

What are the processes driving carbon allocation to stem and fine roots in a mature coppice of *Quercus ilex* in the Mediterranean? A data model analysis

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Highlights: Improving carbon allocation in process based model is a challenging issue. A process model was prescribed using an extensive data set of growth and carbon fluxes (11 years) at the stand scale in order to draw new carbon allocation scheme in *Q. ilex*. Our results suggest that a part of summer photosynthesis is used for the renewal of fine roots.

Keywords: Carbon partitioning, sink source limitations, growth, drought, phenology, hydraulic

INTRODUCTION

Anticipating the fate of trees and forest ecosystems under the threats of climate changes involve numerical models. Process based models (PBMs) are predominantly used for this purpose because they were well-parameterized and able to run over spread out area (e.g. regional or continental scale). Despite such models have often been validated on the short term (from hour to year) through extensive comparisons with eddy covariance fluxes (water and carbon fluxes), they often fail to accurately represent the longer term processes that determine the growth of the different tree compartments. This is because processes related to carbon allocation inherently rely on multiple and complex interactions involving the source activities of photosynthesis, the sink activity of the different organs as well as the plant hydraulic and allometric structure.

In PBMs, carbon allocation is often computed using empirical coefficients that set which proportion of the current NPP (*i.e.* photosynthesis – autotrophic respiration) is used for the growth of the plant compartments (*e.g.* stem, roots, fine roots, leaves, storage). Such coefficients may be set empirically or may vary according to structural and biological rules (*e.g.* allometry, phenology or hydraulic constraints). Identifying the most important rules of carbon allocation for a given species in a given ecosystem is fundamental to improve the simulations of forest growth productivity and tree species persistence in a changing future (Leuzinger and Thomas 2011).

The Mediterranean climate is seasonal, winters are cool and wet whereas summers are dry and hot. The growth activity of stems of the evergreen *Quercus ilex* matches this climatic pattern as it takes place principally during the short favorable season of spring whereas little activity are observed during the rest of the year. Because the climate seasonality affects simultaneously most functions of trees, it is often difficult to figure out which of the source (Photosynthesis) or the sink (tissues development) activity are limited first and exerts the strongest influence on growth. An ongoing study using automatic dendrometers on a Mediterranean *Q. ilex* site (Lempereur *et al.*, in prep) suggests that the decrease of plant water potential that occurred during early summer is likely to preclude the development of tissue well before gross photosynthesis reaches zero. In such a situation a surplus of carbon substrate might be available for the growth of reproductive tissue, fine roots, or non structural carbohydrate (NSC) storage. Using a data-model approach, we first tested whether the decrease of stem growth of *Q. ilex* during summer was source or sink driven. Further, we attempted to identify the most likely sink for a surplus of carbon available. The implications our findings are discussed in terms of plant hydraulic architecture, structure and functioning in order to draw new carbon allocation rules.

MATERIALS, METHODS & SIMULATIONS

All simulations were performed for the period 2000-2010, using the PBM CASTANEA (Dufrene *et al.*, 2005), on a mature Mediterranean coppice largely dominated by *Q. ilex* and located in southern France on the experimental site of Puéchabon (hereafter PSite, see Rambal *et al.*, 2003, 2004, <http://puechabon.cefe.cnrs.fr/> for details). CASTANEA is a forest soil-vegetation-atmosphere model coupled with a growth module. It simulates carbon (photosynthesis and respiration) and water fluxes (transpiration

soil water content, soil water potential) at a half hourly to daily time step for an average tree in a homogeneous stand of forest. A carbon allocation module that uses empirical coefficients assign a proportion of the daily NPP toward the different plant compartment considered (stem, roots, fine roots, flowers, acorn, leaves and storage). Carbon and water fluxes, including gross and net ecosystem photosynthesis, respiration, transpiration, latent heat fluxes, soil water content and plant water potential were previously validated on the site (Davi *et al.*, 2005; Delpierre *et al.*, 2012; Martin-StPaul 2012). Discrete measurements of biomass and productivity (annual forest inventories, monthly litter collection) combined with allometric relationships established on the PSite as well as leaves, flowers and radial growth phenologies were used to constrain the carbon allocation module of CASTANEA. Carbon allocation to leaves, flowers, acorn, stem and coarse roots, was prescribed seasonally using phenological models for each compartment. Conversely, allocation toward storage and fine roots occurred all over the year.

In order to explain the decreased carbon allocation toward woody tissue during the summer drought period and to understand the fate of carbon allocation in summer we tested **three alternative assumptions**. The source limitation hypothesis (hereafter **SL**) states that the decrease C allocation to woody tissue during the summer is caused by a decreased source activity (drought induces stomatal closure and a decrease of the photosynthetic activity). The sink limitation hypothesis in favor of fine roots (**SkFr**), states that the decrease C allocation to woody tissue during summer is caused by a decreased sink activity (*e.g.* decreased growth due to turgor losses of woody tissue) and that carbon allocation is prioritize toward the renewal of the water acquisition tissue (*i.e.* fine roots). The sink limitation hypothesis in favor of storage (**SkSt**) is similar to the latter hypothesis with the exception that the carbon allocation during summer is prioritized to storage. The simulated seasonal pattern of C allocation under the 3 hypotheses is depicted on Fig. 1a. The likelihood of each hypothesis was assessed based on the temporal behavior of i) the storage concentration and, ii) the ratio of fine roots biomass over foliar biomass. We assumed that to be likely, the simulations of both the storage concentration and the fine root to leaf biomass ratio (BFR/BL) should remain stable over the simulation period.

RESULTS AND DISCUSSION

Simulations performed under **SkFr** and **SkSt** hypothesis yielded better predictions of the inter-annual variations of growth than using the **SL** (Fig 1b). This result confirms the general assumption that in drought prone ecosystems growth is mostly sink-driven (Korner 2003). Simulations using the **SkSt** hypothesis showed stable BFR/BL ratio over the study period but, NSC contents of the sapwood increased dramatically; from the 10% prescribed at the beginning of the simulations, NSC reached up to 60% in 2010 (Fig 1c). Such an increase seems very unlikely. It indicates that the surplus of carbon accumulated during the growth interruption in summer, could not be consumed neither by the maintenance respiration nor by the growth of the different tissues. Conversely, assuming that the carbon sequestered during the summer is allocated in priority to the fine roots renewal - as set in the **SkFr** hypothesis - lead to both, stable BFR/BL and stable storage content (Fig 1c). Whereas the BFR/BL was close 1.5 using the former hypothesis, it was close to 2 when simulations were performed using the **SkFr**. We do not have direct estimation of fine roots biomass and production on our experimental site, but measurements performed on a similar *Q. ilex* coppice (same age, climate and management) on a nearby site indicate that BFR/BL should be close to unity (Lopez *et al.*, 2001). The difference between our simulations and the data reported by Lopez *et al.*, (2001) suggests that we probably underestimated fine roots turnover. As fine roots are known to be highly sensitive to water-stress-induced cavitation, and are often considered as the bottleneck of the soil plant hydraulic systems, it is therefore possible that the surplus of carbon sequestered during summer was used to repair the hydraulic systems by building new roots in deeper and wetter soil horizons. Ongoing developments of a hydraulic and allometric model of carbon allocation will be used to test the latter hypothesis.

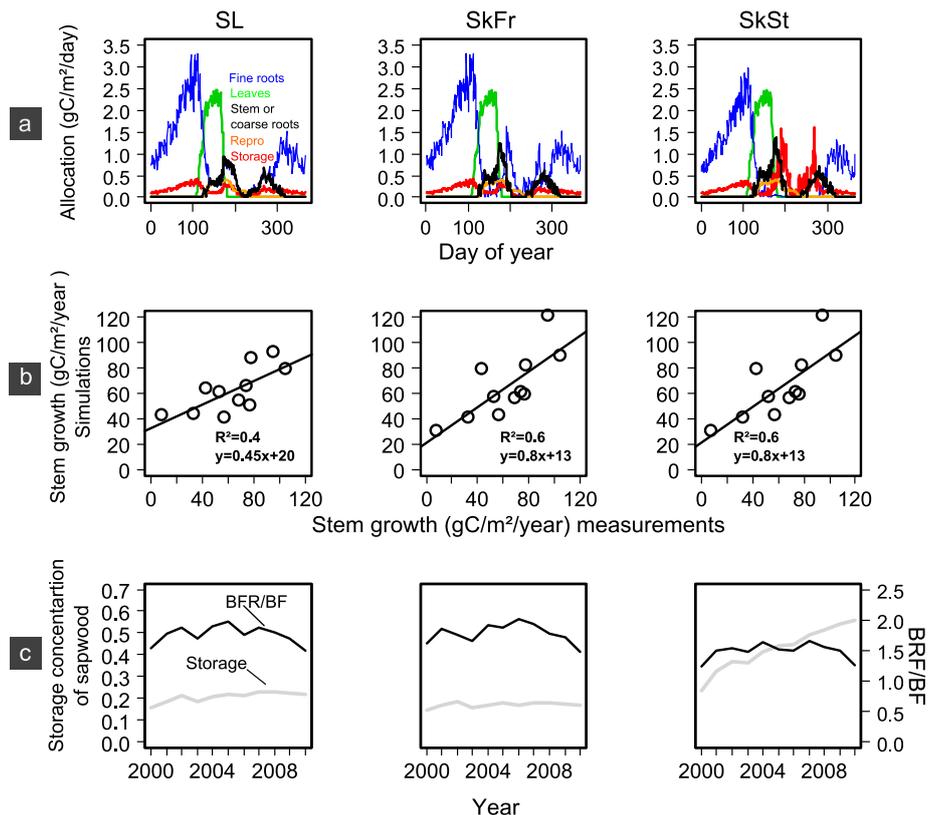


Figure 1 Results of simulations under the 3 hypotheses tested (SL, SkFr, SkSt, see text). (a) Simulations of the seasonal pattern of carbon allocation towards different tree compartments. (b) Yearly stem growth simulated vs. yearly stem growth measured on a *Q. ilex* stand over the study period (2000-2010), the R^2 and the fitted relationships are shown. (c) Yearly temporal dynamic of sapwood storage content and of the ratio of fine root biomass over leaf biomass.

LITERATURE CITED

- Davi H, Dufrêne E, Granier A, et al. 2005.** Modelling carbon and water cycles in a beech forest Part II: Validation of the main processes from organ to stand scale. *Ecological Modelling* **185**:387-405.
- Delpierre N, Soudani K, François C, et al. 2012.** Quantifying the influence of climate and biological drivers on the interannual variability of carbon exchanges in European forests through process-based modelling. *Agricultural and Forest Meteorology* **154**, 99-112.
- Dufrêne E, Davi H, François C, Le Maire G, Le Dantec V, Granier A. 2005.** Modelling carbon and water cycles in a beech forest Part I: Model description and uncertainty analysis on modelled NEE. *Ecological Modelling* **185**:407-436.
- Korner C. 2003.** Carbon limitation in trees. *Journal of Ecology* **91**: 4-17.
- Lempereur M, Martin-StPaul NK, Damesin C, Ourcival JM, Rambal S. in prep.** What limits the radial growth of *Quercus ilex* in a Mediterranean coppice?
- Leuzinger S, Thomas R. Q. 2011.** 'How do we improve Earth system models? Integrating Earth system models, ecosystem models, experiments and long-term data', *New Phytologist* **191**(1), 15--18.
- Lopez B, Sabate S, Gracia CA. 2001.** 'Annual and seasonal changes in fine root biomass of a *Quercus ilex* L. forest', *Plant and Soil* **230**(1), 125-134.
- Martin N. 2012.** Ajustements fonctionnels du chêne vert (*Quercus ilex* L.) à la sécheresse à différentes échelles temporelles : Incidences sur la modélisation des processus. PhD thesis, Université Montpellier 2, France.
- Rambal S, Joffre R, Ourcival JM, Cavender-Bares J, Rocheteau A. 2004.** The growth respiration component in eddy CO₂ flux from a *Quercus ilex* mediterranean forest. *Global Change Biology* **10**: 460-1469.
- Rambal S, Ourcival J, Joffre R, et al. 2003.** Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy. *Global Change Biology* **9**: 1813-1824.