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Original article

Ice nucleation and frost resistance of *Pinus canariensis* seedlings bearing needles in three different developmental states

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Abstract – Frost resistance and ice formation in different developmental states of needles of *P. canariensis* seedlings were assessed. Regrowth after frost damage was used to determine the overall frost survival capacity. Two distinct freezing exotherms (E1, E2) were registered. E1 was between –1.7 and –2.0 °C. Initial frost damage (LT_{10}) was 1.5–2.7 °C below E1. E2 was between –5.6 and –6.0 °C, and either corresponded with LT_{50} or occurred in between LT_{10} and LT_{50}. Current year needles were less frost resistant than 1-year-old needles. The overall recuperation capacity of seedlings revealed that frost survival may be underestimated when only needle damage is assessed. Freezing of seedlings with or without roots had no effect on the frost resistance of needles but recuperation capacity was significantly affected. Seedlings survived –10 °C during summer indicating that they withstand the lowest naturally occurring frosts in Tenerife.

extracellular ice formation / freezing exotherm / *Pinus canariensis* / regrowth / subzero temperatures

Résumé – Nucléation de glace et résistance au froid de semis de *Pinus canariensis* portant des aiguilles à trois différents stades de développement. La résistance au froid et la formation de glace dans des aiguilles à différents stades de développement ont été déterminées chez des semis de *Pinus canariensis*. La repousse après les dommages du froid a été utilisée pour déterminer l'ensemble de la capacité de résistance au froid. Deux exothermes de congélation (E1, E2) ont été enregistrés. E1 était entre –1,7 et –2,0 °C. Les premiers dommages du froid (LT_10) ont été constatés entre 1,5 et 2,7 °C sous E1. E2 était entre –5,6 et –6,0 °C et soit correspondait à LT_50 ou arrivait entre LT10 et LT50. Les aiguilles de l'année en cours ont été moins résistantes au froid que les aiguilles âgées de 1 an. La capacité de récupération globale des semis a révélé que la survie au froid pouvait être sous estimée quand on détermine seulement les dommages subis par les feuilles. La congélation des semis avec ou sans racines n'a pas eu d'effet sur la résistance au froid des aiguilles, mais la capacité de récupération a été significativement affectée. Les semis ont survécu à –10 °C pendant l'été indiquant qu'ils étaient capables de résister aux basses températures qui se produisent à Ténérife.

formation de glace extra cellulaire / exotherme de gel / *Pinus canariensis* / repousse / températures en dessous de zéro

Abbreviations: LT_{10}: Temperature at 10% frost damage ; LT_{50}: Temperature at 50% frost damage ; LT_{100} : Temperature at 100% frost damage ; E1: High temperature freezing exotherm ; E2: Low temperature freezing exotherm ; ΦPSII: Photochemical Efficiency of Photosystem II.

1. INTRODUCTION

Freezing stress is one of the most important environmental constraints limiting plant distribution [26]. During sprouting conifers are particularly susceptible to frost damage as their comparatively low frost resistance coincides with subzero temperatures [27, 28]. Frost damage to expanding leaves and shoots of conifers has been repeatedly observed in the timberline ecotone of the European Alps [11, 27]. Even *Pinus cembra,* which is one of the most frost resistant conifers (maximum frost resistance < –90 °C (see [3]); USDA climatic zone 1 (< –45.6)) may get damaged during sprouting. In this species initial frost damage at –4.8 °C which is surprising in an evolutionary sense. Ultra-structural changes during sprouting and cell elongation may result in insufficient frost hardening [27]. Seedlings of European timberline conifers have a mature, fixed growth pattern. Between the formation of shoot and needle primordia in summer there is a considerable time-lapse before sprouting in the following spring. During winter the primordia are protected in buds covered by scales and resinous material. In contrast, seedlings of several Mediterranean pines exhibit a juvenile, free growth pattern where stem units elongate shortly after their formation throughout the year [5, 13]. In seedlings of *Pinus canariensis* C. Sm ex D.C., the free growth habit can persist for 2 to7 years [12]. Due to this juvenile, free growth pattern, seedlings and young plants continuously bear

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