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Cold acclimation of pedunculate oak (*Quercus robur* L.) at its northernmost distribution range

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Abstract

Pedunculate oak (*Quercus robur* L.) grows on the border of its northernmost distribution range in southern Finland. We hypothesised that insufficient cold hardiness (CH) during autumn is a key factor that restricts the northward growth of oak. We tested this hypothesis by monitoring the cold acclimation of oak seedlings growing in central Finland, 300 km north of the present northern limit of the species. For a deep understanding of the events occurring in stems during cold acclimation and freezing, several ecophysiological parameters were measured and compared with the water attributes. When growing 300 km north from its natural distribution range considerable hardening of 2-year-old seedlings took place already at the beginning of September. This was supported by measurements of several ecophysiological attributes related to the cold acclimation. The first symptom of cold acclimation was a decrease in the water content in stems in August, concomitant with a reduction in the relaxation time as assessed by electrical impedance spectroscopy. The CH was approximately −10 °C at the beginning of September and then increased together with an enhancement of the soluble sugar accumulation and a loss of starch. The CH was −36 °C at the beginning of December. The high temperature exotherm (HTE) in current-year stems decreased from −6 °C to −9.4 °C between August and December. Leaf reflectance at 660 nm increased after the first night frosts at the end of September (CH of stem −25 °C), leading to leaf abscission. The apoplastic and symplastic electrical resistance of current-year stems increased substantially in October. The chemical nature of the water (free, bound) within the stem changed under the influence of ice nucleation at HTE and during cold hardening, as determined by ^{1}H NMR microscopy. The free water was distributed unevenly within the cross-section of the cold-hardened stems, i.e., most of it became located at the interface between xylem and cambium. The quantity of non-freezing water at −45 °C was, on average, 0.25 and 0.31 $g_{H_2O}\, g_{DM}^{-1}$ for the cold-hardened current- and previous-year stems, respectively. Even though our results for a single autumn did not provide conclusive evidence in support of our hypothesis, the results suggest that during years with more critical climatic conditions frost may cause damage to the oak seedlings, and in this way disturb their growth in the climatic conditions northwards of the present range of the species.
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1. Introduction

Pedunculate oak (*Quercus robur* L.) is widely spread in Europe. Natural distribution area extends from Ireland (10°W) in west, to Sicily, Italy (37°S) in south, to the Ural mountains (55°E) in east and to central Norway (63°N) in north (Zanetto et al., 1994; Oszako, 2004, op cit). The Finnish oak populations grow at the border of their northern distribution range with a few fragmented oak stands in the coastal part of the south-western Finland (60°N). Short growing seasons, cold winters and the consequent frost damage may be limiting factors for the natural distribution of this species in the north (Jensen, 2000). Oak may also suffer frost damage in southern latitudes. The implications of such damage are symptoms of decline in central Europe that have typically been observed after extreme weather such as cold winters (Auclair, 1992; Hartmann and Blank, 1992; Thomas et al., 2002; Oszako, 2004, op cit).

The correct timing of cold hardening and dehardening is important for the growth and survival of oak. It has been found that, in their nursery stage, oaks are exposed to frost damage in

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early autumn or late spring (Jensen and Deans, 2004). During cold acclimation, physiological changes are driven by changes in the temperature and photoperiod, when the prerequisites for tolerating low winter temperatures are fulfilled. Studies involving several oak populations from different central European countries have shown significant differences in cold hardening between provenances, southern and maritime provenances being the least frost hardy and continental and northern ones the frost hardiest (Deans and Harvey, 1995, 1996; Jensen and Deans, 2004; Morin et al., 2007). However, only a few studies are available concerned with the cold hardening and the accompanying physiological processes of pedunculate oak at its northern distribution limit (Jensen and Deans, 2004). Such studies are much needed, given current predictions of climate change, where the growth conditions may favour a more northerly distribution and growth of southern exotic tree species, e.g. oak, than in the present climate (Dahl, 1990; Cramer et al., 2001; Jensen, 2000).

Ice nucleation in specific tissues is an important event with regard to the cold hardiness of oak. Oaks belong to a species with deep-supercooling in their xylem ray parenchyma cells, whereas cells of other tissues without such a property may avoid freezing by means of dehydration (George et al., 1982). Injury caused by ice nucleation in xylem parenchyma cells is quantitative, i.e. cells with intracellular ice nucleation die, but adjacent cells – which have no ice nucleation – survive (Hong and Sucoff, 1980). Thus, the more that cells are ice nucleated, the more extensive is the injury caused. In terms of slow cooling rates, extracellular freezing is regarded as an equilibrium process. During this process, ice forms in the extracellular spaces and the cells become progressively dehydrated. Winter-hardy cells may tolerate such dehydration. Cells with low water permeability, such as xylem ray parenchyma cells, may supercool, and when that ability is exceeded, ice nucleation occurs. There is a physical limit to deep-supercooling defined by the homogeneous nucleation temperature of water (George et al., 1974; George, 1983; George and Burke, 1984).

While the initiation and spread of ice nucleation in plants are well-known phenomena, according to studies conducted using differential thermal analysis and infra-red thermography (Kitaura, 1967; Wisniewski et al., 1997; Pearce and Fuller, 2001), the spatial dehydration of tissues by means of extracellular freezing is known poorly. Such studies can be conducted by means of nuclear magnetic resonance imaging (^{1}H NMR imaging). Using this technique it is possible to characterize the spatial or two-dimensional distribution (amount and nature) of ^{1}H nuclei of H_2O in plant tissues without using destructive or ionising radiation. The important requirements for successful depiction are sufficient mobility and a sufficiently long relaxation time for protons as well as a sufficiently high content of the proton-bearing compound (Callaghan, 1991; Ritchley et al., 1994; Blümich, 2000). Using ^{1}H NMR imaging, studies have been made of the freezing of leaf buds of Momi fir (*Abies firma* Sieb. et Zucc.) and Japanese red pine (*Pinus densiflora* Sieb. et Zucc) (Ide et al., 1998), the leaf and flower buds of full-moon maple (*Acer japonicum* Thunb.) (Ishikawa et al., 1997), the flower buds of Japanese azalea (*Rhododendron japonicum* (A. Gray) Suringer), and the stems of maple (*Acer cissifolium* (Seib. et Zucc.) K. Koch) and potato (*Solanum tuberosum* L.) (Price et al., 1997a,b).

The objective of this study was to investigate the cold acclimation of pedunculate oak (*Quercus robur* L.) seedlings in field conditions to enhance our understanding of the survivability of this species in its northernmost distribution range. For a deep understanding of the events in stems during cold hardening and freezing, several ecophysiological parameters were measured and compared with the water attributes (amount and chemical nature). We hypothesise that cold hardiness is a key trait that limits the distribution of oak northwards. When growing beyond the northern border of its natural distribution range, oak would be predisposed to freezing injuries in autumn.

2. Materials and methods

2.1. Plant material

The material used in this study consisted of 2-year-old seedlings of pedunculate oak. The seed origin was Malmi, Helsinki, Finland (60°10′N, 24°58′E, seed index G01-95-0051). The acorns were sown in a greenhouse at the Finnish Forest Research Institute, Suonenjoki Research Station (62°39′N, 27°03′E, 130 m asl) in mid-May. At the beginning of June, the seedlings were replanted in styrofoam trays (cell volume 0.58 dm^3), with 22 cells in each tray. One month later they were moved to the winter storage area of the nursery. During the next growing season, on 21 July, 176 seedlings (8 trays) were transported to the botanical garden of the University of Joensuu (62°36′N, 29°43′E, 81 m asl) for monitoring of their cold acclimation between August and December. In the nursery, the seedlings were fertilized once in the greenhouse and twice outside, during the first growing season, with Kekkilä 9 and Kekkilä 5 fertilizers (10–15 g m^{-2}), respectively, (Kekkilä Co., Tuusula, Finland) and once during the second growing season with Kekkilä 5 fertilizer (15 g m^{-2}) (Kekkilä Co.).

2.2. Differential thermal analysis and cold hardiness

Samples (8 mm long) for DTA were cut from the middle part of the current- and previous-year stems of the seedlings on six occasions between 8 August and 24 November. On each occasion, nine seedlings were sampled. The high and low temperature exotherms (HTE and LTE, respectively) of the moistened current- and previous-year stems were determined by means of custom-designed DTA equipment. The differential temperature of the sample and reference junction was measured using iron–constantan thermocouples (diameter 0.2 mm). The amplified differential signal and the sample temperature were recorded (Yokogawa LR 4110, Japan). In a DTA run, the initial temperature was 5 °C and the cooling rate to the target temperature of −45 °C was 5 °C h^{-1}.

The cold hardiness of the current- and previous-year stems was determined using the electrolyte leakage method on four occasions between early September and late November (Sutinen et al., 1992; Repo et al., 1994; Luoranen et al., 2004). On each occasion, shoots from 36 seedlings were dissected at the root col-

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