



Can decision rules simulate carbon allocation for years with contrasting and extreme weather conditions? A case study for three temperate beech forests



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ABSTRACT

The allocation of carbohydrates to different tree processes and organs is crucial to understand the overall carbon (C) cycling rate in forest ecosystems. Decision rules (DR) (e.g. functional balances and source-sink relationships) are widely used to model C allocation in forests. However, standard DR allocation schemes lack a strong environmental sensitivity and their ability to simulate the year-to-year variability and the impact of extreme events is questioned. In this study, we aimed to compare the performance of a standard DR allocation scheme to the performance of an improved DR allocation scheme taking into account drought-induced changes in allocation dynamics and acclimation of respiration. Model validation was performed against extensive datasets of C fluxes and C pools for a 9 years period (2000–2008) for the site of parameterisation (the beech forest of Hesse, France) and for two contrasting sites not used for parameterisation (the beech forest of Sorø, Denmark, for 1999–2006, and Collelongo, Italy, for 2005–2006). At Hesse, 2003 was characterised by a severe and extreme drought and heat wave.

The standard DR allocation scheme captured the average annual dynamics of C allocation and wood growth at beech stands with contrasting climate and standing stock. However, the allocation model required high quality GPP input and errors (even modest) in GPP resulted in large errors in the growth of the tree organs lowest in the modelled sink hierarchy (woody organs). The ability of the standard DR allocation model to simulate year-to-year variability was limited. The amended DR allocation scheme improved the annual simulations and allowed capturing the stand growth dynamics at Hesse during the extreme 2003 summer and its important lag effect on next year's wood production. Modelling of drought-induced changes in fine root dynamics and of short-term thermal acclimation of maintenance respiration should not be overlooked when simulating the C cycle of forests, particularly for sites likely to experience extreme drought and heat waves. The most relevant model bias was the inaccurate estimation of leaf biomass production (up to 15%) and a poor description of its interannual variability. Future studies should focus primarily on this limitation.

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1. Introduction

Forest ecosystems globally store about 1200×10^{15} g carbon (C), equivalent to 52% of the terrestrial C pool (Adams et al., 1990), and are estimated to be the largest terrestrial C sink, accumulating about 1 to 3×10^{15} g C year⁻¹ (Malhi et al., 1999). Small changes in the C balance of these ecosystems can therefore have a large impact on the atmospheric CO₂ concentration and on the global climate. The allocation of assimilates among different processes (e.g. biomass production vs. respiration) and plant organs with different life spans and decomposition rates (e.g. leaves vs. stem wood) is a key process in the C cycle because it determines the long term rate of the ecosystem respiration (Trumbore, 2006) and thus the residence time of C in the ecosystem. Nonetheless, assimilate allocation is among the processes described in lesser detail in C cycle models.

The development of allocation procedures for C cycle models can rely on different strategies used to simulate C allocation in forest growth models (Cannell and Dewar, 1994; Laointe, 2000; Le Roux et al., 2001). Assimilate allocation can be modelled following three main approaches: decision rules, mechanisms and system dynamics (Mäkelä, 2012). (1) Decision rules (DR) describe a priori growth pattern and the C allocation process is considered more as a consequence than a determinant of this pattern (Laointe, 2000). Decision rules comprise allometric relationships (e.g. the relationship between sapwood and foliage i.e. the Pipe-Model, Shinozaki et al. (1964)), functional balances (e.g. the root-shoot ratio, Davidson (1969)) and source-sink relationships. According to the latter strategy, trees are considered as a collection of semi-autonomous, yet interacting sinks (e.g. fine roots, stems) competing for the supply of assimilates from sources (leaves, reserves) (Le Roux et al., 2001). The amount of C allocated to the sinks depends on specific sink demands. In case the available C is not sufficient to satisfy these demands, then every sink is partly satisfied on the same degree, or a sink hierarchy is established. (2) The mechanistic approaches attempt to describe accurately the (eco)physiological processes underlying allocation. Such approaches are based on biochemical/hormonal control, sink strength or transport-resistance (TR) (Mäkelä, 2012). For instance, the well known TR models simulate C allocation by modelling the C transport within the tree (based on concentration gradients and flow resistances, Münch (1930)) and the C consumption by the organs (sinks), whose growth is modelled following a bi-substrate kinetic (De Schepper and Steppe, 2010; Thornley, 1972, 1991). (3) Approaches based on system dynamics simulate allocation following laws that are assumed to control the overall dynamics of the system of interest (Mäkelä, 2012). For example, such strategies might rely on biological laws of traits variability and natural selection (e.g. adaptive dynamics of populations) or physical laws of thermodynamics (e.g. maximum entropy production) (Franklin et al., 2012).

The practical application of mechanistic and system dynamics models remains complex and, for mechanistic models, the model parameters are difficult to estimate. On the other hand, C allocation modules based on DR are more convenient to apply for at least four reasons. (1) Although not explanatory as the other approaches, the DR models describe the basic principles controlling allocation. (2) Their parameters have in general a clear physiological meaning and can be easily obtained from direct measurements or calibration. (3) They can be coupled to the phenological course. (4) They are straightforward and easy to develop and use. Because of these qualities, DR allocation schemes are widely used in models of forest growth (Bartelink, 1998; Bossel, 1996; Hoffmann, 1995; Misson, 2004), of forest C and H₂O cycle (Davi et al., 2005; Dufrêne et al., 2005) and of global vegetation dynamics (Krinner et al., 2005; Sitch et al., 2003). However, most DR allocation schemes have an important drawback, i.e. a poor environmental sensitivity. This might

make standard DR schemes too insensitive to variable environmental conditions and year-to-year variability and might undermine the quality of their future projections. In fact, climate variability is expected to increase with global change (IPCC, 2012). The ability of a standard DR scheme to reproduce allocation and growth dynamics during severe and exceptional weather conditions (i.e. extreme climatic events) is particularly questioned. Uncertainty about the performance of DR schemes under variable environmental conditions is also related to the lack of validation, as model validation exercises are typically limited to one year, one site or a single growth process.

In this study, we addressed three main questions: (1) Is the performance of a standard DR allocation scheme with low environmental sensitivity satisfying when tested against multiple datasets of (inter)annual and seasonal carbon fluxes and pools at different sites? (2) Does the performance of a standard DR allocation scheme improve significantly when drought-induced changes in allocation dynamics and acclimation of respiration are considered? (3) Does such an amended DR allocation scheme (from here on 'environmental DR' scheme) capture the interannual variability in allocation and growth and the impact of extreme weather events such as drought and heat waves? These questions were addressed by testing a standard DR scheme and an environmental DR scheme against extended independent datasets (e.g. annual biomass production of leaves and wood, partitioning of photosynthates, standing biomass, phenological observations and seasonal growth dynamics) for a 9 years period (2000–2008) for the site of parameterisation (the CarboEurope beech site of Hesse, France) and for two contrasting sites not used for parameterisation (the CarboEurope beech sites of Sorø, Denmark, and Collelongo, Italy). The investigated period allowed a modelling analysis of the impact of the European drought and heat wave of the summer of 2003, which was low at Sorø but it was severe at Hesse (Bréda et al., 2006; Granier et al., 2007).

2. Materials and methods

2.1. Terminology

Terminology on C allocation is often confusing. Here, we use only the terms allocation and partitioning, to which we associate a different meaning. 'Allocation' indicates the transfer of assimilates to one (or more) tree organ(s) (e.g. C allocated to fine roots) where they are either used to increase the C stock or for driving physiological processes, e.g. maintenance respiration. 'Partitioning' indicates the fractioning of a certain amount of assimilates among specified organs or processes (e.g. the C allocated to wood is partitioned among coarse roots, stems and branches). In addition, we use the term 'relocation' to indicate the withdrawal of assimilates previously allocated to an organ (e.g. the non-structural carbohydrates in leaves were relocated at the end of the growing season).

2.2. Standard DR allocation model

We integrated the most suitable routines of earlier DR models (in particular the TREEDYN3 model (Bossel, 1996) and the CAS-TANEA model (Dufrêne et al., 2005)) in a straightforward and efficient way (e.g. with the lowest possible number of equations and parameters). The resulting model (defined here as standard DR model) simulates C partitioning among the main tree organs and the reserve pool of non-structural carbohydrates considering the main physiological processes that determine C allocation (biomass production, maintenance and growth respiration, reserve consumption and accumulation, organ turnover and mortality) for single-flush diffuse-porous deciduous species.

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