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Research paper

Nitrogen nutrition and drought hardening exert opposite effects on the stress tolerance of *Pinus pinea* L. seedlings

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Functional attributes determine the survival and growth of planted seedlings in reforestation projects. Nitrogen (N) and water are important resources in the cultivation of forest species, which have a strong effect on plant functional traits. We analyzed the influence of N nutrition on drought acclimation of *Pinus pinea* L. seedlings. Specifically, we addressed if high N fertilization reduces drought and frost tolerance of seedlings and whether drought hardening reverses the effect of high N fertilization on stress tolerance. Seedlings were grown under two N fertilization regimes (6 and 100 mg N per plant) and subjected to three drought-hardening levels (well-watered, moderate and strong hardening). Water relations, gas exchange, frost damage, N concentration and growth at the end of the drought-hardening period, and survival and growth of seedlings under controlled xeric and mesic outplanting conditions were measured. Relative to low-N plants, high-N plants were larger, had higher stomatal conductance (27%), residual transpiration (11%) and new root growth capacity and closed stomata at higher water potential. However, high N fertilization also increased frost damage (24%) and decreased plasmalemma stability to dehydration (9%). Drought hardening reversed to a great extent the reduction in stress tolerance caused by high N fertilization as it decreased frost damage, stomatal conductance and residual transpiration by 21, 31 and 24%, respectively, and increased plasmalemma stability to dehydration (8%). Drought hardening increased tissue non-structural carbohydrates and N concentration, especially in high-fertilized plants. Frost damage was positively related to the stability of plasmalemma to dehydration ($r = 0.92$) and both traits were negatively related to the concentration of reducing soluble sugars. No differences existed between moderate and strong drought-hardening treatments. Neither N nutrition nor drought hardening had any clear effect on seedling performance under xeric outplanting conditions. However, fertilization increased growth under mesic conditions, whereas drought hardening decreased growth. We conclude that drought hardening and N fertilization applied under typical container nursery operational conditions exert opposite effects on the physiological stress tolerance of *P. pinea* seedlings. While drought hardening increases overall stress tolerance, N nutrition reduces it and yet has no effect on the drought acclimation capacity of seedlings.

Keywords: carbohydrates, drought tolerance, frost damage, Mediterranean, plasmalemma stability, residual transpiration, root growth capacity, stomatal conductance, survival.

Introduction

Water stress and frost are major limiting factors for plant life in Mediterranean continental climate areas (Larcher 1981, Castro et al. 2004). Seedlings planted in forest projects in these areas must therefore be cold resistant and able to withstand drought. Water stress applied in the nursery can enhance drought and