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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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