A model of nitrogen distribution and senescence in virtual wheat

Jessica Bertheloot[1], Bruno Andrieu[1], Christian Fournier[1], Pierre Martre[2]
[1] *INRA, UMR1091 Environnement et Grandes Cultures, AgroParisTech, F-78850 Thiverval – Grignon*
[2] *INRA, UR874 Agronomie, F-63100 Clermont-Ferrand*

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Introduction

Modelling nitrogen dynamics is essential to model plant productivity. Indeed, foliar nitrogen is a major compound of the photosynthetic apparatus and is remobilized from the senescent leaves during grain filling. This remobilisation results in a decrease of leaf photosynthetic activity and finally leaf death (Masclaux, et al., 2001). It is a general observation that within a canopy, leaf nitrogen distributions are related to light gradients and that the most shaded leaves are also the first ones to die (*e.g.*, Ono et al., 2001). It results from nitrogen remobilisation from the oldest leaves to the new emerging ones. As a consequence, maximum photosynthetic capacity is found in the most lit leaves, as if the plant would adjust its nitrogen distribution for maximizing carbon gain. Authors used this optimization theory to model nitrogen distribution as function of light level (Hirose and Werger, 1987) and extended it to include prediction of leaf life span (Hikosaka, 2005). However, this idea was criticized since it is difficult to conceive that an optimization process can be a leading force in a plant. Chen et al. (1993) proposed a coordination theory to predict nitrogen distribution between leaves as the equilibrium between two rates limiting the photosynthetic processes, the rate of Rubisco carboxylation and the rate of electron transport. None of these two theories allowed closed simulation of the dynamics of vertical nitrogen distribution observed in the field. Moreover, these models are difficult to apply during the reproductive stage, where non leaf organs, such as stems and ears, represent a large fraction of plant nitrogen. Some models attempt to simulate nitrogen distribution based on a more explicit description of the processes (*e.g.*, Tabourel-Tayot and Gastal, 1998a,b; Thornley 1998, 2004). However, the processes in such models are significantly simplified, and need further evaluations against experimental data (Kull, 2002). Moreover, these models do not address the reproductive stage.

Here we present a simple "mechanistic" model aiming at predicting nitrogen and senescence distributions between leaves in a wheat shoot (*Triticum aestivum* L.) after flowering. The objective was to evaluate whether a simple mechanistic model could account for (i) the observed relationship between leaf nitrogen and light distribution within the canopy, and (ii) the acropetal sequence of leaf senescence. This work is based on a theoretical model described by Thornley (1998) for a single leaf. We extended this model to represent a wheat mainstem within a canopy, consisting of a series of leaves, a stem and a growing ear, and also to consider the sequential death of leaf tissues.

Model description and parameterization

The model described below focuses on nitrogen dynamics inside a wheat mainstem during the reproductive stage. In the current version of the model, carbon dynamics are not considered, thus no interaction was supposed to occur between carbon and nitrogen dynamics. Modelling is restricted to the grain filling period, which is after the completion of leaf growth.

The model starts at flowering and runs with a time step of 1 °Cday, with a base temperature of 0°C. Since the main objective is to predict nitrogen distribution between leaf laminae, individual modules are developed for each of them. Other vegetative organs (i.e., leaf sheaths, internodes, ear chaffs) are not considered individually and are pooled in a single module (termed stem), in order to give an appropriate context to the leaf laminae functioning. The grains are defined as one other module. Three nitrogen forms are considered: photosynthetic nitrogen, mobile nitrogen (representing amino acids and nitrate), and structural nitrogen that does not participate to the fluxes. Each lamina and the stem are characterized by their photosynthetic nitrogen content and their structural nitrogen. Mobile nitrogen is

treated as a common pool shared by all modules. In addition, each lamina is characterized by a quantity of green and dead tissues.

The main processes expressed in the lamina and grain modules are that:

(i) photosynthetic nitrogen is synthesized from the mobile nitrogen pool according to a Michaelis function depending on the concentration of mobile nitrogen, and on the irradiance intercepted by the lamina. This results in a flux of nitrogen from the mobile nitrogen pool to the lamina.

(ii) in green tissues, photosynthetic nitrogen is degraded at a constant rate. This results in a flux of nitrogen from the leaf to the mobile nitrogen pool, proportional to the amount of photosynthetic nitrogen in green tissues.

(iii) an additional degradation flux of photosynthetic nitrogen is induced if the quantity of photosynthetic nitrogen per unit area is lower than a given threshold. This nitrogen fluxes contributes to the mobile nitrogen pool and results in tissue death. The rate of photosynthetic nitrogen degradation is constant in thermal time.

(iv) grains take up nitrogen from the common pool. Potential rate of grain nitrogen accumulation follows an expolinear function, where the initial exponential phase correspond to the endosperm cell division period, and the linear phase correspond to the effective grain-filling period. The duration of each phase is constant in thermal time. At each time step, the actual rate is either equal to the potential rate, if sufficient nitrogen is available in the mobile pool, or is null.

Parameter values defining the photosynthetic apparatus turnover were taken from Thornley (1998). The other ones, specific to our model, were adjusted empirically: these are the threshold nitrogen concentration for tissue death, the maximum flux for the additional photosynthetic nitrogen degradation in dying tissues and the coefficients of the function for potential grain filling. Model was defined and evaluated with an experiment held on the bread wheat cultivar 'Apache' during the 2004-2005 growing season at Clermont-Ferrand, France, in condition of high nitrogen fertilisation. The dataset includes extensive description of the time course of biomass, total nitrogen and surface area of ear chaffs, internodes, leaf laminae (green and senescent parts) and sheaths, and grain biomass and total nitrogen. Irradiance distribution at various depths within the canopy was determined at weekly interval around noon from anthesis to total canopy senescence using a linear ceptometer. We used this dataset to (i) estimate model constants: these are structural biomass and structural nitrogen of each module, the number and the areas of the laminae containing green tissues at flowering and the light gradient, (ii) calculate the time course of forced variables, these are the time course of total shoot nitrogen and of stem nitrogen, and (iii) evaluate model predictions: these are time courses of each lamina nitrogen and tissue death, and of grain nitrogen.

The present version of the model is implemented in ModelMaker version 4.0 (Cherwell Scientific, UK), and it is currently being translated into L+C language (Karwowski and Prusinkiewicz, 2003), which will allow us to study the responses to changing plant density or architecture.

Results

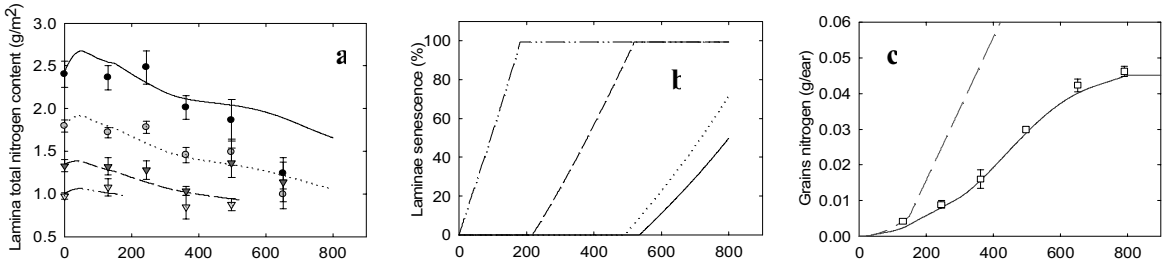

Fig 1. Time course of (a) lamina nitrogen content per unit area; (b) lamina senescence (% of tissue death); (c) Simulated potential (dashed line) and actual (solid line) grain nitrogen per ear, during the grain filling period for the bread wheat cultivar 'Apache' grown in the field under non-limiting nitrogen supply. Laminae 1 to 4 are represented respectively by solid, dash, long dash, and dotted lines (simulated) and by black circles, grey circles, black triangles, grey triangles (observed). Observed data are means $\pm$ 1 s.e. for $n = 3$.

At flowering, the fifth lamina (counted from the top of the canopy) was completely dead, thus four laminae were considered in the model. Simulation results showed that model behaviour was consistent with trends reported in the literature. In accordance with experimental data, simulated lamina nitrogen content decreased during the post-flowering period (Fig. 1a), due to nitrogen uptake by the grains, but the differences between leaves remains fairly stable. The model did reproduce the quasi linear relationship observed between the irradiance intercepted by the laminae and their area-based nitrogen content (not shown). The acropetal sequence of laminae senescence was also reasonably well simulated (Fig. 1b). However, in the simulation, the two upper leaves started senescing almost synchronously, and were not fully senesced at maturity when grain filling was completed. Insufficient experimental data were available to allow comparisons with simulations, but the simulated behaviour is reported to occur in some conditions, depending on cultivar and nitrogen fertilisation. Finally, the model predicted accurately the time course of grain filling (Fig. 1c). This, and the large difference between potential and actual grain filling, are strong indications that the time course of mobile nitrogen was also correctly simulated.

Discussion and conclusion

We have shown that a model based on some key nitrogen dynamics processes and with a restricted number of parameters (eight in the current version) is able to describe the main trends found in the literature in terms of nitrogen distribution among leaf laminae, leaf life span, and grain nitrogen accumulation. A virtue of the approach is that it does not rely on a predicted global behaviour, such as optimisation of canopy carbon assimilation, but rather show that this can be seen as an emerging property of simple local rules. This gives inherent plasticity and should make the model to cope with important perturbations, such as when new sinks of nitrogen are created by insects or diseases.

Several approximations were made in order to avoid the difficulties related to parameter estimations. The high nitrogen mobility and the existence of nitrogen exchange between phloem and xylem led us to approximate that all organs were connected to a single pool of mobile nitrogen. This avoids the problem of estimating resistance of the nitrogen transfer pathways between individual laminae and the common mobile nitrogen pool. Another main simplification deals with the restricted number of nitrogen forms. Only the most relevant ones in the process studied (here photosynthetic apparatus turnover) were taken into account.

The simple model presented here reproduces the behaviour of the shoot compartments reasonably well when shoot nitrogen absorption is forced to experimental data. The next step will be to include a feedback control on post-flowering absorption, involving nitrogen availability in the soil, the concentration in the mobile nitrogen pool and leaf photosynthesis. This will allow investigating responses in a wider range of experimental conditions. Inclusion of a photosynthesis model will allow to analysis carbon – nitrogen interactions.

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