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Cold hardiness of *Pinus nigra* Arnold as influenced by geographic origin, warming, and extreme summer drought

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ABSTRACT

Adaptation to the adverse effects of climate change is being investigated more and more through the introduction of species from warmer and drier climates, such as the (sub-) mediterranean *Pinus nigra* to dry sites in temperate Central Europe. Winter survival, however, may pose a serious threat to this strategy as cold extremes, which naturally determine the poleward range limits of forest trees, are not expected to follow the general warming trend in the near future.

Here, juveniles of *P. nigra* from eight provenances throughout Europe were exposed to different climate change scenarios (factorial combinations of 42 days of drought and warming by 1.6 °C) in a common garden experiment in Bayreuth, Germany. Cold hardiness (LT50) was determined by the Relative Electrolyte Leakage method (REL) in two consecutive winters.

Cold hardiness of foliage differed by 10 °C between the provenances studied and a local adaptation to minimum temperature was found. Cold hardiness was further affected by extreme summer drought, increasing cold hardiness by 3.9 °C on average in the subsequent winter, and by summer warming, increasing cold hardiness by 3.4 °C. Year-round warming had no significant effect on cold hardiness. Cold hardiness was related to the content of soluble carbohydrates and to the composition of fatty acids and alkanes in the needles. Juveniles of *P. nigra* exhibited a comparable cold hardiness as juveniles of species native to Central Europe (*Pinus sylvestris, Picea abies, Fagus sylvatica* and *Quercus petraea*) under the same climatic conditions. Cold hardiness of the fine roots of *P. nigra* averaged -16.5 °C compared to -23.8 °C on average for needles.

Our results imply that the cold hardiness of the foliage is adaptive to both long-term growing conditions at the seed origin (genetic heritage) and short-term alterations of these conditions (individual plasticity), while first hints suggest that cold hardiness of the roots is high and might not be adaptive. For *P. nigra*, below- and above-ground cold hardiness of selected provenances in mid-winter appear suitable for cultivation in temperate regions.

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1. Introduction

Species respond to climate change by poleward range shifts (Parmesan and Yohe, 2003). The speed of warming, however, is expected to exceed natural migration rates in many cases (Thomas et al., 2004). In forestry in particular, human-assisted range shifts are proposed to counter long generation cycles and modest dispersal abilities of forest trees (Schaberg et al., 2008b; McKenney et al., 2009). Yet, the importance of winter conditions is often overlooked, especially in the ecology of temperate regions (Kreyling, 2010). Absolute minimum temperatures have strong implications for species distributions by often determining their poleward range limits (Sakai and Weiser, 1973; Repo et al., 2008). A single cold extreme can offset any distributional adaptations to the general warming trend (Jalili et al., 2010) and in spite of the mean warming and their decreased frequency of occurrence, both the intensity and the duration of such cold extremes may not decrease within this century due to atmospheric circulation changes and internal atmospheric variability which counteract the warming trend from greenhouse forcing (Vavrus et al., 2006; Kodra et al., 2011).

Phenotypic plasticity and the adaptive potential of forest trees are determined by their high genetic diversity, allowing forest trees to develop local adaptations to environmental stressors (Hosius et al., 2006; Schaberg et al., 2008b). The cold hardiness of *Pinus*

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devoniana, for instance, increases with increasing frost risk along an altitudinal gradient (Saenz-Romero and Tapia-Olivares, 2008). Similarly, changes to the cold hardiness of Fagus sylvatica indicate local adaptation to the prevailing minimum winter temperatures (Visnjic and Dohrenbusch, 2004) and to late spring frost risk (Kreyling et al., 2011b) across Europe, and the frost tolerance of Tsuga heterophylla is adapted to frost risk along latitudinal and altitudinal gradients in North America (Kuser and Ching, 1980). Provenance trials demonstrate a differential performance between the provenances of different geographic origins of Pinus nigra (Varelides et al., 2001), which is the target species of this study. P. nigra was selected because it is discussed in forestry as target species for translocations to Central Europe (Kölling, 2007; Huber, 2011) and because of its high genetic diversity (Nkongolo et al., 2002; Jagielska et al., 2007). Based on its fragmented submediterranean range, one could assume that it lacks adaptation to winter frost, at least in some provenances. Provenance trials suggest that frost damage occurs around -20°C and in particular those provenances from Corsica do not survive -25 °C (summarized in Huber, 2011).

The cold hardiness of evergreen tree species fluctuates over the course of the year. During acclimation in autumn, the plant organs become increasingly tolerant to the damaging effects of tissue freezing, particularly protecting cellular membranes which are a prime place of freezing injury (Bigras et al., 2001). Even though the genetic controls of the protective processes in conifers are complex and not yet sufficiently understood (Holliday et al., 2008), data has been summarized on the chemical components that are involved (Thomashow, 1999). During acclimation, lipid composition in the plasma membrane shifts towards more unsaturated lipids (Bakht et al., 2006) in addition to accumulation of soluble carbohydrates, hydrophilic polypeptides, antioxidants and chaperones in the membranes (Thomashow, 1999). Increased concentrations of all these chemical components serve the general purpose of preventing intra-cellular ice crystallization (Bigras et al., 2001).

Plants grown under generally warmer conditions, however, may lose their functional adaptations to frost (Eccel et al., 2009). Plants can further cope with different environmental stressors by similar responses at the cellular and molecular level when these stressors trigger similar signal chains. Drought and frost, for instance, lead to similar physiological responses in a coniferous forest tree – aiming to prevent cellular dehydration (Blodner et al., 2005). More frequent drought events may therefore make up for diminished acclimation due to warming.

The (sub-) mediterranean distribution of our target species P. nigra is reflected in high drought tolerance (Isajev et al., 2004) relative to temperate species such as Pinus sylvestris or F. sylvatica. Therefore, translocation of *P. nigra* is discussed as one adaptation strategy against the adverse effects of climate change at dry sites in Central Europe (Kölling, 2007). The minimum temperature in winter, however, is one of the most important factors setting the northern boundaries of the natural ranges of forest tree species (Sakai and Weiser, 1973; Körner and Paulsen, 2004). The cold hardiness of one single provenance of P. nigra was lowest among eight Pinus species (with P. nigra showing the southernmost native range of the tested species) in a common garden experiment in Trondheim, Norway (Strimbeck et al., 2007). As tree species are generally well adapted to the minimum temperatures of their environment (Sakai and Weiser, 1973), the range of frost tolerance of P. nigra across provenances needs to be examined in detail before translocations to other climates are undertaken. This holds particularly true because climate modelling implies that cold extremes will remain stable in their magnitude throughout this century in spite of climate warming (Vavrus et al., 2006; Kodra et al., 2011). With regard to the life span of trees, the expected decrease in frequency of cold spells (e.g. Vavrus et al., 2006; Kodra et al., 2011) is clearly less important than magnitude and duration of individual cold spells, as even with decreased frequency the likelihood of experiencing at least one cold spell is still close to 100%. Furthermore, forests grow slowly and management action aiming at stable and productive forests in future need to be started now. Target species for translocations need therefore not only be adapted to future conditions, but also survive current conditions with prevailing occurrences of cold extremes.

Plant organs differ in their cold hardiness. Generally, roots are the least frost tolerant (Mancuso, 2000; Bigras et al., 2001). The on-going decline of *Chamaecyparis nootkatensis* in the Pacific Northwest of North America, for instance, has been linked to root frost damage due to climate change-induced reductions in the insulating snow cover (Schaberg et al., 2008a). A similar reduction in snow cover is also projected for Central Europe (Kreyling and Henry, 2011). In addition to shoot cold hardiness, root freezing tolerance should therefore be investigated.

Here, eight provenances of *P. nigra* from autochthonous origins and from southern Germany were tested for their cold hardiness in a common garden experiment in southern Germany. We hypothesized that (1) cold hardiness differs between provenances, with provenances from colder origins displaying superior cold hardiness, and that (2) cold hardiness is affected by climatic experiences of the individuals with drought increasing cold hardiness and warming decreasing cold hardiness. We further expected that (3) differences in cold hardiness between provenances are physiologically related to the content of soluble carbohydrates and lipid composition of the needles, and that (4) the (sub-) mediterranean species *P. nigra* is less frost-tolerant than tree species native to Central Europe, while (5) cold hardiness of the fine roots of *P. nigra* is high compared to cold hardiness of its foliage as it naturally occurs in regions without continuous snow cover.

2. Materials and methods

Juveniles of *P. nigra* from eight provenances throughout Europe were exposed to different climate change scenarios (warming and extreme drought) in a common garden experiment. Cold hardiness was determined by the Relative Electrolyte Leakage method (REL) in two consecutive winters. The experiment was established in Bayreuth, Germany (49°55′19″N, 11°34′55″E) in March 2009. The long-term mean annual temperature for the site is 8.2 °C, whereas long-term mean annual precipitation is 724 mm.

2.1. Experimental design

Eight provenances of P. nigra (Fig. 1; Table 1) were obtained as seeds and cultivated at the Bavarian Institute for Forest Seeding and Planting (ASP) in Teisendorf, Germany from April 2008 to April 2009. These provenances are part of an international long-term provenance trial which started in 2009 (Huber, 2011). The provenances stem from autochthonous populations of P. nigra except for the provenance from Zellingen, Germany, which was introduced from Austrian sources in 1909. Subspecies identities of the provenances are assigned geographically and morphologically (Table 1), as genetic analyses are not yet available (Huber, 2011). The Croatian provenance stems from a location very close to one of the few autochthonous stands of *P. nigra* subspecies dalmatica and its assignment to the subspecies nigra is somewhat questionable. The seedlings were transported to Bayreuth and individually planted into 4-l plastic pots filled with sandy silt (pH 7.3, total C 1.9%, total N 0.15%, plant available NO $_3$ ⁻-N 22.5 mg l⁻¹; plant available NH $_4$ ⁺-N 1.8 mg l^{-1}). Selection of the plants occurred randomly for each provenance from all those plants alive at the planting date. The Download English Version:

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