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Interpreting shallow, vertical nitrogen profiles in tree crowns: A three-dimensional, radiative-transfer simulation accounting for diffuse sunlight

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Abstract

The assumed concentration and distribution of active leaf nitrogen (N) within vegetation canopies has a major influence on the gross primary product (GPP) predicted by land-surface models. We couple a Monte Carlo, three-dimensional (3D), ray-tracing simulation to the land-surface model JULES in order to compare the vertical profiles of light and active leaf-N in three forest stands of diverse composition and structure. Our simulations, which are driven by real climate data, strengthen the view that tree canopies are only partially light-acclimated. Notably, our computation demonstrates the importance of both diffuse sunlight and the manner in which the light profile is quantified. For example, when our temperate, broadleaf stand is subjected to diffuse sunlight, the mean leaf irradiance declines steeply in the upper third of crown ($k_{ext} \gtrsim 1$, where k_{ext} is the exponential extinction coefficient) but is relatively shallow below that height ($k_{ext} \leq 0.75$). Under direct sunlight, the foliage divides into sunlit and shaded fractions and a more appropriate measure of the light environment is probably the mode irradiance rather than the mean irradiance. Under direct sunlight, the optimal vertical distribution of Rubisco (i.e. that which maximises GPP for a fixed amount of active leaf-N in the canopy) is calculated to be shallow in both the upper and lower portions of the canopy ($k_{rub} < 0.27$, where k_{rub}, is the exponential N-allocation parameter). Furthermore, an abrupt step, from high to low photosynthetic capacity, is predicted in the upper third of the crown. The theoretical gain in GPP for a stand that is fully light-acclimated compared to one that is only partially light-acclimated (i.e. with $k_{rub} = 0.15$, as measured in real tree canopies) is moderately important (8–13%). Our results are relatively insensitive to canopy architecture, i.e. crown structure, leaf-clumping and the leaf angle distribution.
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Keywords: Radiative-transfer; Diffuse sunlight; Light acclimation; Nitrogen cycle

1. Introduction

The acclimation hypothesis states that the vertical gradient of photosynthetic capacity is proportional to that of the average light profile through the canopy (Meir et al., 2002). The leaf photosynthetic capacity is equivalent to the photosynthetic rate at light saturation and is determined by the concentration of RUBP carboxylase-oxygenase (Rubisco) in the foliar photosynthetic apparatus. The acclimation hypothesis is implicit in the big leaf radiative-transfer (RT) scheme (Sellers et al., 1996) and is often assumed in other formulations of RT implemented in regional/global land-surface models (LSMs). Typically, these LSMs are coupled to a Global Circulation Model (GCM) and can, therefore, undergo quite computationally intensive simulations. The assumption of full acclimation facilitates the calculation of gross primary product (GPP) for the canopy considerably (e.g. Schulze et al., 1994). Furthermore, strong adaptation to the light

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environment might be expected for biomes of high Leaf Area Index (LAI) where GPP may be light-limited for prolonged periods of the day (Nemani et al., 2003). Although measurements of leaf-N and photosynthetic capacity can vary considerably at the same height within a tree (≃30%; Dang et al., 1998), a majority of empirical data in the literature suggest that light acclimation might be incomplete, at least within tree canopies (Carswell et al., 2000; Lewis et al., 2000; Meir et al., 2002; and references therein). The question of acclimation is important for several reasons: (i) the GPP predicted by LSMs varies strongly (20–35%) for typical uncertainties in both the photosynthetic capacity at the top of the crown and the vertical gradient of Rubisco (Alton et al., 2007a, 2007c); (ii) the distribution of active leaf-N is important for dynamic models of nutrient cycling; and (iii) the understanding of current constraints on plants and their ecosystems (light-, water- or N-limited) is a prerequisite to predicting the response of the terrestrial biosphere to future climate change (e.g. Nemani et al., 2003).

Various attempts have been made to explain the shallow Rubisco gradients measured in vegetation canopies (Chen et al., 1993; Kull and Kruijt, 1999; Friend, 2001). However, to cite Frak et al. (2002), '. . .there is presently no consensus about the factor(s) driving photosynthetic acclimation'. Furthermore, many previous studies are rather theoretical, containing ecological concepts which are difficult to test. In this paper, we adopt a different approach. We simulate light interception in tree canopies using a 3D, ray-tracing model which has recently been enhanced so that it discriminates between diffuse and direct sunlight (Alton et al., 2005). Our RT-scheme takes explicit account of leaf orientation and sunfleck penetration. This is an important consideration under sunny conditions when the dispersion in leaf irradiance, at any given height in the canopy, is observed to be large (Parker et al., 2002). Meir et al. (2002) attribute an important role to diffuse sunlight in influencing the Rubisco gradient within tree canopies. Until now, this idea remains untested as modellers have a tendency to concentrate on the impact of *direct* sunlight on the distribution of foliar N (e.g. Chen et al., 1993). The diffuse sky flux produced by clouds and aerosols is known to have a large impact on carbon assimilation, increasing light-use efficiency by up to a factor of two compared to direct sunlight (Hollinger et al., 1994; Gu et al., 2002; Niyogi et al., 2004; Alton et al., 2007b).

The current investigation differs from previous studies in several other important aspects: (i) our ray-tracing simulations are three-dimensional taking explicit account of crown shape and canopy heterogenity; (ii) we conduct simulations for three quite different tree stands with known biophysical parameters (a sparse, boreal needleleaf site; a dense, tropical, broadleaf stand; and a moderately dense, temperate, broadleaf location); and (iii) we use real climate data to infer the light environment in the canopy at each timestep, including the fraction of diffuse sunlight. Our RT-scheme is coupled to a LSM to ensure realistic simulation of other biophysical processes, such as stomatal conductance, as well as environmental variables such as canopy temperature and humidity.

Our main objective is to interpret the vertical profile of photosynthetic capacity (hence Rubisco) recorded in tree canopies. This is achieved in three steps: (i) by quantifying the light profile within the stand; (ii) by determining the exponential profile of Rubisco which maximises canopy GPP when the total amount of Rubisco within the stand is fixed (hereafter 'optimal' Rubisco distribution); and (iii) by using the theoretical results from (i) and (ii) to interpret the profiles of Rubisco and light measured in real tree canopies, particularly with respect to light acclimation.

2. Materials and methods

Our methodology requires the coupling of a 3D, ray-tracing simulation to a LSM. The latter is subsequently run for three separate sites using real climate data. The next two sections describe the ray-tracing simulation and the LSM. Section 3 describes simulations conducted to ascertain the average light profile and optimally distributed Rubisco distribution.

2.1. Radiative-transfer

The forest light (FLIGHT) simulation is a ray-tracing, numerical model employing Monte Carlo techniques to sample light propagation and leaf irradiance in both uniform, one-dimensional (1D) vegetation layers and heterogeneous, 3D canopies (North, 1996; Barton and North, 2001; Alton et al., 2005). Our current focus is on 3D canopies, although we also conduct 1D simulations in order to compare with previous modelling of light acclimation (Chen et al., 1993; Kull and Kruijt, 1999; Friend, 2001). For both 1D and 3D simulations, foliage is represented by volume-averaged parameters such as LAI and scattering phase function. Leaf inclinations are modelled explicitly within FLIGHT, rather than adopting a single (mean) leaf orientation which is standard practice in sunlit/shade RT models. Explicit leaf orientation accounts