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Stomatal and non-stomatal limitations to photosynthesis in seedlings and saplings of Mediterranean species pre-conditioned and aged in nurseries: Different response to water stress

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ABSTRACT

The aim of the present work was to compare the physiological responses to water stress and recovery of seedlings and saplings of three different Mediterranean species (*Olea europaea* var. *sylvestris*, *Rhamnus alaternus* and *Cneorum tricoccon*), pre-conditioning and aged in nursery and presenting different ages and pot sizes. Our hypothesis was that the ratio of plant size to soil volume (which constrains root development leading to low root-to-shoot ratios) rather than any of the two factors separately determines the seedling response to water stress. Seedlings (1-y) and saplings (3 to 4-y) were transplanted into pots bigger than those used during growth in the nursery and irrigation was stopped to each species × age/size combination. Leaf water potential (Ψ), net CO_2 assimilation (A_N), stomatal (g_s) and mesophyll (g_m) conductances, and the rate of photosynthetic electron transport (ETR) were determined every few days. Plants were re-watered when A_N dropped below 70% of control values.

Saplings of each species presented larger total leaf area (TLA) and reached lower Ψ than seedlings. Even under irrigation, saplings showed lower A_N, which was not related to g_s but to lower g_m and ETR. During water stress, A_N decreased slowly in seedlings due to stomatal limitations, while in saplings it decreased fast and mainly associated to non-stomatal limitations (g_m and ETR). Upon re-watering, seedlings recovered maximum A_N within a few days, while recovery was slow and incomplete in saplings. At the end of the experiment, significant leaf die-back occurred in saplings but not in seedlings except for *Cneorum*. The minimum Ψ achieved during water stress was strongly linearly related to TLA when pooling all species and ages, and leaf die-back was strongly dependent on Ψ and on the appearance of non-stomatal limitations to photosynthesis. Therefore, we conclude that the total amount of leaf area for a given volume of substrate (i.e., maximum water availability), rather than plants pre-conditioning in nurseries or plant age, determines seedling/sapling responses to water stress and re-watering in Mediterranean species.

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1. Introduction

Mitigation of desertification in Mediterranean areas is an important issue which requires reforestation and afforestation of former woodlands and abandoned agricultural lands. However, the achievement of successful plantations has technical problems imposed by the extreme aridity during summer, which leads to low establishment and high seedling mortality after summer (Vallejo et al., 2005; McDowell et al., 2008; Luis et al., 2009). Strategies based on pre-conditioning and/or hardening seedlings in nurseries have been proposed to improve seedling performance under field conditions (van den Driessche, 1991; Bañon et al., 2006; Vilagrosa et al., 2006). Of the two, hardening (i.e., application of short term stress treatments) has been more often reported. In Mediterranean species, the most common hardening techniques include induced nutrient deficiency (Vilagrosa et al., 2006), acclimation of seedlings to low temperatures and, most often, water deficiency (Villar-Salvador et al., 1999, 2004a,b; Vilagrosa et al., 2003a). However, although hardening techniques are often reported to increase seedling resistance to environmental stress when tested in nurseries, their success for improving seedling survival and growth when planted in the wild is far from being demonstrated. For instance, recent studies suggest than nutrient fertilization rather than deficiency improves field performance (Villar-Salvador et al.,

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