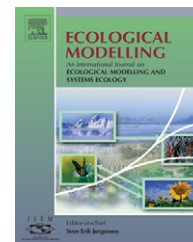


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GRAAL-CN: A model of GRowth, Architecture and ALlocation for Carbon and Nitrogen dynamics within whole plants formalised at the organ level

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ABSTRACT

A functional–structural model has been developed to analyse the dynamics between morphogenetic processes and assimilate (carbon and nitrogen) management processes, the dynamics between carbon and nitrogen metabolism (acquisition and allocation) as well as the regulations of those processes during the vegetative development of individual plants. It associates models of plant morphogenesis and models simulating the growth of plant compartments as related to assimilate availability. Using object-oriented modelling methods, knowledge is formalised at the organ level (local rules of development and resource management), and the behaviour of the plant arises from interactions between those organs and the integration of the processes into the whole plant. Shoot and root organs are initiated as a function of temperature. Using the source–sink concept, organ growth is calculated from its individual potential growth and assimilate availability within the plant. Simulations using maize illustrate the capacity of the model to mimic the main features of plants in relation to development and resource allocation (e.g., dynamics of root:shoot ratio for carbon and nitrogen, changes in priority between organs as well as plant plasticity to assimilate availability). Conceptually, the model constitutes a generic framework for testing and sorting out hypotheses on functioning processes involved in plant development. In the fields of systems biology and ecology, it is a highly suitable tool for analysing the interactions between genotypic and environmental characteristics affecting plant behaviour.

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1. Introduction

Many crop and plant models have been developed over recent years to simulate the main fluxes (e.g., CO₂, water, or nitrogen) between the plant and its environment (soil and atmosphere). They aimed at studying the effects of various environmental factors on crop and forest growth, soil and groundwater quality and/or air and surface water quality (e.g., Suzuki et al.,

1993; Hauhs et al., 1995; Tiktak and van Grinsven, 1995; Brisson et al., 1998; Riedo et al., 1998; Kirschbaum, 1999; Tanaka, 2001; Welch et al., 2005). For these purposes, the soil, root system, canopy, and atmosphere were considered as homogeneous in the horizontal plane, and thus all components of the model were described as one-dimensional. However, to study heterogeneous populations or competition within the population at a lower scale, it is necessary to explicitly consider the

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architecture of individual plants. Such a description needs to provide both (i) spatial information, which is essential for understanding plant-medium exchanges and thus inter-plant competition (see e.g., Chelle, 2005, for light interception; Caldwell, 1987, for water and nutrients uptake), and (ii) structural information making it possible to represent plant organs and thus intra-plant interactions (e.g., by using a source/sink approach, Warren-Wilson, 1972; Drouet and Pagès, 2003).

Among the numerous models of plant architecture that have been developed and published, most of them have focused on the developmental processes which combine and repeat within the plant, and lead to a complex and highly structured system (e.g., Diggle, 1988; Pagès et al., 1989; Kurth, 1994; Jourdan et al., 1995; Perttunen et al., 1996; de Reffye and Houllier, 1997; Fournier and Andrieu, 1998; Prusinkiewicz, 1999). These development-focused models simulate realistic plants, but in a narrow range of environmental conditions related to the data used to develop and calibrate the model. By producing plant mock-ups, these simulations have been shown to be useful for getting an insight into the influence of the plant architecture on various aspects of plant functioning, like resource capture (e.g., for the shoot system, Dauzat et al., 2001; for the root system, Dunbabin et al., 2003), mechanical constraints related to plant weight (Pearcy et al., 2005), interactions with other living organisms (Hanan et al., 2002) or transport within the branching system (Doussan et al., 1998; Früh and Kurth, 1999; Daudet et al., 2002).

To further develop this approach, and to give virtual plants the architectural plasticity that real plants exhibit in response to medium heterogeneity and its changes, it is necessary to model at the organ level the response of the developmental processes to their environment *sensu lato*. For a given individual organ, this environment has an external component (i.e., exogenous environment) and an internal component (i.e., within the plant, endogenous environment, as defined by Pagès, 2000). The former has been the subject of much experimental and modelling work on various organs, using several major variables like temperature, air vapour pressure deficit, and soil mechanical impedance (Ben Haj Salah and Tardieu, 1995; Bengough et al., 2006). The latter is much more difficult to formalise and quantify, and has received little attention.

The main means by which architectural models have linked individual organ growth and development to other plant parts is through carbohydrate availability (Thaler and Pagès, 1998; Balandier et al., 2000; Drouet and Pagès, 2003; Yan et al., 2004; Allen et al., 2005; Eschenbach, 2005). If carbohydrate availability has often been shown to be a limiting factor or a signal for root growth (Bingham and Stevenson, 1993; Thaler and Pagès, 1996; Freixes et al., 2002), there is nevertheless little evidence of its prominent influence for determining shoot or leaf growth under usual, not extreme, conditions. Other resources, or other signalling substances, like nitrogen metabolism products, should also be considered for representing the variations of development in a whole plant model, as proposed in the pioneer work of Thornley (1972). Using various species, experimental work has shown the impact of nitrogen nutrition on leaf growth (e.g., Gastal and Nelson, 1994; Vos et al., 1996; Fricke et al., 1997). Furthermore, resources (carbon and nitrogen especially) interact through several functions:

acquisition, transport, and utilisation for growth. It is worth evaluating the impact of these interactions on organ and plant behaviour.

We pursue this modelling approach, integrating both architectural development and resource management, hereafter carbon (C) and nitrogen (N). For this purpose, we consider the shoot and root systems with the same amount of detail and represent for the organs of each system the main processes regarding C and N management. These processes are explicitly described as functions of external factors (temperature, light, nitrogen supply) and endogenous factors (carbon and nitrogen availability within the plant). The present model, called GRAAL-CN, follows up and generalises the work of Drouet and Pagès (2003), which considered carbon assimilates alone. GRAAL-CN is founded upon dynamics between organ development and assimilate partitioning for C and N as well as interactions between C and N metabolism within the whole plant. After a detailed description of the model, we focus on its conceptual advances based on simulations of the architectural plasticity of virtual plants in relation to varying C and N inputs.

2. Model description

2.1. General principles

GRAAL-CN associates two aspects of plant functioning: (i) morphogenetic processes that determine the initiation of new organs and plant topology as well as (ii) resource acquisition (carbon and nitrogen) and assimilate exchange between organs that modulate their extension and growth in assimilate mass (see e.g., Lemaire and Millard, 1999). Both assimilates, carbon and nitrogen, have the same status within the plant: they interact symmetrically and regulate both resource acquisition and developmental processes. The model is based on a source–sink approach (Warren-Wilson, 1972; see Marcelis, 1993; Lacoïnte, 2000) and uses only one simple rule for assimilate partitioning: the effective growth of a given organ is proportional to its potential growth rate and assimilate availability (ratio between supply and demand). There is no predetermined coefficient of partitioning between organs. The potential growth rate of each organ depends on temperature and its developmental stage. The effective growth rate in dimension and in assimilate mass of each organ depends on both external and endogenous factors. As regards external factors, carbon acquisition depends on light intensity, while nitrogen uptake depends on external nitrogen concentration. Carbon acquisition, nitrogen uptake as well as assimilate partitioning are regulated by endogenous carbon and nitrogen availability (Fig. 1).

The model was developed for maize plants during the vegetative period (until silking). It was formalised using object-oriented methods with the help of the Unified Modelling Language (UML; Muller and Gaertner, 2003). The general principle is to divide the given system (the plant) into entities (or objects; Fig. 2). Objects are linked by relationships of composition or association (see Drouet and Pagès, 2003; for more details). Each leaf (resp. root) is then divided into successive leaf segments (resp. root segments), each segment corre-

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