From Forest Nursery Notes, Winter 2009

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Functional Plant Biology, 2008, **35**, 725–737

Relating leaf photosynthetic rate to whole-plant growth: drought and shade effects on seedlings of four *Quercus* species

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Abstract. Understanding the impacts of combined resource supplies on seedlings is critical to enable prediction of establishment growth, and forest dynamics. We investigated the effects of irradiance and water treatments on absolute growth, and relative growth rate (RGR) and its components, for seedlings of four *Quercus* species differing in leaf habit and with a wide variation in seed mass. Plants were grown for 6.5 months at three levels of irradiance (100, 27, and 3% daylight), and treated during the last 2.5 months with two watering treatments (frequent watering *v.* suspended watering). Both shade and drought reduced seedling growth rates, with a significant interaction: under full irradiance the drought treatment had a stronger impact on RGR and final biomass than under deep shade. For three species, seed mass was positively related to absolute growth, with stronger correlations at lower irradiance. The evergreen species grew faster than the deciduous species, though leaf habit accounted for a minor part of the interspecific variation in absolute growth. Seedling biomass was determined positively either by RGR or seed mass; RGR was positively linked with net assimilation rate (NAR) and leaf mass fraction (LMF), and seed mass was negatively linked with RGR and LMF, but positively linked with NAR. Seedling RGR was not correlated with light-saturated net photosynthetic rate, but was strongly correlated with the net carbon balance estimated, from photosynthetic light-response curves, considering daily variation in irradiance. These findings suggest an approach to applying short-term physiological measurements to predict the RGR and absolute growth rate of seedlings in a wide range of combinations of irradiance and water supplies.

Additional keywords: biomass allocation, carbon balance, growth analysis, leaf habit, Mediterranean oak, relative growth rate, seed mass, specific leaf area.

Introduction

Seedlings' rates of growth and survival are strongly determined by irradiance (e.g. Poorter 2001; Montgomery 2004; Sánchez-Gómez *et al.* 2006), and water availability (Grant *et al.* 2005; Matthes and Larson 2006; Engelbrecht *et al.* 2007). Recently, there has been strong interest in the combined effects of irradiance and water on plant performance across scales, from leaves (Aranda *et al.* 2005; Quero *et al.* 2006), to plants (Sack and Grubb 2002; Sack 2004; Sánchez-Gómez *et al.* 2006), to communities (Zavala and de la Parra 2005). This understanding is critical as droughts are occurring with increasing severity (Piñol *et al.* 1998; De Luís *et al.* 2001; Peñuelas *et al.* 2002); climate change scenarios predict a 20% decrease in rainfall in Mediterranean areas in the next century (IPCC 2007). Irradiance and water supplies may vary strongly even at the meter or centimetre scale (Maestre *et al.* 2003; Quero 2006), driving coexistence of different species (Montgomery and Chazdon 2002; Valladares 2003; Sack 2004). Indeed, in different natural systems, irradiance and water supplies may vary independently, or they may be correlated positively or negatively (e.g. Abrams and Mostoller 1995; Valladares and Pearcy 2002; Niinemets and Valladares 2006). Given this complexity, we need to understand how plant responses to drought can vary across irradiances. Some authors have hypothesised that the impact of drought should be stronger in deeper shade (Smith and Huston 1989; Aranda *et al.* 2005). However, studies have shown that for leaf-level physiology and for absolute plant growth and survival, the impact of drought is typically reduced in shade (e.g. Canham *et al.* 1996; Holmgren 2000; Sack and Grubb 2002; Sack 2004). In a previous

10.1071/FP08149
1445-4408/08/080725