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Ontogeny, understorey light interception and simulated carbon gain of juvenile rainforest evergreens differing in shade tolerance

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• *Background and Aims* A long-running debate centres on whether shade tolerance of tree seedlings is mainly a function of traits maximizing net carbon gain in low light, or of traits minimizing carbon loss. To test these alternatives, leaf display, light-interception efficiency, and simulated net daily carbon gain of juvenile temperate evergreens of differing shade tolerance were measured, and how these variables are influenced by ontogeny was queried.

• *Methods* The biomass distribution of juveniles (17–740 mm tall) of seven temperate rainforest evergreens growing in low (approx. 4 %) light in the understorey of a second-growth stand was quantified. Daytime and night-time gas exchange rates of leaves were also determined, and crown architecture was recorded digitally. YPLANT was used to model light interception and carbon gain.

• *Results* An index of species shade tolerance correlated closely with photosynthetic capacities and respiration rates per unit mass of leaves, but only weakly with respiration per unit area. Accumulation of many leaf cohorts by shade-tolerant species meant that their ratios of foliage area to biomass (LAR) decreased more gradually with ontogeny than those of light-demanders, but also increased self-shading; this depressed the foliage silhouette-to-area ratio (STAR), which was used as an index of light-interception efficiency. As a result, displayed leaf area ratio ($LAR_d = LAR \times STAR$) of large seedlings was not related to species shade tolerance. Self-shading also caused simulated net daily carbon assimilation rates of shade-tolerant species to decrease with ontogeny, leading to a negative correlation of shade tolerance with net daily carbon gain of large (500 mm tall) seedlings in the understorey.

• *Conclusions* The results suggest that efficiency of energy capture is not an important correlate of shade tolerance in temperate rainforest evergreens. Ontogenetic increases in self-shading largely nullify the potential carbon gain advantages expected to result from low respiration rates and long leaf lifespans in shade-tolerant evergreens. The main advantage of their long-lived leaves is probably in reducing the costs of crown maintenance.

Key words: Biomass distribution, leaf display, leaf angle, leaf area ratio, leaf lifespan, light-interception efficiency, self-shading, shade tolerance, silhouette-to-area ratio, YPLANT.

INTRODUCTION

Understanding the forces controlling forest succession has been a prime goal of ecologists and foresters for >100 years (Warming, 1909). In humid forests, where intervals between stand-destroying disturbances often exceed the lifespan of individual trees, species turnover is thought to be driven mainly by differences in the ability to tolerate shade (Pacala *et al.*, 1994), as light is the resource most diminished by vegetation development and best correlated with juvenile tree survival and growth (Denslow *et al.*, 1990; Finzi and Canham, 2000).

A long-running, evolving debate centres on whether shade tolerance is mainly a function of traits maximizing photosynthetic carbon gain in low light, or of traits minimizing losses (reviewed by Valladares and Niinemets, 2008). The first attempt at a general theory of adaptation to sun and shade proposed that shade tolerance is determined mainly by traits that enhance net energy capture in low light (Givnish, 1988). Shade-tolerant species were therefore expected to develop a large ratio of leaf area to plant biomass (leaf area ratio, LAR) by allocating heavily to leaf production, and to gain more carbon gain per unit leaf area than light-demanding species when grown in low light. However, subsequent comparative studies of young seedlings failed to support most of these predictions. First-year seedlings of shade-tolerant species develop a smaller LAR than light-demanding associates of the same age – reflecting a large initial allocation to roots, and small specific leaf areas (SLA) – as well as growing more slowly even in light as low as 2–5 % of full sun (Kitajima, 1994; Veneklaas and Poorter, 1998; Walters and Reich, 1999). The robust construction (small SLA) of the leaves of shade-tolerant evergreen seedlings is associated with resistance to physical stresses and unattractiveness to natural enemies (Coley and Barone, 1996; Kitajima and Poorter, 2010).