and Smith (1983,1986) and Murray et al. (1989) developed a simulation approach to examine the effects of the climatic warming on the timing of height growth onset and on the incidence of frost damage in the trees. They found various patterns of change in the timing of growth onset for scenario conditions in Scotland, some of the patterns suggesting an increased incidence of frost damage. Hänninen (1991) applied a similar simulation approach in Finnish conditions, using a model developed for Finnish tree species (Sarvas 1972,1974, Hänninen 1990a). In the scenario simulations, growth onset took place in some years during mild spells in winter, which were followed by periods of frost reaching –25 °C. According to these simulations, the predicted climatic warming will cause heavy frost damage to trees in Finnish conditions.

The simulation models of height growth onset have been developed in close connection with experimental studies (see Fuchigami et al. (1982), Cannell (1989,1990) and Hänninen (1990b) for reviews). Most of the experiments, however, have been carried out in strictly artificial conditions, i.e. in growth chambers or in greenhouses. The purposes of the present study were (i) to test the model for height growth onset (Sarvas 1972,1974, Hänninen 1990a) with saplings of Scots pine (*Pinus sylvestris* L.) in semi-controlled Finnish field conditions corresponding to one extremely warm winter among those predicted to prevail at the site after climatic warming; and (ii) on the basis of the test, to assess the risk of increased incidence of frost damage in the trees following climatic warming.

2 Materials and methods

2.1 Study area and experimental set up

The experiment was carried out in a naturally regenerated 20–30-year-old Scots pine stand in eastern Finland near the Mekrijärvi Research Station (62°47'N, 30°58'E, 144 m a.s.l.). The trees are growing on sandy soil of low fertility. The mean annual temperature and rainfall at the site are +2.0 °C and 600 mm, respectively. No management practices had been carried out at the site.

Four experimental saplings of Scots pine (height 2–3 m) were surrounded by chambers (2.5 m × 2.5 m × 3.5 m) in October 1990 (Fig. 1). The south- and westward walls of the chambers were constructed of radiative heating glass, and the north- and eastward walls of greenhouse plastic. Below ground level, the walls were constructed by placing styrox plates (50 mm in thickness) about a half meter into the soil. A shutter of 1.5 m × 1.5 m in size was constructed on top of the chambers. During wintertime, the shutters were kept closed and snow was shovelled into the chambers to keep the precipitation similar to open air conditions. In spring the shutters were opened during sunny weather to prevent excess heating of the saplings. Artificial heating of the chambers ceased at the beginning of May 1991. Thereafter the shutters were kept open.

At the time the chambers were constructed, two control saplings growing in the open were selected for the experiment. The air temperature was monitored in one chamber and in the open by thermohydrographs (model 'Lambrect 252') located in standard meteorological screens. The daily maximum, mean, and minimum temperatures were determined on the basis of 24 hourly observations.

Fig. 1. Chambers used in the study. Photograph by Jaakko Kettunen.

2.2 Temperature treatment

The air temperature in the chambers was regulated during the winter according to a predetermined pattern. The temperature pattern was designed on the basis of two criteria.

(i) The pattern is expected to be realized in the future at the site as a result of a doubled level of atmospheric carbon dioxide. The patterns fulfilling this criterion were determined by increasing the daily mean temperatures in a temperature record over 73 years based on the predicted increase, i.e. by 4.3–5.1 °C, depending on the month (Bach 1987, Kettunen et al. 1987, Hänninen 1991).

(ii) Among the 72 potential patterns obtained in (i), the experimental temperature pattern applied in the study was selected by requiring it to cause premature growth onset during winter, according to the simulations of Hänninen (1991). This criterion specified that the experimental temperature pattern had to have more above zero temperatures during winter than an average winter in the predicted conditions (Fig. 2). Further, contrary to many of the potential patterns, heavy frosts were not allowed in the experimental temperature pattern (Fig. 2c). Air temperature in the open (control saplings) during winter was most of the time below 0 °C (Fig. 2). Daily minimum temperatures in the open during winter were frequently between –20 °C and –30 °C (Fig. 2c).

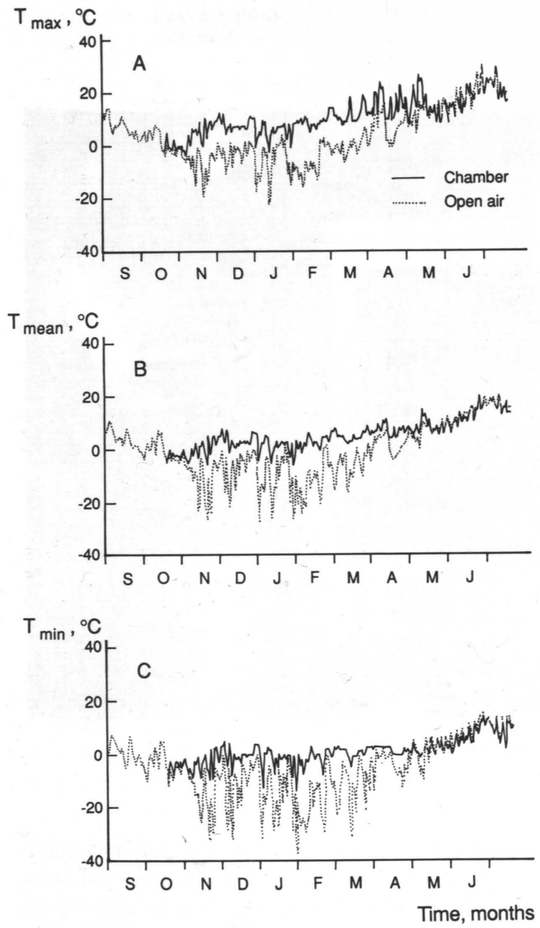

Fig. 2. Daily (A) maximum, (B) mean, and (C) minimum temperatures in the open air (control saplings) and in one of the chambers (experimental saplings) during the experiment. Until mid-October both the control and the experimental saplings were exposed to open-air temperatures.

2.3 Determination of height growth onset

The height growth of nine buds in each of the four experimental and two control saplings was observed from September 1990 to October 1991. The selected buds in each sapling were the terminal bud of the sapling, and the terminal buds of two twigs in each of its four uppermost whorls. A small needle was pushed through the stem approximately two centimeters below the bud, and the distance between the tip of the bud and the needle was measured twice a week. The height growth values for days without a measured value were determined with linear interpolation. The time for growth onset of each of the buds was determined as the day elongation exceeded ten percent of the final elongation of the shoot (Hänninen and Pelkonen 1988).

2.4 Test of the model for height growth onset

In the model tested in the present study (Sarvas 1972,1974, Hänninen 1990a), air temperature is the only environmental factor affecting the timing of height growth onset. After growth cessation, prolonged exposure to chilling temperatures is required for rest break, i.e. for attaining the growth competence of the buds. After rest completion, prolonged exposure to temperatures above 0 °C is necessary for ontogenetic development leading to growth onset. These temperature requirements are simulated in the model by accumulating specific developmental units on the basis of temperature data. Chilling units (CU) are accumulated in order to describe the effects of chilling on the rest break of the buds. The rate of chilling at time instant t, $M_{chl}(t)$ (unit CU day^{-1}), is calculated in the model as follows:

$$M_{chl}(t)=\begin{cases} 0\ \text{CU day}^{-1}, & T(t)\le -3.4\ \text{C°} \\ a_1\cdot T(t)+a_2, & -3.4\ \text{C°}< T(t)\le 3.5\ \text{C°} \\ a_3\cdot T(t)+a_4, & 3.5\ \text{C°}< T(t)\le 10.4\ \text{C°} \\ 0\ \text{CU day}^{-1}, & T(t)>10.4\ \text{C°} \end{cases} \qquad (1)$$

where T(t) = air temperature, a_1 = 0.159 CU day^{-1} °C^{-1}, a_2 = 0.506 CU day^{-1}, a_3 = –0.159 CU day^{-1} °C^{-1}, and a_4 = 1.621 CU day^{-1}. The state of chilling at time instant t, $S_{chl}(t)$ (unit CU), is calculated by integrating the rate of chilling from the moment of rest initiation, t_{RI}, up to the time instant t:

$$S_{chl}(t)=\int_{t_{RI}}^{t} M_{chl}(\tau)\,d\tau \qquad (2)$$

The moment of rest initiation, t_{RI}, is arbitrarily set at September 1. Rest is completed when S_{chl} attains a genotype-specific critical value CU_{crit} (chilling requirement of rest completion):

$$S_{chl}(t)\ge CU_{crit} \qquad (3)$$

After rest completion, forcing units (FU) are accumulated in order to describe the effects of high temperature exposure on the ontogenetic development towards growth onset. The rate of forcing at time instant t, $M_{frc}(t)$ (unit FU day^{-1}), is calculated as follows:

$$M_{frc}(t)=\begin{cases} 0\ \text{FU day}^{-1}, & T(t)\le 0\ \text{C°} \\ \dfrac{a_5}{1+\exp(a_6\cdot(T(t)-a_7))}, & T(t)>0\ \text{C°} \end{cases} \qquad (4)$$

where T(t) = air temperature, a_5 = 28.361 FU day^{-1}, a_6 = –0.185 °C^{-1}, and a_7 = 18.431 °C. The state of forcing at time instant t, S_{frc} (unit FU), is calculated by integrating the rate of forcing from the time of rest completion, t_{RC}, up to the time instant t:

$$S_{frc}(t)=\int_{t_{RC}}^{t} M_{frc}(\tau)\,d\tau \qquad (5)$$

Height growth onset occurs when S_{frc} attains a genotype-specific critical value, i.e. the forcing requirement of growth onset:

$$S_{frc}(t)\ge FU_{crit} \qquad (6)$$

The model (1)–(6) predicts that growth onset of a specified tree genotype takes place in any given temperature conditions when the accumulation of chilling units from September 1 attains a given critical value, and the subsequent accumulation of forcing units attains another critical value. The model was tested in the present study by analysing the accumulation of chilling and forcing units for the control and experimental saplings. In the test, the units were accumulated with a time step of one day, i.e. the daily mean rates of chilling (Eqn. 1) and forcing (Eqn. 4) were calculated as a function of the daily mean temperature, and the integrations (Eqns. 2 and 5) were carried out by summing the corresponding mean daily rates.

Starting from September 1, chilling units were first accumulated until they attained a critical value, CU_{crit}. Five values of CU_{crit}, ranging from 10 to 50 chilling units, were used in the calculations, since the exact chilling requirements of rest completion for the examined trees are not known (Hänninen 1990b). Subsequently, the accumulation of forcing units from the day following the attainment of the specified value of CU_{crit} until the mean day of growth onset (mean value of the 18 and 36 buds in the control and experimental saplings, respectively), was calculated for each applied value of CU_{crit}. If the model is valid, then the accumulation of forcing units at the time of growth onset must be approximately the same for the control and experimental trees with one of the applied values of CU_{crit}.

3 Results and discussion

On the average growth onset took place on May 30 in the control saplings and on April 3 in the experimental saplings (Table 1). The accumulation of forcing units required for growth onset after the accumulation of 30 chilling units was about 150 units in the control (Fig. 3a) and 230 units in the experimental saplings (Fig. 3b). According to the model prediction, the height growth onset of the experimental trees should have taken place at approximately the beginning of March, i.e. with the same accumulation of forcing units (150 FU) as in the case of the control trees (Fig. 3). Thus, the experimental treatment hastened growth onset by about two months, but the hastening was about one month less than what the model tested in the present study had predicted.

The difference in accumulation of forcing units between the control saplings and experimental saplings was similar with all five values of CU_{crit} applied in the calculations (results given only for CU_{crit} = 30 CU in Fig. 3), i.e. the model failed to predict the timing of growth onset with all of the applied values of CU_{crit}. Thus, the model needs to be developed further, either by modifying the modelled effect of air temperature or by intro-

Table 1. Julian dates of height growth onset in control (total: 18 buds in two saplings) and experimental saplings (total: 36 buds in four saplings).

	Control	Experimental
$\bar{x}$	150 (May 30)	93 (Apr 3)
S.D.	2	6
Min	146	80
Max	153	109

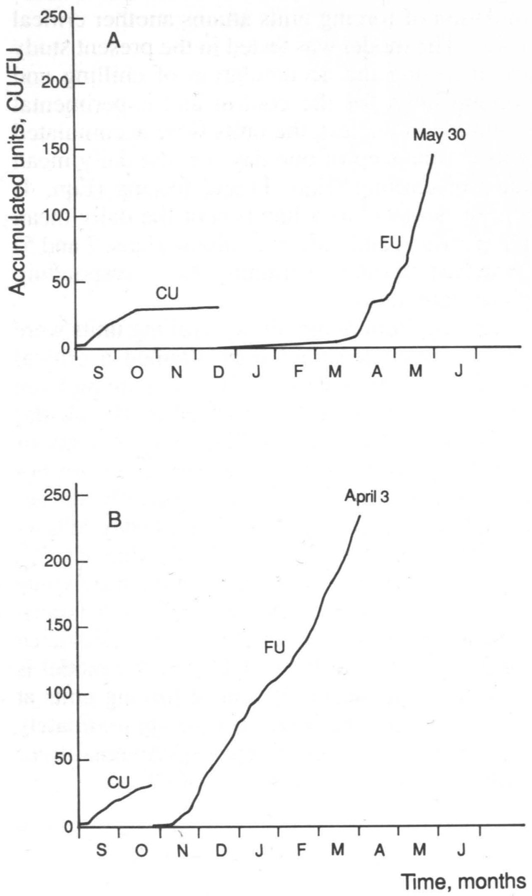

Fig. 3. Accumulation of chilling units from September 1 until the value of 30 CU is attained, and subsequent accumulation of forcing units until the mean day of growth onset, in (A) control and (B) experimental saplings.

ducing other environmental factors.

The model tested in the present study (Sarvas 1972,1974, Hänninen 1990a) involves two types of parameters. The first type, a_1–a_7, determine the temperature response of the rates of the two biological processes considered, i.e. rest break (Eqn. 1) and ontogenetic development (Eqn. 4). The second type, CU_{crit} (chilling requirement of rest break) and FU_{crit} (forcing requirement of growth onset), indicate values of the time integrals of the two temperature responses that are required for the completion of the two respective processes (Eqns. 2,3,5,6).

In the present study, the chilling requirement of rest completion, CU_{crit}, covered the range from 10 to 50 chilling units, i.e. a range exceeding at both extremes the range observed earlier for Scots pine (Hänninen 1990b). The forcing requirement of growth onset, FU_{crit}, was used as a test variable whose value was calculated in each case from the growth onset data (Fig. 3). A fixed value was used for each of the parameters a_1–a_7 that determine the two temperature responses. The values of these parameters were obtained earlier by Hänninen (1990a), who fitted the response functions to data concerning rest break (Sarvas 1974) and ontogenetic development (Sarvas 1972) of Finnish forest tree species. In this way, the test of the present study concerns only the specific model developed for Finnish forest trees, and used later by Hänninen (1991) for assessing the implications of climatic change in Finland; not any other model sharing with it the same basic assumptions of chilling and forcing, but having different temperature responses for their rates.

The results of the present study suggest that the risk of premature height growth onset during winter and subsequent frost damage in trees following climatic warming is not so high as predicted in an earlier simulation study (Hänninen 1991). To assess the risk quantitatively, the model used in the present study must be developed in order to describe the regulation of the timing of growth onset in the trees better. Furthermore, it has to be taken into account that growth onset is only a rough indicator of frost hardiness of the trees: the only thing that is clear is that the trees are susceptible to frost after the observed onset of growth. Thus, in order to properly assess the effects of climatic warming on the incidence of frost damage in the trees, a realistic and accurate model for the annual cycle of frost hardiness must be developed. Modelling the growth phenology of the trees provides a good basis for such a model of frost hardiness (Fuchigami et al. 1982, Kobayashi et al. 1983, Kellomäki et al. 1992).

The results of the present study should be regarded as preliminary, since the study involves several limitations. The experimental material consisted of only four saplings, and the experiment covered only one winter. Furthermore, the temperature treatment concerned one exceptionally warm winter among those predicted to prevail at the site as a consequence of a doubled level of atmospheric carbon dioxide. The experimental saplings did not have tens of years to acclimate to the gradually increasing temperatures, which according to the predictions will be the case in naturally growing trees in the future. However, as far as the present authors know, the present study is the first in which the effects of climatic warming on the growth of boreal trees have been examined in semicontrolled field conditions. Thus, despite all the limitations, the results of the present study provide important clues for further studies of the effects of climatic warming on the growth and development of boreal trees.

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