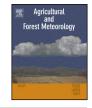
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Frost hardening of Scots pine seedlings in relation to the climatic year-to-year variation in air temperature



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ABSTRACT

The study addressed the effect of year-to-year variation in air temperature on the early needle frost hardening of first-year Scots pine (Pinus sylvestris L.) seedlings in autumn. To this end a novel method, combining biometeorological and plant ecophysiologal research, was introduced. In the biometeorological part, climatic year-to-year variation in air temperature during August and September was examined by analysing a 51-year set of daily air temperature data from central Finland. The cumulative occurrence of low air temperatures in August and September was quantified by calculating a cold sum for that period each year, and the climatic year-to-year variation of the cold sum accumulation was subsequently determined. Similar cold sum calculations were carried out for different air temperature treatments in hypothetical growth chamber experiments. By comparing the results of these two sets of calculations, experimental designs were defined for air temperature treatments covering the climatic year-to-year variation of cold sum accumulation in August and September. In the ecophysiological part of the study, the effects of low air temperatures on the early needle frost hardening of Scots pine seedlings were studied experimentally over two years in central Finland, using the air temperature treatments defined in the first part of the study. The hardening treatments were implemented in growth chambers under conditions simulating natural autumn conditions: gradually increasing night length combined with decreasing and diurnally fluctuating air temperature. Out of the eight air temperature treatments applied, only one had a clear effect of accelerating the hardening. Comparisons of the cold sum accumulations in the experimental treatments with those in natural conditions suggest that low air temperatures do not accelerate the early frost hardening of Scots pine seedlings in most years; further experimental studies are needed in order to determine the frequency of the years when they do. The results of the cold sum comparisons in the present study will help to identify the experimental designs needed in forthcoming studies.

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1. Introduction

Boreal forest trees grow in seasonal climates where the air temperature range between the lowest winter minima and the highest summer maxima is dozens of degrees Celsius (Archibold, 1995; Bonan, 2008). These tree species have adapted to the seasonal climate with their annual cycle of development, so that the frost-tolerant dormant phase and the susceptible active growth phase are synchronised with the annual cycle of air temperature (Weiser, 1970; Sarvas, 1972, 1974; Fuchigami et al., 1982; Repo, 1992; Hänninen and Tanino, 2011; Junttila and Hänninen, 2012). The synchronisation is regulated by an interaction of genetic and environmental factors, so that each tree genotype responds in its specific way to the environmental cues regulating the annual cycle, with air temperature and night length being the most important ones (Perry and Wang, 1960; Ekberg et al., 1979; Billington and Pelham, 1991; Toivonen et al., 1991; Repo et al., 2000; Aitken and Hannerz, 2001; Hannerz et al., 2003; Viherä-Aarnio et al., 2005; Hänninen and Kramer, 2007).

In practical forestry, information on the genetic and environmental regulation of the annual cycle is essential when artificial regeneration is applied. The seed origin of the regeneration material should be sufficiently close to the regeneration site, or else the annual cycle of the seedlings may not be synchronised with the local climatic conditions (Heikinheimo, 1949; Viherä-Aarnio and Heikkilä, 2006). Furthermore, when seedlings are produced in nurseries, the annual cycle of the developing seedlings is controlled by regulating the environmental factors of the seedlings. For instance, growth cessation and frost hardening are induced by

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means of short-day treatments (Colombo et al., 2001; Konttinen et al., 2003, 2007; Luoranen et al., 2009), and the planting window in spring is extended by using freezer storages (Luoranen et al., 2005; Hänninen et al., 2009). If exceptionally early and heavy autumn night frost exceeds the frost hardiness of the seedlings grown in nurseries, considerable mortality may occur. The seedlings can be protected by frost irrigation (Rose and Haase, 1996) or by covering them with frost fabrics (Heiskanen and Raitio, 1992). However, frost protection is expensive and irrigation can also lower the quality of the seedlings. For these reasons, frost protection measures should be taken only when night frosts exceeding the frost hardiness of the seedlings are forecast.

It has been shown experimentally that similarly to several other boreal tree species (Weiser, 1970; Bigras et al., 2001), the hardening of Scots pine (Pinus sylvestris L.) seedlings in autumn is regulated by increasing night length and decreasing air temperature (Aronsson, 1975; Christersson, 1978; Repo et al., 2001; Zhang et al., 2003). Studies addressing the role of night length and air temperature are based on experiments under controlled conditions in growth chambers. The experiments have often made use of unnatural conditions, such as constant photoperiods and air temperatures or combinations of long nights and high air temperatures. While necessary for disentangling the effects of night length and air temperature, the artificial experimental conditions prompt questions about the relevance of the results for natural conditions. We addressed the effect of climatic year-to-year variation in air temperature on the early needle frost hardening of first-year Scots pine (Pinus sylvestris L.) seedlings in autumn. To this end, a novel method combining biometeorological analysis of long-term air temperature data with frost hardiness experiments in controlled conditions was introduced. The experiments were carried out in growth chambers under conditions simulating natural autumn conditions: gradually increasing night length combined with decreasing and diurnally fluctuating air temperature.

2. Material and methods

2.1. Defining the experimental design by analysing long-term climatic data

2.1.1. Climatic year-to-year variation in air temperature

Rather than being fixed *a priori*, the experimental air temperature treatments were designed to cover the climatic year-to-year variation in the cumulative occurrence of low air temperatures over August and September. To this end, a 51-year (1952–2002) set of air temperature data collected by the Finnish Meteorological Institute in Jyväskylä, central Finland ($62^{\circ}24'$ N, $25^{\circ}40'$ E, 139 m asl), was analysed. The data comprised the daily mean air temperature (T_{mean}), determined by recordings made in standard meteorological screens at the height of 2 m above ground, and the daily minimum temperature (T_{min}), measured at the height of 5 cm from the soil surface. For each calendar day in August and September, the yearto-year variation of the T_{min} was described by determining, over the 51 years, the minimum, mean, and maximum of the T_{min} for the particular day (Fig. 1). The year-to-year variation of T_{mean} was described similarly (see the Supplementary material).

The cumulative occurrence of low air temperatures in autumn was quantified by calculating an arbitrary cold sum (Timmis et al., 1994). It was calculated for the August and September of each of the 51 years covered in the air temperature data from Jyväskylä. According to earlier studies, air temperatures lower than +10 °C cause frost hardening in Scots pine (Aronsson, 1975; Repo, 1992; Leinonen et al., 1996; Leinonen, 1996), and the full hardening effect of air temperature is attained when the air temperature drops to -16 °C (Leinonen et al., 1996; Leinonen, 1996). On the basis of these

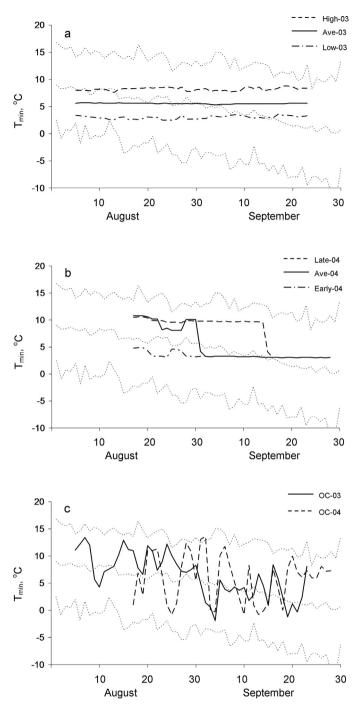


Fig. 1. Daily minimum air temperature, T_{min} , (a) in the experimental treatments of 2003, (b) in the experimental treatments of 2004, and (c) in natural conditions (outdoor controls) in 2003 and 2004. The legend at the upper right-hand corner of each panel indicates the treatment or outdoor control (Table 2) represented by each curve. The thin dotted curves are identical in all the three panels and represent the long-term (1952–2002) climatic minimum (lower curve), mean (middle curve), and maximum (upper curve) of T_{min} for each calendar day in Jyväskylä, located 100 km southwest of the experiment location.

studies, the daily accumulation rate of arbitrary cold units (ACUs) was calculated as follows:

$$R(i) = \begin{cases} 26, & T_{\min}(i) < -16 \,^{\circ}\text{C} \\ -T_{\min}(i) + 10, & -16 \,^{\circ}\text{C} \le T(i) < 10 \,^{\circ}\text{C} \\ 0, & T(i) \ge 10 \,^{\circ}\text{C} \end{cases}$$
(1)

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