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ORIGINAL ARTICLE

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Carbohydrate storage, survival, and growth of two evergreen *Nothofagus* species in two contrasting light environments

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Abstract A number of traits have been attributed important roles in tolerance of shade by plants. Some explanations emphasize traits enhancing net carbon gain; others emphasize energy conservation traits such as storage of non-structural carbohydrates (NSC). To date, cross-species studies have provided mixed support for the role of NSC storage in low-light survival. We examined NSC status, survival, biomass, and growth of large seedlings of two evergreen species of differing shade tolerance (*Nothofagus nitida* and *N. dombeyi*) grown in deep shade and 50% light for two growing seasons. We expected to find higher NSC concentration in the more shade-tolerant *N. nitida* and since allocation to storage involves sacrificing growth, higher growth rate in the shade-intolerant *N. dombeyi*. NSC concentration of both species was >twofold higher in 50% light than in deep shade, and in roots and stems did not differ significantly between species in either environment. NSC contents per plant were also similar between dead and living plants in deep shade. *N. dombeyi* outgrew *N. nitida* in 50% light, while this pattern was reversed in deep shade. Survival in deep shade was not correlated with NSC concentration. Leaf mass fraction was similar between species in 50% light, but lower in *N. dombeyi* in deep shade. Results provide little evidence of a link between carbohydrate storage and low-light survival in *Nothofagus* species, and support the view that understorey survival is primarily a function of net carbon gain. Patterns of variation in NSC concentration of the temperate species we studied are likely dominated by more important influences than adaptation to shade, such as limitation of growth or adaptation to cold stress.

Keywords Allocation · Carbon gain · Non-structural carbohydrates · Shade tolerance · Temperate forest

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Introduction

A central question in the physiological ecology of forest succession is whether tolerance of shade has more to do with carbon gain or carbon conservation (Valladares and Niinemets 2008). Early explanations emphasized traits likely to enhance whole-plant carbon gain in low light, such as development of a large ratio of leaf area to biomass through high allocation to foliage production, and low respiration rates and light compensation points (Bazzaz 1979; Givnish 1988). Some studies of young seedlings have lent little support to this concept of shade tolerance (Kitajima 1994; Walters and Reich 1999), although other studies of larger seedlings and saplings are more supportive (e.g., King 1991; Lusk 2002; Baltzer and Thomas 2007).

Another view of shade tolerance emphasizes storage and defensive traits favoring energy conservation (Kitajima 1994; Kobe 1997; Canham et al. 1999; Walters and Reich 1999). Non-structural carbohydrates (NSC) storage is potentially valuable in buffering against temporary resource deprivations: reserves could be mobilized to meet maintenance costs during periods of heavy shading, or to replace leaves lost to herbivores (Chapin et al. 1990; Kitajima 1994; Kobe 1997; Canham et al. 1999). Allocation to storage necessarily involves sacrificing growth and forgoing opportunities for increasing