



Differences in frost hardiness of two Norway spruce morphotypes growing at Mt. Brocken, Germany

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ABSTRACT

Norway spruce (*Picea abies* (L.) Karst.) exhibits strong ecotypic variation along altitudinal gradients in morphological traits, e.g. slenderness of crowns or arrangement of second-order branches. We were interested whether montane and lowland morphotypes differ in a key trait for the survival in cold environments, i.e. frost hardiness, and asked: (i) are montane morphotypes more resistant to frost damage and (ii) do they have a lower risk of frost damage by late frosts in spring than lowland morphotypes?

We used the electrolyte leakage-method to measure frost hardiness on a monthly basis from October 2006 to May 2007 in stands of the montane and lowland morphotypes at Mt. Brocken in the Harz Mountains, Germany.

LT₅₀ (i.e. the temperature that results in 50% of maximum electrolyte leakage) was assessed by freezing treatments in a frost chamber and was significantly influenced by morphotype, month and minimum ambient temperatures. LT₅₀ was significantly lower in the montane than in the lowland morphotype, with -107°C and -49°C , respectively. However, the interactions between morphotype with minimum ambient temperature or month were not significant. Thus, as frost hardiness of the two morphotypes responded to temperature in the same way, both morphotypes can be supposed to be exposed to the same risk of frost damage during hardening in autumn and dehardening in spring.

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Introduction

A key trait for the survival of coniferous tree species in the boreal zone is frost hardiness. Frost hardiness of plants is associated to a multitude of physiological processes (Sutinen et al., 2001). Water loss by extracellular ice formation results in concentrating cellular solutes, decreasing water potentials and changes in membrane potentials (Beck et al., 2004, 2007), which the protoplast can tolerate by preceding synthesis of specific proteins and membrane lipids (Kozłowski and Pallardy, 2002). A widely distributed mechanism to prevent intracellular freezing and thus frost damage is deep supercooling (Sutinen et al., 2001). In some plants such as conifers, the concentrated cell solution can even turn into a state of glass (vitrification; Strimbeck et al., 2007). Plant tissues in this stage survive even temperatures of -196°C (Larcher, 1994; Strimbeck et al., 2007).

In principle, frost hardiness consists of three determining components: first, genetically fixed traits, second, epigenetic effects and third, the physiological adaptation of individuals to environ-

mental conditions. The genetically fixed component determines absolute thresholds of frost tolerance among species and is controlled by several genes (Beck et al., 2004). A considerable amount of genetic variation in frost hardiness has been found among and within conifer populations (Aitken and Hannerz, 2001; Savolainen et al., 2004), which is the basis of both present and future adaptations to the environment. The review by Aitken and Hannerz (2001) revealed that the degree of genetic control differs for different aspects of frost hardiness. The heritability for spring frost hardiness is generally high, while heritability for frost hardiness in autumn is lower and more variable. In addition, frost hardiness underlies epigenetic effects (Johnsen et al., 2005), i.e. changes in gene function which are mitotically and/or meiotically heritable but are not associated with changes in the DNA sequence (Wu and Moris, 2001). For example, in a study on *Picea abies* Johnsen et al. (1996) demonstrated that the environmental conditions experienced by the parent trees, especially in the period of female flowering, had a major impact on the frost hardiness of progenies. Flowering in an early and warm spring created less hardy progenies than flowering in a late and cold spring. Finally, frost hardiness is determined by the ability of physiological adjustment of individuals to the ambient environmental conditions, i.e. the ability of hardening and dehardening (Beck et al., 2004). Hardening and dehardening are strongly affected by ambient temperature (Jönsson et al., 2004; Søgaard et

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al., 2009), day length/photoperiod (Beck et al., 2004; Beuker et al., 1998), nutrients (Jönsson et al., 2001) and drought stress (Beck et al., 2007). While the initiation of hardening in autumn is mainly driven by photoperiod, the dehardening in spring is mainly regulated by temperature (Beck et al., 2004). For *P. abies* it has been demonstrated that dehardening starts already after five days with temperatures over +5 °C (Jönsson et al., 2004). This type of environmental control can be particularly crucial in the context of ongoing climate change, because higher temperatures will result in earlier dehardening (Hänninen et al., 2001). With an expected increase of magnitude and frequency of weather extremes (Hundecka and Bárdossy, 2005), the IPCC report predicts a rise in minimum and maximum temperatures as well as of mean temperatures in winter for the northern hemisphere (Solomon et al., 2007). The result will be an earlier dehardening, which might increase the risk of late frosts in spring, and thus, the risk of frost damage.

To assess this frost damage various methods have been developed, such as *in situ* determination (Buchner and Neuner, 2009; Taschler and Neuner, 2004) or visual assessment (Jensen and Deans, 2004) and, most commonly, electrolyte leakage measured as relative conductivity (Bruelheide and Heinemeyer, 2002; Bruelheide and Lieberum, 2001; Murray et al., 1989; Thomas and Sporns, 2009). Jensen and Deans (2004) compared the visual assessment and measurement of relative conductivity and demonstrated that the latter provided the most statistically consistent results.

Picea abies (L.) H. Karst. is one of the major coniferous tree species of the boreal zone in Europe with a high ability to tolerate low temperatures (Hannerz and Westin, 2005; Sakai and Okada, 1971) and a strong ecotypic variation along altitudinal and latitudinal gradients in frost hardiness (Johnsen and Skråppa, 2000). Ecotypic variation is not only encountered at the continental scale, but also regionally. For example, Skråppa (1991) found differences in frost hardiness between *P. abies* populations that were separated by only 60 km at the same altitude and longitude. When seedlings from origins of high and low altitudes were grown together at sea level, the latter developed their frost hardiness later (Skråppa et al., 2007). Recently, regional, native ecotypes of *P. abies* have become the focus of nature conservation efforts because they represent valuable genetic resources from a time before industrial forestry started in the 18th century throughout Central Europe, and before lowland genotypes were planted at high altitudes. This mixing of provenances bears the risk of genetic erosion through introgression (Akimoto et al., 1999), and in consequence, the loss of certain traits such as a decrease in frost hardiness.

One well known example of such a risk is the native, i.e. montane morphotype of *P. abies* in the core zone of the Harz National Park at Mt. Brocken, Germany, which is today surrounded by planted, lowland morphotypes. This montane population includes individuals that are older than the initiation of forest management in this area. So far, the main evidence for its native status is its morphology, visible in a slender, cylindrical and tall growth habit (Greger, 1991) as well as in a higher number and reduced length of second-order branches, which are less horizontal compared to the lowland morphotype (Geburek et al., 2008; Greger, 1991). Consequently, the native, montane morphotype is known to show an increased resistance to snow and ice break (Greger, 1991) and is considered to be better adapted to the harsh environment at high altitudes, probably at the expense of lower growth rates (Oleksyn et al., 1998). That said, there is so far no empirical evidence for higher frost resistance of the native genotype. Likewise, no attempt has been made to relate frost hardiness to morphological traits that differ between montane and lowland morphotypes. Such morphological variation with regard to climatic variables has been ascribed for example to *Betula pendula* (Li et al., 2002), where an increase of frost hardiness was accompanied by an increase in specific leaf mass. Similarly, ecotypic variation in *Pinus sylvestris* was found for leaf dry matter

content, which is in turn correlated to frost hardiness (Bresinsky et al., 2008).

We addressed the question of differences in absolute frost tolerance and timing in frost hardiness between different provenances of lowland and montane ecotypes of *P. abies* in the Harz Mountains, Central Germany. In particular, we first hypothesised that montane morphotypes are more resistant to frost damage than lowland morphotypes, and second, that montane morphotypes have a lower risk of frost damage by late frosts in spring than lowland morphotypes.

Materials and methods

Study area and sampling design

The study was conducted in the Harz Mountains in Saxony-Anhalt, Germany. Two different sampling sites were selected separated by a linear distance of about 6 km. Lowland morphotypes were taken from a planted Norway spruce (*Picea abies* (L.) Karst.) stand adjacent to the core zone in the Harz National Park at Mt. Brocken (51°44'08"N, 10°40'39"E, 550 m a.s.l.) and native (montane) morphotypes were sampled from spruce stands inside the core zone (51°47'21"N, 10°38'27"E, 930 m a.s.l.).

We selected 10 adult *P. abies* individuals per site at the edge of the stand to ensure that the sampled individuals did not differ in frost exposure. Only individuals with a minimum height of 15 m, a minimum circumference at breast height (cbh) of 1.0 m and without any crown break or indications of fungal infections were chosen. One first-order branch was selected per individual and marked. Second-order branches from all marked branches were sampled in monthly intervals and subsequently subjected to measurements of frost hardiness in the laboratory between October 2006 and April 2007 (sampling dates: 22/10/2006, 26/11/2006, 17/12/2006, 21/01/2007, 18/02/2007, 25/03/2007, 22/04/2007).

One of the lowland individuals broke down in January 2007 as a result of the storm "Kyrill". Accordingly, from January onwards, only nine individuals of the lowland morphotype were sampled.

Ambient temperatures at both sampling sites were monitored with data loggers (Type Tinytag, Gemini), one installed per site on the marked branch of one of the target individuals. Temperature was logged every 30 min from October 2006 until May 2007.

Measurements of frost hardiness

Frost hardiness was assessed using the method of electrolyte leakage according to Murray et al. (1989). This method is based on the release of electrolyte leakage through membranes which have been damaged by intracellular ice formation. The increase of electrolytes in a solution is measured as electrical conductivity. Branches were exposed to the following temperature levels in a climate test chamber (Sanyo, MTH-4400): +4 °C (control), 0 °C, –8 °C, –16 °C, –24 °C, –32 °C, –40 °C, –80 °C and to liquid nitrogen (–196 °C). The temperature level of –80 °C was starting in December. All temperature levels lasted for 30 min in the climate test chamber, with the first four temperature levels having a cooling rate of –4 °C h^{–1}, and the last four temperature levels in the climate test chamber having a cooling rate of –6 °C h^{–1}. These cooling rates are in the range of those commonly applied in frost experiments (e.g. Hannerz and Westin, 2005; Thomas and Ahlers, 1999), but might represent a more extreme situation than normally encountered in field. At the end of each temperature level, twigs as parts of the branches from each individual were removed from the climate test chamber and stored at +4 °C in a refrigerator. One twig from each individual was placed into liquid nitrogen for 10 min after receiving all eight temperature levels in the climate chamber.

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