Contribution of Leaf Orientation and Leaf Physiology to the Maximization of Plant Carbon Gain

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Introduction

Optimal nitrogen allocation theory predicts that plant photosynthesis will be maximized if the photosynthetic capacity of individual leaves (A_{max}) in a canopy scales proportionally to the availability of light in the vicinity of a leaf (Field 1983, Farquhar 1989, Field 1991). However, many plants do not follow the expected distribution (e.g., Hirose and Werger 1987, Evans 1993, Hollinger 1996). This discrepancy has generally been interpreted as being the results of physiological constraints and ecological trade-offs that impede plants to reach the predicted "true" optimal A_{max} distribution. Yet, optimal allocation resource allocation theory does not take into consideration the potentially important role of leaf orientation as a modulator of the light environment of individual leaves. Moreover, it is not yet clear that the predicted optimal A_{max} distribution does in fact maximize plant photosynthesis. The objective of our study was to find the distribution of leaf functional traits that maximized plant carbon gain when both leaf A_{max} and leaf orientation were allowed to vary with the light gradients in the canopy.

LIGNUM Simulations

We did three-dimensional simulations of trees using the functional-structural plant model LIGNUM. We grew realistic 1-4 m tall trees of *Acer saccharum* and *Populus deltoids* and used them as plant architectural "templates" to search for distributions of leaf traits that maximized plant photosynthesis. Light above the trees was distributed assuming standard overcast conditions. Self-shading between leaves generated a gradient of photosynthetic photon flux density (PPFD) within the canopy and LIGNUM calculated PPFD incident at the point of emergence of each individual leaf bud. The function relating leaf A_{max} to PPFD incident on buds varied hyperbolically while leaf inclination changed linearly with PPFD. We used quasi-Newton and simulated annealing methods to find combinations of parameter that maximized whole tree carbon gain. A_{max} defined the photosynthetic light response of each individual leaf assuming a linear relationship between A_{max} and dark respiration (R_d) while apparent quantum yield (ϕ) and curvature (θ) were kept constant.

Results and Discussion

One-dimensional optimizations showed that plants that gradually increased the inclination of leaves with PPFD had higher carbon gain than leaves with either horizontal or vertical leaves. When individual leaf A_{max} changed linearly with PPFD plant photosynthesis was higher than if all leaves had the same A_{max}, supporting the initial predictions of optimal allocation theory. However, when leaf A_{max} changed as a hyperbolic function of PPFD plant carbon gain was enhanced further contradicting the above predictions. Furthermore, the hyperbolic A_{max} functions were qualitatively similar to distributions observed in natural conditions. Maximum plant carbon gain was obtained when both leaf inclination and leaf A_{max} changed with PPFD availability in the canopy. Our simulations show that plant photosynthesis was maximized when the leaf array in the canopy attained maximum average photosynthetic light use efficiency. Thus, these results suggest that natural selection should favor a distribution of A_{max} that maximizes photosynthetic efficiency of all individual leaves.

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