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A model to simulate the dynamics of carbohydrate remobilization during rice grain filling

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ABSTRACT

The remobilization of carbon reserves accumulated in stems during vegetative growth is known to significantly contribute to yield formation in many cereals, and to be modulated by water and nitrogen availability during grain filling. However, despite the extensive use of crop models to support irrigation and fertilization plans, current knowledge on carbohydrate remobilization is rarely formalized in the available simulation tools. This paper presents a model to simulate carbohydrate remobilization in rice, based on the balance between source (i.e., the carbon reserves in stems) and sink (i.e., the grains) strength and on the impact of water stress and nitrogen luxury consumption. The new approach was included in the WARM model and evaluated using data from published experiments where two cultivars were grown under two nitrogen fertilization levels and two irrigation strategies. Results highlighted the model effectiveness in reproducing the amount of remobilization under non stressed conditions ($R^2 = 0.99$), as well as the impact of water and nitrogen availability (average $R^2 = 0.97$) for Indica and Japonica rice cultivars. The proposed model can be easily plugged into available rice simulators to increase their adherence to the underlying system.

1. Introduction

Carbon (C) supply in cereal kernels at maturity depends both on the photosynthates produced during grain filling and on the remobilization of assimilates from vegetative tissues (Schnyder, 1993). For rice, the contribution of the reserves remobilized from stems can reach up to 40% of final yield (Yoshida, 1972), depending on the interaction between the genotype and the environmental and management conditions. These reserves are mostly represented by non-structural carbohydrates (NSC) in the parenchyma cells of culms, and are constituted by starch and soluble sugars synthetized during the vegetative phase (Slewinski, 2012). The amount of NSC can reach up to 4 t ha^{-1} in rice culms at heading (Fu et al., 2011), and a significant portion remains in straw at maturity (Park et al., 2011). Enhancing the efficiency of remobilization could therefore lead to an increase in final yield (Yang and Zhang, 2010a), and this encouraged many authors to investigate the dynamics between source and sink strength (e.g., Yang et al., 2001a, Yang et al., 2003) and the impact of alternate management practices (e.g., Yang and Zhang, 2010a; Pan et al., 2011). Most of available studies agree on considering all these factors as strongly interconnected: low activity of the key enzymes involved in C metabolism (Yang and Zhang, 2010b) and reduced sink size (Fu et al., 2011) may explain the reduced NSC remobilization and the poor filling of inferior spikelets, especially in modern rice cultivars. Other studies underlined how the NSC remobilization from stems-associated with α-amylase activity (Yang et al., 2001a) is triggered by senescence (Gan and Amasino, 1997; Noodén et al., 1997). As a consequence, factors delaying senescence, like excessive nitrogen (N) fertilization or the adoption of "stay green" cultivars, can decrease the contribution of NSC remobilization to crop production (Yang et al., 2001b). Under these conditions, Yang and Zhang (2010a) demonstrated that a controlled water stress during grain filling can favor NSC remobilization and, in turn, increase water and N use efficiency, harvest index and even yield.

The formalization of the available knowledge on such processes in simulation models would contribute to the interpretation of experimental data (Pan et al., 2007), to enhance models' ability to predict crop performance at field level, and to better support crop management. Remobilization of C reserves during grain filling was addressed by crop models specific for different crops, such as wheat (Asseng and Van Herwaarden, 2003), tomato (Wilson et al., 1986) and rice. For the latter, Wu and Wilson (1998) proposed an approach based on the balance between C demand and supply,

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with NSC remobilization exploited to meet the possible difference between these components, whereas Oryza2000 (Bouman et al., 2001) calculates the remobilization of stem reserves from flowering as the ratio between the simulated weight of stems and a time coefficient. More detailed approaches are currently implemented within functional structural plant models, which aim to explain the relationships between source andsink balances and the impact of environmental constraints on plant C use, morphogenesis and production (Pallas et al., 2013). However, most of available models (including rice specific ones) do not consider the processes involved in NSC remobilization. Nevertheless, most rice models dynamically simulate photosynthates partitioning and the effects of water and N availability on crop growth and development (Li et al., 2015). This means that they provide suitable simulation environments where algorithms specific for C remobilization can be plugged in. The accurate simulation of NSC remobilization would increase the adherence of rice models to real systems and this, in turn, would enhance their suitability as supporting tools for water and N management at field/farm level and for in silico analyses to evaluate management scenarios under different agro-climatic conditions.

We present here a new model simulating NSC remobilization during grain filling of rice, able to respond to water and nitrogen availability and coherent with the level of detail used in rice models to reproduce processes involved with growth and development.

2. Materials and methods

2.1. A novel model for NSC remobilization in rice

The model for NSC remobilization is based on the balance between sink and source strengths ($\mathrm{g\,NSC\,m^{-2}\,d^{-1}}$), defined as the product of *size* and *activity* of sink and source organs (Venkateswarlu and Visperas, 1987; Ho, 1988). Size represents (i) the physical restraint to remobilization for sink organs ($\mathrm{Sink}_{\mathrm{size}(d)}$, $\mathrm{g\,grains\,m^{-2}}$; a proxy of the number of cells and cell size of the endosperm; Eq. (1)) and (ii) the amount of NSC in source organs ($\mathrm{Source}_{\mathrm{size}(d)}$, mainly in stems for rice; $\mathrm{g\,NSC\,m^{-2}}$; Eq. (1)). Activities represent the physiological constraint limiting the import/export of C from a source to a sink organ. Source activity ($\mathrm{Source}_{\mathrm{activity}(d)}$, $\mathrm{g\,g^{-1}\,NSC\,d^{-1}}$; Eq. (1)) is here defined as the relative amount of NSC available for translocation in a given time step, whereas sink activity ($\mathrm{Sink}_{\mathrm{activity}(d)}$, $\mathrm{g\,NSC\,g^{-1}}$ grains $\mathrm{d^{-1}}$; Eq. (1)) refers to the relative demand of NSC per unit of grain dry matter.

During the reproductive phase, the daily rate of carbohydrate remobilization from stems ($\mathrm{NSC}_{\mathrm{rate}(d)}$, $\mathrm{g\,m^{-2}\,d^{-1}}$) is obtained as the minimum, i.e., the most limiting factor, between source and sink strengths (Eq. (1)). The transport path between source and sink is not accounted for in the model as phloem does not limit translocatory flux (Marcelis, 1996).

$$\mathrm{NSC}_{\mathrm{rate}(d)} = \min\left(\left(\mathrm{Source}_{\mathrm{size}(d)} \cdot \mathrm{Source}_{\mathrm{activity}(d)}\right), \left(\mathrm{Sink}_{\mathrm{size}(d)} \cdot \mathrm{Sink}_{\mathrm{activity}(d)}\right)\right) \qquad (1)$$

$\mathrm{NSC}_{\mathrm{rate}(d)}$ is used to reduce the total amount of NSC in culms (i.e, the source size) from anthesis (Eq.(2)).

$$\mathrm{Source}_{\mathrm{size}(d)} = \mathrm{Source}_{\mathrm{size}(d-1)} - \mathrm{NSC}_{\mathrm{rate}(d)} \qquad (2)$$

Respiration losses during remobilization and translocation influence the efficiency of the process, which falls in the range from 65% to 80% (Cock and Yoshida, 1972). This term (i.e., η, Eq. (3)) should be accounted for, in the estimation of the amount of remobilized NSC effectively used for grain filling (i.e., $\mathrm{NSC}_{\mathrm{grainfill}(d)}$, Eq. (3)).

$$\mathrm{NSC}_{gra\inf ill(d)} = \mathrm{NSC}_{\mathrm{rate}(d)} \cdot \eta \qquad (3)$$

$\mathrm{Source}_{\mathrm{activity}}$ at day d ($\mathrm{Source}_{\mathrm{activity}(d)}$, Eq. (4)) is a function of the main factors modulating NSC remobilization from stem storage parenchyma (Eq. (4)), i.e., the genetic component associated to the “stay-green” trait (α, unitless, 0–1), and the effects of water (W_{effect}, unitless) and N (N_{effect}, unitless) availability on the enzyme activity. The gradual effect of plant senescence on $\mathrm{Source}_{\mathrm{activity}}$ is reproduced via the S-shape of the function (Eq. (4)).

$$\mathrm{Source}_{\mathrm{activity}(d)} = \mathrm{Source}_{\mathrm{activity}(d-1)} + \alpha \cdot (1 + W_{\mathrm{effect}} + N_{\mathrm{effect}}) \cdot \mathrm{Source}_{\mathrm{activity}(d-1)} \cdot \left(\frac{\mathrm{Source}_{\mathrm{activity(max)}} - \mathrm{Source}_{\mathrm{activity}(d-1)}}{\mathrm{Source}_{\mathrm{activity(max)}}}\right) \qquad (4)$$

$\mathrm{Source}_{\mathrm{activity}(d)}$ is initialized at $0.001\ \mathrm{g\,g^{-1}\,NSC\,d^{-1}}$ at flowering; a maximum value of $1\ \mathrm{g\,g^{-1}\,NSC\,d^{-1}}$ is set ($\mathrm{Source}_{\mathrm{activity(max)}}$). The term W_{effect} is calculated according to Eq. (5):

$$W_{\mathrm{effect}} = \beta \cdot \psi_{\mathrm{soil}} \qquad (5)$$

where, β ($\mathrm{MPa^{-1}}$, −30 to 0) is an empirical parameter representing the cultivar sensitivity to water stress and ψ_{soil} (MPa) is the soil water potential. This term can be derived as a function of the actual to potential transpiration ratio, commonly used by crop models to compute the daily water stress factor. Consistently with available data, in this study the soil water potential was adopted; the conversion between ψ_{soil} and the relative transpiration can be performed according to the approach proposed by Wopereis et al. (1996).

The daily value of N_{effect} is computed according to Eq. (6):

$$N_{\mathrm{effect}} = \gamma \cdot (N_{\mathrm{status}} - 1) \qquad (6)$$

where, γ (unitless,−5 to 0) is an empirical parameter used to discriminate between the susceptibility of different cultivars to non-optimal (insufficient availability or luxury consumption) N availability and N_{status} (unitless) is the ratio between actual and critical N concentration in shoots. With critical N concentration, we mean here the concentration below which the plant is stressed and above which the plant experiences luxury consumption (Sheehy et al., 1998). Thus, a value of N_{status} higher than 1 indicates N luxury consumption, whereas values below 1 convey the degree of N stress sensed by the crop. According to our approach, high values of W_{effect} and N_{effect} cause a steep increase of source activity: in other words, negative values of β and γ parameters favor NSC remobilization under insufficient water and N availability and reduce it under N luxury consumption.

Sink size is mainly determined by the number of cells and the cell size in the endosperm (Fu et al., 2011). The cumulated grain weight ($\mathrm{g\,m^{-2}}$) is used here as a proxy for sink size, given that it is dynamically simulated by most rice crop models.

The value of $\mathrm{Sink}_{\mathrm{activity}}$ at day d ($\mathrm{Sink}_{\mathrm{activity}(d)}$, $\mathrm{g\,NSC\,g^{-1}}$ grains $\mathrm{d^{-1}}$ Eq. (7)) is dependent upon the metabolism of carbohydrates in developing the rice endosperm. This process is regulated by 33 major enzymes (Nakamura et al., 1989), with sucrose synthase and adenine diphosphoglucose pyrophosphorylase playing key roles. The pattern of their activities observed during grain filling (Yang et al., 2003; Fu et al., 2011) highlights an exponential decay after early development of rice endosperm, leading to the following expression (Eq. (7)):

$$\mathrm{Sink}_{\mathrm{activity}(d)} = \mathrm{Sink}_{\mathrm{activity(max)}} \cdot \exp(-\mathrm{DPA} \cdot \varepsilon) \qquad (7)$$

where, $\mathrm{Sink}_{\mathrm{activity(max)}}$ ($\mathrm{g\,NSC\,g^{-1}}$ grains $\mathrm{d^{-1}}$) is set to 1 and ε (unitless, 0–0.3) is a cultivar-specific parameter; high values of ε reflect low activities and/or gene expressions of enzymes involved in the conversion of sucrose to starch, which have been observed especially in inferior spikelets of modern rice cultivars (Yang and Zhang, 2010b), such as “super” hybrid rice (Cheng et al., 2007) and New Plant Type (Peng et al., 1999). The tendency to overestimate the sink activity at low DPA can be considered negligible because according