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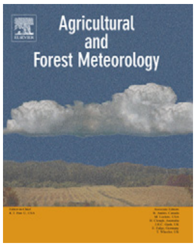

The fundamental role of reserves and hydraulic constraints in predicting LAI and carbon allocation in forests

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ABSTRACT

A model simulating forest carbon and water fluxes was improved to simulate carbon allocation to roots, reserves and aboveground woody biomass and to estimate maximum leaf area index of the current year (LAI_{max}). LAI_{max} was calculated from the carbohydrates reserve, which integrates past ecological conditions. Allocation coefficients to the various compartments were originally fixed constant in the basic version, with no temporal and spatial variation. In the improved version, these coefficients were modified spatially and temporally according to functional rules. Carbon allocation to fine roots was simulated by accounting for hydraulic constraints. An empirical model was developed to simulate allocation to reserves. Allocation to aboveground woody biomass was the residual; remaining carbon after allocation to reserves and fine roots. Then, this residual carbon was partitioned into stem diameter and height growth. The allocation model was tested on 20 stands of oak and beech in the Fontainebleau forest. The model reproduced wood growth and LAI_{max} dynamics between 1994 and 1999. While the basic version of the model overestimated the growth (364 $g_C\,m^{-2}\,year^{-1}$ vs. 261 $g_C\,m^{-2}\,year^{-1}$) and did not reproduced the growth variability well between sites ($r = 0.4$), the new version better reproduced the average level of growth (235 $g_C\,m^{-2}\,year^{-1}$ vs. 261 $g_C\,m^{-2}\,year^{-1}$) and the variability ($r = 0.64$). That model also reproduced the decline of productivity with age and the processes leading to temporal variability in LAI, such as water stress in the previous year.

1. Introduction

1.1. *Improve allocation modelling to bridge the gap between process-based and empirical models*

Some process-based models have coupled water vapour and carbon dioxide exchange between vegetation and the atmosphere that explicitly integrate climate effects (Kramer et al., 2002; Dufrêne et al., 2005; Davi et al., 2006c). On the other hand, wood production has been estimated during the last century using statistical models based on empirical field measurements that account for management and age effect (Schober, 1975; Dhote, 1991). To improve predictions of forest production with global change, it has been necessary to couple mechanistic approaches with empirical forestry knowledge (Mäkelä, 1988; Sievänen and Burk, 1993; Johnsen et al., 2001; Landsberg and Waring, 1997; Valentine et al., 1997; Bartelink, 2000; Mäkelä et al., 2000; Landsberg, 2003).

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To couple process-based and empirical models, the allocation of carbon between different compartments inside the tree and between the various individuals must be improved (Litton et al., 2007). The allocation of carbon can be simulated either by focusing on the series of carbon translocation processes or solely on the requirements of the tree. Carbon translocation processes include transformation to saccharose, phloem loading, transport by diffusion and unloading to the sinks of maintenance and growth (Thornley, 1972). At the stand level, models based on the potential sink (requirements of the tree) are easier to use. Allocation coefficients can be kept constant for the various compartments (MacMurtrie and Wolf, 1983) or allowed to vary according to site fertility (MacMurtrie, 1985), tree social status (Mäkelä and Hari, 1986) or stand age (Magnani et al., 2000). To model allocation coefficients, a priority system (Bossel, 1987) can be used where carbon is first allocated to leaves (Weinstein and Yanaï, 1994) to reach a level calculated according to allometric laws (Landsberg, 1986), or according to relations between the leaf/root ratio and the nitrogen or magnesium concentration in the soil (Wikström and Ericsson, 1995). Other nutriment limitations could be important: P was the nutrient limiting net primary production in many ecosystems (Herbert and Fownes, 1995; Gradowski and Thomas, 2006) and consequently can also drive the allocation (Ericsson, 1995). The relationships among the functional compartments of a tree (fine roots, large roots, trunk, branches and leaves) are also highly constrained by the need to maintain a hydraulic continuum from fine roots through to the leaves (Shinozaki et al., 1964; Magnani et al., 2000).

1.2. *The different approaches for LAI prediction*

Leaves are an important carbon sink and leaf area (LAI) and leaf mass (leaf mass per area) are key ecosystems parameters strongly impacting the Net Ecosystem Exchange. Consequently, LAI and LMA modelling are an important challenge. A method to simulate LMA was already given in Davi et al. (2008). Here, we will focus on LAI.

LAI is an index of canopy structure which controls different processes of a forest ecosystem such as light and rain interception (Gash, 1979), gross productivity (Jarvis and Leverenz, 1983; Linder, 1985; Vose and Allen, 1988; Coyea and Margolis, 1994; Maguire et al., 1998) and transpiration (Granier et al., 2000a). In addition, soil respiration which contributes a significant part of carbon fluxes (Granier et al., 2000b; Janssens et al., 2001) is correlated to litterfall (Davidson et al., 2002).

Some models simulate LAI from the carbon budget of the current year (Garcia et al., 1999; Running and Gower, 1991). LAI thus calculated can be corrected according to nitrogen and water availability (Running and Gower, 1991). Another method consists of optimizing LAI to either maximize carbon uptake or limit the effect of drought (Woodward, 1987; Kergoat, 1995).

In this paper, the stand-level model CASTANEA (Dufrêne et al., 2005) was modified to (1) simulate the stand LAI from reserves level and (2) to improve the carbon allocation model by including reserves and hydraulic constraints. The new model is then tested using aboveground biomass and LAI from 20 stands dominated by two different deciduous species in the Fontainebleau forest near Paris.

2. Materials and methods

2.1. *The model*

2.1.1. *General characteristics of the CASTANEA model*

CASTANEA is a multi-layer model based on physiological and physical processes simulating carbon, water and energy balances in forest stands. Tree structure was a combination of four functional compartments: leaves, aboveground woody biomass, coarse and fine roots. A reserve compartment is also represented but does not have a physical location.

The canopy was horizontally homogeneous and vertically subdivided into layers. Three radiation balances were calculated: PAR [400-700 nm], total radiation [400-2500 nm], and thermal infrared. Incident light was divided into direct and diffuse radiation using equations given by Spitters, 1986. The radiation extinction and diffusion were based on the scattering from arbitrarily inclined leaves (SAIL) model (Verhoef, 1984, 1985). Canopy clumping was taken into account in the model of radiation transfer by using a clumping factor which adjusts the leaf area used by the SAIL sub-model.

Canopy gross photosynthesis was calculated every half-hour according to Farquhar et al. (1980) and modified with a stomatal conductance model according to Ball et al. (1987). Leaf nitrogen effect on photosynthesis was taken into account assuming a linear relationship between the maximum carboxylation rate (V_{cmax}) and leaf nitrogen content per unit area (N_a) with a slope of α_{Na}. A fixed ratio (β) between V_{cmax} and the potential rate of electron flow (V_{jmax}) is used (Leuning, 1997).

All phenological events were calculated daily depending on day-degrees and day duration. Maintenance respiration (RM) depended on temperature and nitrogen content of various organs (Ryan, 1991a), while growth respiration (RG) depended on a construction cost fixed for an organ type (Dufrêne et al., 2005). Soil water balance and heterotrophic respiration (Parton et al., 1987) were also simulated.

After accounting for leaf growth and maintenance respiration the remaining carbon was allocated to the four other compartments (aboveground woody organs, reserve, coarse and fine roots). The growth of the different organs ($\mathrm{GB_{org}}$) was a proportion (allocation coefficients) of the available carbon:

$$\mathrm{GB_{org}} = \frac{\mathrm{AG_{org}}}{\mathrm{CR_{org}}}(A_{\mathrm{can}} - \mathrm{RM} - \mathrm{RG_{leaf}} - \mathrm{GB_{leaf}}) \tag{1}$$

where $\mathrm{AG_{org}}$ is the allocation coefficient per organ type (the sum of the four coefficients is one), A_{can} the gross canopy photosynthesis, $\mathrm{CR_{org}}$ the organ construction cost, RM the total maintenance respiration (all organs), $\mathrm{RG_{leaf}}$ the leaf growth respiration and $\mathrm{GB_{leaf}}$ the leaf growth. $\mathrm{GB_{leaf}}$ is the product of growth in area and mass. The dynamics of leaf growth in area followed degree-day according to Dufrêne et al. (2005) and the dynamics of leaf mass per area depended on degree-day and total radiation sum as in Davi et al. (2008).

In the basic version of the model, $\mathrm{AG_{org}}$ is a parameter either considered as constant for a species or calibrated with measurements for a site. The initial parameterization was done on two sites (see Dufrêne et al., 2005; Barbaroux, 2002) independent from the validation site (Fontainebleau Forest).