**EcoMeristem, a model of morphogenesis and competition among sinks in rice. 1. Concept, validation and sensitivity analysis**

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**Abstract.** Because of rapid advances in functional genomics there is an increasing demand for models simulating complex traits, such as the physiological and environmental controls of plant morphology. This paper describes, validates and explores the behaviour of the structural–functional model EcoMeristem, developed for cereals in the context of the Generation Challenge Program (GCP; CGIAR). EcoMeristem constructs the plant on the basis of an organogenetic body plan, driven by intrinsic (genetic) behavioural norms of meristems. These norms consist of phenological–topological rules for organ initiation and pre-dimensioning (sink creation) and rules enabling feedbacks of the plant’s resource status on the organogenetic processes. Plant resource status is expressed by a state variable called Internal Competition Index (\(I_c\)) calculated daily as the ratio of assimilate source (supply) over the sum of active sinks (demand). \(I_c\) constitutes an internal signal analogous to sugar signalling. \(I_c\) affects potential phytomer size, tiller initiation, leaf senescence, and carbohydrate storage and mobilisation. The model was calibrated and tested on IR64 rice grown in controlled environments, and validated with field observations for the same cultivar (Philippines). Observed distributions and dynamics of soluble sugars and starch in plant organs supported the model concepts of internal competition and the role of reserves as a buffer for \(I_c\) fluctuations. Model sensitivity analyses suggested that plant growth and development depend not only on assimilate supply, but also on organogenesis-based demand. If true, this conclusion has important consequences for crop improvement strategies.

**Keywords:** architecture, complex traits, meristem, modelling, organogenesis, *Oryza sativa* L., phenotypic plasticity.

**Introduction**

A major scientific challenge that has evolved during the past decade is how to improve crop-breeding methodologies on the basis of new molecular genetic knowledge (Dubcovsky 2004; Frey et al. 2004; Moreau et al. 2004). Molecular maps of genomes and information on gene function are increasingly becoming available for global crops such as rice. This is a field opening up new applications for crop models, both in the areas of phenotyping (measuring phenotypic traits that can be related to gene expression) and phenotype prediction (modelling the phenotypic impact of genes and alleles for variable environments). New models are thus needed to help build a bridge between emerging genomic knowledge and observable crop behaviour in the field. This study presents the crop model, EcoMeristem, developed in this context for the CGIAR Generation Challenge Program (GCP 2005) for cereals using rice as a model plant.

In a previous paper, the authors discussed various types of plant models with respect to potential applications in genomics research (Dingkuhn et al. 2005). They concluded that such models, if they are to describe the whole plant (deemed essential for field applications) in variable environments (essential for breeding objectives), should be able to simulate phenotypic plasticity. Phenotypic plasticity of plant architecture, morphology and phenology is a result of genotype x environment interactions (\(G \times E\)) (Wright and McConnaughay 2002; Luquet et al. 2005). It is, therefore, necessary not only to accurately predict the function of a gene or allele of interest, but also its phenotypic impact in a variable agronomic context. Conversely, where phenotyping...
is the objective, models can be applied in reverse mode in order to predict genotypic parameters while using phenotype information as input. This heuristic approach is particularly relevant with respect to process-based traits and genotypic reaction norms that cannot be measured directly, such as adaptive responses of crop architecture and phenology (Hammer et al. 2002; Dingkuhn et al. 2005).

The present study does not aim at relating gene expression to whole-plant phenotype, an objective that would require tools that are currently unavailable. It only elaborates, as a first step, a modelling approach that integrates, in an interactive and dynamic way, development and growth processes in order to predict major feedbacks of environment on morphogenesis and plant structure. The objective is to achieve this with a minimal number of crop parameters and maximal ease of model parameterisation. Furthermore, emphasis is given to behavioural norms of the meristems, which are considered to be the tissues that drive plant development and which probably express many genes involved in adaptive plasticity (Jitla et al. 1997; Itoh et al. 1998; Kobayazi et al. 2002). With this, the authors hope to operate with model parameters that are closer to the effects of relevant genes, potentially enabling parameter \( v \cdot \) gene (or parameter value \( v \cdot \) allele) associations later on.

Since the number of interactions between development and growth processes is presumably very large, some strategic choices were made. This study focused on vegetative development only, although the entire life cycle including yield formation will be considered eventually. Furthermore, we will consider here only temperature and photosynthetically active radiation (PAR) and their effects on development rate, carbon assimilation, organogenesis and competition among growing organs for assimilates, while ignoring any specific effects of physiological stresses. This paper describes the EcoMeristem model, its calibration and validation for one rice genotype, and explores the model’s behaviour. A sequel to this paper will extend the study to contrasting genotypes and a nutritional stress, phosphorus deficiency.

Materials and methods
The model
Underlying concepts
EcoMeristem is a whole-plant, deterministic, dynamic, radiation- and temperature-driven crop model. (The model also has a soil and plant water balance but these modules were not used in this study.) The specificity of the model is its capability to simulate competition for assimilates (supply) among growing organs (demand) (Fig. 1).
Supply is thereby simulated at the scale of the whole plant (either isolated or situated within a canopy formed by a homogeneous population), whereas demand is simulated at the individual organ level, and then aggregated to provide a whole-plant demand term. This procedure allows comparison of plant level supply and demand for each time step (24 h) and to simulate feedbacks of supply/demand imbalances on organ number (organogenesis), growth rate and final size (morphogenesis). Supply/demand relationships are measured with a state variable called \( I_c \) (Index of internal competition, Table 1), calculated as aggregate supply divided by aggregate demand for each time step of model execution. Values of \( I_c \) lower than one trigger adaptive adjustments in plant organogenesis and morphogenesis, resulting in phenotypic plasticity.

Excess assimilates (when \( I_c > 1 \)) are reversibly stored as reserves, or, if the reserve compartment is saturated, feed back on photosynthesis (product inhibition). Asimilate deficiency (when \( I_c < 1 \)) causes two types of adaptive responses. First, the current assimilate shortfall for growth is buffered by reserve mobilisation, organ senescence (followed by recycling) and ultimately, delays in organogenetic cycles, in this order; and second, organs that are being initiated are down-sized, leading to smaller demand when they turn into active sinks. The \( I_c \) conditions also branching events (in the case of grasses, tiller initiation). This system of feedbacks stabilises plant carbon balance by adjusting plant development to resources.

In contrast to assimilate supply (or source), a term that has an established physiological basis (Penning de Vries et al. 1989; Dingkuhn and Kropff 1996), demand for assimilates is less understood. Most agronomic crop models simply assume that incremental assimilate production (after subtraction of respiration and other losses) is reinvested in growth without limitation, and simply partitioned among organ types according to developmental stage (Penning de Vries et al. 1989; Sultan et al. 2005). This simplification cannot be upheld when we consider a dynamic body plan involving a tree structure, as well as meristems that initiate and differentiate new organs before they expand to their final size (Cookson et al. 2005). The plant, therefore, continuously makes commitments to new sinks, constituting demand functions that need to be adjusted to resources. A well-known example is the resources-dependent size of rice panicles (Hasegawa et al. 1994; Kropff et al. 1994; Yoshida et al. 2006), maize cobs (Andrade et al. 1999; Gambin et al. 2004) and wheat ears (Reynolds et al. 2004, 2005).

### Table 1. Description of EcoMeristem parameters, method of calibration and estimated values for IR64 rice

Some of this information, differing slightly because an earlier version of the model was used, has been published previously in a conceptual paper on various modelling approaches (Dingkuhn et al. 2005; with the kind permission of the Australian Journal of Agricultural Research).

<table>
<thead>
<tr>
<th>Parameter Name</th>
<th>Definition</th>
<th>Unit</th>
<th>Method of calibration</th>
<th>Value for IR64</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed DW</td>
<td>1st leaf DW</td>
<td>mg</td>
<td>Measurement</td>
<td>28</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>LSDW</td>
<td>Root/shoot DW ratio at 1st leaf stage</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Measurement</td>
<td>1.0</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>RSR</td>
<td>1st leaf specific leaf area</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Measurement</td>
<td>0.047</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>PLAs.</td>
<td>Plant population</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BUE</td>
<td>Potential radiation use efficiency</td>
<td>g m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Optimisation</td>
<td>2.88</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Krm</td>
<td>Coefficient for the calculation of daily maintenance respiration</td>
<td>g g&lt;sup&gt;−1&lt;/sup&gt;</td>
<td>Penning de Vries et al. (1989)</td>
<td>0.015</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>RESeed</td>
<td>Fraction of seed DW mobilised&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–</td>
<td>Asch et al. (1999)</td>
<td>0.45</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Tb</td>
<td>Basic temperature</td>
<td>°C</td>
<td>Dingkuhn and Miezan (1995)</td>
<td>9.55</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Kd</td>
<td>PAR extinction coefficient&lt;sup&gt;b&lt;/sup&gt;</td>
<td>g g&lt;sup&gt;−1&lt;/sup&gt;</td>
<td>Dingkuhn et al. (1999)</td>
<td>0.65</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>StoRmax</td>
<td>Upper limit of assimilate storage in green tissues (leaf blades and sheaths)</td>
<td>g g&lt;sup&gt;−1&lt;/sup&gt;</td>
<td>Samonte et al. (2001)</td>
<td>0.3</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>BSR</td>
<td>Leaf blade/sheath DW ratio</td>
<td>–</td>
<td>Measured</td>
<td>0.55</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>RSDem</td>
<td>Root/shoot assimilate demand ratio</td>
<td>–</td>
<td>Optimisation</td>
<td>0.310</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>SLAp</td>
<td>SLA decrease for successive leaf ranks</td>
<td>–</td>
<td>Measured</td>
<td>0.006</td>
<td>0.0003</td>
<td></td>
</tr>
<tr>
<td>Kls</td>
<td>Leaf shape index (area/L x W)</td>
<td>–</td>
<td>Tivet et al. (2001)</td>
<td>0.725</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

### Allometric parameters

<table>
<thead>
<tr>
<th>Parameter Name</th>
<th>Definition</th>
<th>Unit</th>
<th>Method of calibration</th>
<th>Value for IR64</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>BSR</td>
<td>Leaf blade/sheath DW ratio</td>
<td>–</td>
<td>Measured</td>
<td>0.55</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>RSDem</td>
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<tr>
<td>SLAp</td>
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<td>Measured</td>
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<td>0.0003</td>
<td></td>
</tr>
<tr>
<td>Kls</td>
<td>Leaf shape index (area/L x W)</td>
<td>–</td>
<td>Tivet et al. (2001)</td>
<td>0.725</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

### Parameters governing organogenesis

<table>
<thead>
<tr>
<th>Parameter Name</th>
<th>Definition</th>
<th>Unit</th>
<th>Method of calibration</th>
<th>Value for IR64</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>PLAs</td>
<td>Plantochron</td>
<td>°Cd</td>
<td>Optimisation</td>
<td>47.3</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>MGR</td>
<td>Potential meristem Growth rate</td>
<td>PLAS&lt;sup&gt;−1&lt;/sup&gt;</td>
<td>Optimisation</td>
<td>1.60</td>
<td>0.08</td>
<td></td>
</tr>
<tr>
<td>Ic</td>
<td>Ic threshold for tillering</td>
<td>–</td>
<td>Optimisation</td>
<td>1.00</td>
<td>0.09</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Asch et al. (1999) reported seed lost 75% of initial DW during germination, of which 60% reappeared in the seedling. The product of the two fractions is 0.45.

<sup>b</sup>Dingkuhn et al. (1999) reported values between 0.45 and 0.65 for Kd. The higher value was chosen here because leaves were comparatively lax under phytochrome conditions.
determined long before these sinks become active. EcoMeristem applies this concept to all organs of the plant except the root system (studies on root system morphogenesis are in progress to permit its detailed simulation as well).

The model assumption that a rice phytomer (entry consisting of leaf, sheath, tiller bud and internode) undergoes a dimensioning process before attaining its final size (in EcoMeristem a function of apical meristem size and current carbon resources) is somewhat intuitive, although it is known that (i) both meristem size (Itoh et al. 2005) and leaf size (Tivet et al. 2001) increase for subsequently formed phytomers, and (ii) leaf size of rice is strongly affected by resources such as nitrogen (Veerma et al. 2004; IRRI 2005), presumably through its effects on assimilability. Cockson et al. (2005) confirm for *Oryza sativa* that leaf size is, in fact, determined at an early stage of leaf development. The exact developmental period during which final leaf size is sensitive to resources is currently under study and for lack of detailed information, we assume here that the dimensioning process happens between leaf initiation and appearance.

### Functional components

The main functional components of the model are: (i) assimilate production (supply function), (ii) implementation of a body plan (generation of demand functions) and (iii) allocation between supply and demand functions (physiological feedbacks).

(i) Assimilate production

For carbon supply, the EcoMeristem version used here implements modules of the simple crop model SARRA-II (Doungkham et al. 2003, Sultana et al. 2005), which assumes that plants are part of a homogenous population having a canopy with random leaf distribution. To descend from population to plant scale, the soil surface area attributed to a single member of the population is used as basis for computations. Also adopted from SARRA-II was the simulation of an initial carbon reserve whose size depends on grain dry weight (DW) (parameter RESseed, Table 1) and the mobilisable fraction thereof (RESEvolve). Daily assimilate production and the initial seed reserves (which gradually disappears after germination) form a common pool available to all organs.

Plant area index PAI [the single-plant equivalent of leaf area index (LAI)] is computed from green-leaf dry weight by applying an empirical, allometric rule for blade/sheath DW ratios (Luquet et al. 2005; Table 1) and the specific leaf area (SLA, m\(^2\) g\(^{-1}\)) attributed to leaf blades according to their position in the stem. SLA is a steadily decreasing function of leaf rank \(r\) (Luquet et al. 2005) computed here with two parameters: \(SLA_{ini}\) and \(SLA_{p}\) (Table 1):

\[
SLA = SLA_{ini} - SLA_{p} \times \ln(r) \tag{1}
\]

This equation reproduces the development-stage-dependent decrease of SLA observed in rice (Asch et al. 1999) and generally in cereals, using leaf rank as measure of development stage. For model output, a distinction is made between structural SLA \(SLA_{ini}\) as computed with Eqn (1) and actual SLA, which includes simulated transitory carbon reserves, considered to be equally distributed among all green leaf sheaths and blades. For this reason, observed data used for model calibration should be based on measurements made in the morning, when transitory reserves are smallest. No structural effects on temperature or radiation levels on SLA are taken into account.

Lambert-Beer's law of logarithmic light quenching (Verhoef 1985) is applied to LAI to compute PAR interception using an extinction coefficient \(K_{df}\) (Table 1). Then carbohydrate assimilation is computed by multiplying intercepted PAR with a radiation-use efficiency (RUE) parameter. Contrary to common definitions of RUE (Montrith 1994; Knuy et al. 2001), this parameter is calibrated so as to include root growth and maintenance respiration, which is subsequently calculated and subtracted from the assimilation term (this provision was made because RUE is known to decrease in the presence of a large biomass due to maintenance respiration; Penning de Vries et al. 1989). The model provides for drought stress effects on assimilation (function of fraction of transpirable soil water, FTSW), but this was not used in this study.

Maintenance respiration (RM) was considered to be proportional to shoot DW (SDW) and a power function of air temperature (Ta) according to the \(Q_{10} = 2\) rule (doubling of rate for every increase of Ta by 10°C) according to Penning de Vries et al. (1989).

(ii) Implementation of a body plan

Developmental processes were implemented along thermal time, starting with germination (1st-leaf stage). The thermal time clumping in 1D was defined as the difference between the mean daily air temperature and the base temperature \(T_{b}\) (Table 1). Organ initiation (new leaves and tillers) was implemented with a genotypic plastic schedule (Table 1) which spanned several days and was statistically optimised against a target file containing morphological observations (Table 2).

The topology of the plant consists of a principal axis or main stem, constituted by a sequence of phytomers (Fig. 1). Each phytomer consists of a leaf (blade and sheath), a virtual auxiliary node and an internode (internodes were not attributed mass and dimensions in this study because rice plants remained vegetative). An open-ended number of tillers can be created, depending on an evolving number of potential sites (one bud per phytomer on main stem and tillers), but their actual number depends on assimilate availability and genotypic sensitivity to this (it will be explained farther below). Each tiller is defined by its time of initiation and the leaf on the main stem with which its first leaf will be synchronous, according to principle of cohorts (Hanada 1993; Tivet et al. 2001). All subsequent leaves produced on the tiller, as well as internode elongation and panicle growth (not simulated in this study), are from then on synchronised with the main stem.

The expansion of a new leaf to its final size happens during a single phyllochron after initiation of the corresponding phytomer. Carbon demand of an expanding leaf is thus considered only once it tips emerges from the enclosing sheath of the previous leaf (i.e. when its sink strength becomes significant), and subsides when the next leaf appears.

This is a major simplification because in fact, the periods of expansion of successively appearing leaves overlap to some extent in rice. Two or three leaves queue up in the tube formed by several sheaths, and leaf initiation therefore happens earlier than simulated by the model (Jitsla et al. 1997; Itoh et al. 1998; Miyoshi et al. 2004). As in all grasses, the development and growth events on shoot axes of rice are highly coordinated (Fourrier et al. 2005). At leaf tip appearance, the ligule of the same leaf differentiates at its junction with the sheath (collar), which is at that time hidden in the previous leaves' sheaths. Once the collar of emerges from the enclosing sheath, the elongation of the leaf blade ends (Williams 1975; Skinner and Nelson 1995), probably involving long-distance signalling (evidence summarised by Fourrier et al. 2005).

There are major differences among grass species regarding the number of successive phytomers whose development overlaps in time. In *Poa pratensis* L., a new leaf is initiated only once the previous leaf is nearly fully expanded, whereas in maize five leaves having different development stages grow at the same time (Sy/estes et al. 2001). Rice is intermediate, with a total of three leaves developing at the same time (Sy/estes et al. 2001). Their development is coordinated such that the appearance of the tip of leaf \(n\) coincides with the ligule emergence (and thus, the end of rapid elongation) of leaf \(n - 1\). Consequently, only one visible leaf per culm is undergoing rapid (linear) elongation at any given time, while two or three leaves hidden in the sheath elongate much more slowly (exponential elongation phase).

Since little evidence of this specific behaviour of rice can be found in referenced journals, we present here an example of elongation kinetics.
Morphogenesis of rice: 1. EcoMeristem model

Table 2. EcoMeristem model input variables, output variables and measured variables used for statistical parameter optimisation

<table>
<thead>
<tr>
<th>Variable</th>
<th>Physical scale</th>
<th>Temporal scale</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model input variables&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean air temperature Ta – daily</td>
<td></td>
<td>daily</td>
<td>°C</td>
</tr>
<tr>
<td>PAR – daily</td>
<td></td>
<td>daily</td>
<td>MJ m&lt;sup&gt;−2&lt;/sup&gt; d&lt;sup&gt;−1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Model output variables (available for each time step)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organ dry weight</td>
<td>Leaf blades, sheaths, root system</td>
<td>daily</td>
<td>g plant&lt;sup&gt;−1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Leaf area</td>
<td>Per leaf, tiller or plant</td>
<td>daily</td>
<td>m&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>Leaf and tiller number</td>
<td>Whole plant</td>
<td>daily</td>
<td>–</td>
</tr>
<tr>
<td>Senescent leaf number</td>
<td>Whole plant</td>
<td>daily</td>
<td>–</td>
</tr>
<tr>
<td>Organ length</td>
<td>Individual leaf, total shoot (plant height)</td>
<td>daily</td>
<td>m</td>
</tr>
<tr>
<td>Specific leaf area (SLA)</td>
<td>Per leaf blade or plant</td>
<td>daily</td>
<td>m&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;−1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Leaf growth rates</td>
<td>Individual leaf</td>
<td>daily</td>
<td>mm d&lt;sup&gt;−1&lt;/sup&gt;, mg d&lt;sup&gt;−1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Carbon reserve pool</td>
<td>Plant</td>
<td>daily</td>
<td>g plant&lt;sup&gt;−1&lt;/sup&gt;, mg g&lt;sup&gt;−1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Index of competition (Ic)</td>
<td>Plant</td>
<td>daily</td>
<td>–</td>
</tr>
<tr>
<td>Variables measured for parameter optimisation (target file for this study)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf number</td>
<td>Main stem</td>
<td>36 DAT</td>
<td>–</td>
</tr>
<tr>
<td>Leaf number</td>
<td>Whole plant</td>
<td>36 DAT</td>
<td>–</td>
</tr>
<tr>
<td>Leafblade length and dry weight</td>
<td>Last fully expanded leaf on main stem</td>
<td>36 DAT</td>
<td>m, g</td>
</tr>
<tr>
<td>Tiller number</td>
<td>Whole plant</td>
<td>36 DAT</td>
<td>–</td>
</tr>
<tr>
<td>Shoot dry weight</td>
<td>Whole plant</td>
<td>36 DAT</td>
<td>g</td>
</tr>
</tbody>
</table>

<sup>1</sup>Input variables for soil moisture and atmospheric demand are not provided because water balance was not simulated in this study.

of subsequently appearing leaves on IR64 rice (Fig. 2: observations on one plant taken from the experiment described below). Therefore, the simulation of leaf growth confined to the duration of a single phyllochron, as done here in EcoMeristem, is a simplification because it ignores the slow (exponential) growth of leaves before their appearance, but this probably causes only a small bias with respect to the timing of carbon demand in expanding leaves.

On the main stem, potential leaf size increases from one phytomer to the next (Tivet et al. 2001), a trend that is associated with an increase of the size of the apical meristem (Itoh et al. 1998, 2005; Asai et al. 2002). In EcoMeristem, the apical meristem grows during each plastochron by a constant factor (parameter Meristem Growth Rate, MGR; Table 1) if assimilate supply is non-limiting. It grows less if Ic < 1. The potential DW of a new leaf is assumed to be proportional to the meristem size at its appearance. Therefore, potential DW of leaf n on the main stem is equal to final, structural DW of leaf n−1, multiplied by MGR. Final DW of leaf n is equal to its potential DW, or smaller if Ic < 1. The down-sizing of the leaf when Ic < 1 is non-linear (using Ic<sup>2</sup> as factor, instead of Ic) because a linear function was found to have unrealistic, disruptive effects on the simulation process. In summary the final DW of a new leaf on the main stem depends on that of its predecessor, the genotypic value of MGR and the resource situation (value of Ic) at the time of its appearance.

Leaves produced by tillers are initially smaller than other leaves of the same cohort, but leaves appearing subsequently catch up in size with those on the main stem (Tivet et al. 2001). In the model, we assume that the first leaf produced by a tiller has an intermediate (mean) size between the leaf simultaneously produced on the main stem (same cohort), and the very first leaf produced on the main stem. Subsequent leaves produced by the tiller are pre-dimensioned at the time of their initiation as the mean weight of the previous leaf on the main stem and that on the concerned tiller, multiplied by MGR. Consequently, the weight of leaves appearing on tillers asymptotically converges towards 0 as thermal time (°Cd) 100 200 300 400 500 600

Fig. 2. Kinetics of the elongation of seven successive leaf blades on the main culm of IR64 rice (L2–L8, visible parts only), from tip appearance (app) to constant length. The continuous, bold line indicates plant height from shoot base to the tip of the youngest, fully expanded leaf. Kinetics of aggregate sheath length can be estimated from the difference between plant height and the length of the longest leaf present on the culm. Only one of four replications is shown.
that of leaves appearing on the main stem, and leaf size on older tillers (having several phytomers) is similar to that on the main stem.

The root system is not simulated with the same amount of detail as the shoot, although a detailed version is being developed. The present version of EcoMeristem considers the root system as a bulk compartment of the plant, with a daily carbon demand that is equal to the total plant carbon demand simulated on the previous day, multiplied with a genotypic parameter \( k_{RSmow} \) (Table 1).

Contrary to some other architectural models (e.g. GREENLAB, Yan et al. 2004), organ lifespan is not forced by EcoMeristem. Senescence is triggered by assimilate shortage, resulting in 'recycling' of the oldest leaves and youngest tillers on the plant. Leaf longevity is known to depend also on nitrogen supply (Dhungana et al. 1992), which is not simulated at present. However, the feedbacks of assimilate shortage on leaf size and mortality implemented here are bound to occur as well when RUE is reduced by N deficiency, or any other physiological stress for that matter. Future modules for mineral and other stresses can thus make use of the existing mechanism for senescence, provided that their effect resembles that of assimilate starvation.

(iii) Arbitration between supply and demand functions

At the core of this modelling concept is the hypothesis that plant growth is not only supply driven (which is the case for most agronomic models such as APSIM (Wang et al. 2002), STICS (Bossion et al. 1998) or DSSAT (Jones et al. 2005)), but also demand driven. The underlying assumption is that organ development begins with cell divisions (determining potential size and thus, sink capacity) and ends with expansion (during which demand for resources is greatest). Although cell division and expansion phases overlap (Tardieu et al. 2000), there is reason to assume that meristem activity must be regulated through supply-related feedbacks in order to efficiently adjust organ size to fluctuating resources (Luquet et al. 2005; Murchie et al. 2005). In fact, recent findings on sugar signals regulating meristem activity support this concept at the molecular scale (Sherston et al. 2003; Heyer et al. 2004).

In EcoMeristem, the ratio between aggregate carbon supply and demand at the whole-plant scale (state variable \( I_c \)) serves as a signal influencing development processes. In order to keep the model reasonably simple and transparent, \( I_c \) directly affects only two processes deemed crucial for adaptive responses of morphogenetic processes: down-sizing of new organs at the time of their initiation if \( I_c < 1 \) and enabling of tiller production if \( I_c > 1 \), with \( I_c \) being a threshold parameter potentially smaller or larger than 1.

These two effects of \( I_c \) are strategic in the sense that they do not alleviate assimilate shortfalls immediately, but during subsequent plastochron phases when they have an impact on sink activity (growth of the organs initiated). There are, however, also immediate effects of supply and demand imbalances, required to keep the carbon balance intact.

Case of \( I_c > 1 \):

- Storage of excess assimilates in vegetative tissues (leaf blades, sheaths and internodes, once simulated).

- Proportional reduction of photosynthesis if storage reaches its physiological limits (parameter \( k_{STHom} \)).

Case of \( I_c < 1 \):

- Mobilisation of stored assimilates.

- Senescence of the oldest leaf; if reserve mobilisation is insufficient to satisfy demand, senescence of the youngest tillers — if leaf recycling is insufficient — is not yet implemented in the current version of the model.

- Delay of organ expansion and extension of current plastochron if the above are insufficient.

These processes, generally known but insufficiently studied to model them quantitatively, were programmed rather intuitively. They are necessary, however, to account for the fact that plant development is not only based on organogenesis but also on organ death and recycling of internal resources.

Model parameters and input/output variables

When applied to non-water limited environments, the EcoMeristem model uses 18 crop parameters (Table 1). Preliminary, unpublished observations indicated that most of these parameters vary little among rice cultivars. Strong genotypic variation, and thus the need for careful parameterisation, was found in seed DW (SDW), a parameter necessary for the calculation of the initial pool of carbon reserves; first-leaf DW (LDW1st), plastochron (PLAS), meristem growth rate (MGR) and the critical \( L_e \) value for tillering (\( L_{till} \)). The first two parameters can be easily observed on seeds and seedlings in the course of germination tests, but the last three parameters calibrate organogenetic responses and thus, are quite inaccessible to measurement.

For applications that do not consider water deficit or photoperiodism, the model uses only two weather input variables: mean daily air temperature and PAR (Table 2). When applied to water-limited environments and photoperiod-sensitive genotypes, additional input variables such as potential evapotranspiration (PET), soil depth and water holding capacity, rainfall/irrigation and geographic latitude are needed.

Programming aspects

The current version of EcoMeristem, which is a prototype for research purposes, was programmed with Matlab software (version 6.5, Mathworks Inc., Natick, MA). The model is now being implemented in a third generation programming environment (Delphi, version 5, Borland-France, Paris, France) using an object approach, destined for routine phenotyping applications in the context of genetic and functional-genomics research, marker development for breeding, and plant ideotype development. The object approach permits delining generic entities (such as organ types) that can be more easily adapted to different plant topologies.

Model calibration

The model was calibrated for IR64 (Oryza sativa L. indica type) rice grown under the controlled, experimental conditions described later Parameterisation, where it used experimental data, was performed separately for each of the four experimental replications, in order to obtain standard errors for parameter values. Results of parameter optimisation are summarised in Table 1.

Information on parameter values was derived from three sources (Table 1), and implemented in the following order: (1) generic information from the literature, (2) direct calibration with measured observations, and (3) indirect calibration with statistical parameter optimisation against measured observations by running the model. Parameters derived from the literature included coefficients for calculating temperature- and biomass-dependent maintenance respiration \( (K_{rm}) \), the DW fraction of seed available as reserves \( (R\text{ESeeds}) \), and the extinction coefficient for PAR \( (k_{PAR}) \) (literature citations in Table 1). There is considerable uncertainty on the accurate
value of these parameters and on their variability. For 2b, we used a value for fRB4 obtained heuristically by model fitting to field observations (Dingkuhn and Meinzer 1999). For Kw, a genetic value proposed by Penning de Vries et al. (1989) was used, but since maintenance is very small during vegetative growth, the accuracy of this parameter value has little bearing on the results of this study. Growth models are very sensitive to Kw, a parameter that is difficult to measure. We used a value adapted from Dingkuhn et al. (1999), a study that compared several methods for the estimation of Kw. Also uncertain is the value of SDDmax. partly because reserves are rarely measured in vegetative-stage plants and partly because it is difficult to estimate the upper limit of storage. We assumed here that the storage capacity of leaves and stems observed by Samonte et al. (2001) for leaves and sheaths of several rice cultivars at heading stage can be extended to these organs during vegetative growth stages as well.

Parameters adjusted manually with direct measurements included all initial crop parameters derived from germination tests (individual seed DW, SaDFW, first-leaf DW, LoDFW, first-leaf SLA, SLA; and root/shoot DW ratio at first-leaf stage, RsR0m), as well as some parameters adjusted manually on the basis of plant observations at 36 d after transplanting (DAT) (individual leaf blade/shoot DW ratio, root/shoot DW partitioning ratio and a coefficient setting the decrease in SLA for subsequently appearing leaves, eqs 1). Lastly, some less accessible parameters describing morphogenetic behaviour (PLAS, MgK and Ix and W2Isp) were optimised statistically by running the model while varying parameter values.

Optimisation was done with utilities available on the Matlab software package, which also served as programming environment. The Nelder–Mead method (Nelder and Mead 1965) was applied to a maximum of three parameters at a time. The optimisation procedure required establishing a standardised target file containing the observations in a format that corresponds to model output, in order to evaluate prediction errors. Table 2 (bottom) provides details of this target file.

Model validation

The model was field-validated with a published field experiment conducted in the Philippines in the 1988 dry season (site of Malas, 120° 56’ E, 15° 45’ N, altitude 48 m, mean daily PAR 11.2 MJ m−2 d−1; Schneid et al. 1998), with the same cultivar IR64 for which the model had previously been calibrated under controlled, growth chamber conditions (parameter values as in Table 1 except plant population, which was 180 plants m−2 in the field and 30 plants m−2 in controlled environments). Plant establishment method was similar in both cases (wet, direct seeding of pre-germinated seed). For the field experiment, sequential observations were available on bulk leaf blade and stem (essentially, sheath) DW, plant height, tiller number and leaf area. Since these data were based on soil surface area, values were transformed to single-plant scale. Global solar radiation data from the experiment were converted to PAR with a factor of 0.49 (Kropff and van Laar 1993). The field experiment was composed of six nitrogen input treatments between 0 and 150 kg ha−1, converted to PAR with a factor of 0.49 (Kropff and van Laar 1993). The experiment had four replications in a block design, with several pots per block to permit destructive sampling at several growth stages. After each destructive sampling, pots were rearranged to form a plant canopy at 30 plants m−2 including single rows of border plants. All remaining plants were harvested at 36 DAT for measurements constituting the target file for model calibration (Table 2).

Measured variables and measurement schedule are summarised in Table 3. Sample size per replication was one plant. Destructive sampling was done in the morning in order to avoid DW variation caused by transitory reserve accumulation in leaf blades, which is most pronounced in the afternoon (Mann et al. 1981; Walter and Schuur 2005). Root systems were sampled in bulk and washed thoroughly to remove sand. All samples taken for DW measurements were dried in ventilated ovens at 70°C until constant weight, and then weighed with a precision balance (resolution 0.1 mg). Samples for sugar analyses were deep frozen and processed as described in the following section. Leaf blade area was estimated from blade length and width using an allometric coefficient of 0.725 (Tivet et al. 2001). Specific leaf area (SLA) was calculated by dividing individual leaf blade area by the corresponding DW. Leaf appearance was defined as the time when the leaf tip emerged from the enclosing sheath. Blades were considered to have achieved their final length when the ligule had emerged from the previous leaf’s sheath.

Analytical methods

Dry matter and sugar concentrations of bulk plant parts were determined after lyophilisation. Samples were ground with liquid nitrogen with a ball grinder (Mixer Mill MM 200, Retsch, Germany). Sugars were extracted

Table 3. Measurement schedule (days after transplanting, DAT) and derived variables (underlined)

<table>
<thead>
<tr>
<th>Measured or estimated variables</th>
<th>DAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature at plant base and PAR at level of plant tops</td>
<td>Continuous</td>
</tr>
<tr>
<td>Individual leaf blade and sheath DW on all stems; root DW</td>
<td>12, 19, 25, 30, 36</td>
</tr>
<tr>
<td>Individual specific leaf area (SLA), shoot DW ratio, blade-shoot DW ratio</td>
<td>12, 19, 25, 30, 36</td>
</tr>
<tr>
<td>Individual leaf blade and sheath size (length, width and area)</td>
<td>Daily</td>
</tr>
<tr>
<td>Leaf appearance and dissection (thermal time between appearance of 2 leaves)</td>
<td>Daily</td>
</tr>
<tr>
<td>Tiller appearance</td>
<td>Daily</td>
</tr>
<tr>
<td>Plant height (distance from ground to tip of last fully expanded leaf on the main stem)</td>
<td>12, 19, 25, 30</td>
</tr>
<tr>
<td>Glucose, fructose, sucrose and starch concentration (bulk blades, sheaths and roots)</td>
<td>12, 19, 25, 30</td>
</tr>
</tbody>
</table>

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three times from 30-mg samples with 1 mL 80% ethanol for 30 min at 80°C, and then centrifuged. Soluble sugars were contained in the supernatant and starch in the sediment. The supernatant was filtered in the presence of polyvinyl polypyrrolidone and activated carbon to eliminate pigments and polyphenols. After evaporation of solute with Speedvac (RC 1022 and RCT 90, Jouan SA, Saint Herblain, France), fructose, glucose and sucrose were quantified by high performance ionic chromatography (HPIC; standard Dionex) with pulsed amperometric detection (HPAE-PAD). The sediment was solubilised with 0.02% soda at 90°C for 2h and then hydrolysed with α-amylglucosidase at pH 4.2 for 1.5 h. Glucose was quantified as described by Boehringer (1984) with hexokinase and glucose-6-phosphate dehydrogenase, followed by spectrophotometry of NADPH at 340 nm (spectrophotometer UV/VIS V-530, Jasco Corporation, Tokyo, Japan).

Results

Model parameter values for IR64 rice obtained in controlled environments

The model parameter values obtained for IR64 are presented in Table 1. Due to a very homogenous population and controlled culture conditions, measurement-derived parameter values were very similar among the four replications, even in the case of statistical parameter optimisation, as indicated by the standard errors of the mean (SE). The threshold parameter for tillering ($I_c$) was 1.6, indicating that IR64 did not require any assimilate surplus (relative to current demand) to initiate a tiller. The meristem growth rate ($MGR$) was 1.6, indicating that each subsequent leaf produced on the main stem was up to 60% heavier (if supply was not limiting) than its precursor. Whether the meristem actually grew in size at this rate remains to be confirmed, although non-quantitative, microscopic observations on dissected apical meristems appeared to confirm the hypothesis (results not presented). Detailed observations on meristem development are currently in progress.

Simulation of observed plants

Morphogenesis

The calibrated model accurately reproduced the observed time courses of shoot and whole-plant dry weight, as well as tiller production (Fig. 3). Furthermore, the observed distribution of dry weight and leaf area between the main stem and various tillers, and among leaf positions on the culms, was simulated accurately (Fig. 4: individual leaf area of fully expanded leaves; dry weights and physical dimensions were simulated but not presented here).

Carbon dynamics

Since the EcoMeristem model simulates carbon reserve dynamics in the plant and their feedbacks on development processes, we investigated the distribution among organs of soluble sugars and starch in the course of vegetative development (Fig. 5). No significant amounts of polysaccharides were found. Hexose (glucose and fructose) concentrations increased consistently with plant age in leaf blades and sheaths ($P<0.05$), but not significantly in roots. Sucrose concentrations were greatest in blades, smaller in
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Sheaths and smallest in roots. They did not change during the period of observation in leaf blades, but decreased significantly in sheaths. Lastly, starch concentrations were greatest in sheaths and decreased significantly over time. They were intermediate in leaf blades and very small in roots, with no significant trend over time.

It is difficult to relate these observations to variables simulated by the model, because the model considers only a general assimilate reserve pool in the plant without specifying substance classes and organs. In Fig. 6, observed sucrose and starch concentrations (supposed to constitute main reserve compounds) in sheaths (considered a storage organ) were compared with the model outputs \( I_c \) (which is an index of assimilate abundance) and weight fraction of reserves in the shoot. Although these variables cannot be compared in quantitative terms, the simulated and observed variables showed the same trend and appeared to be correlated (although with four points, this cannot be asserted statistically). Note that for model calibration, only morphological observations and no chemical measurements were used.

Field validation

The model as calibrated for IR64 under growth chamber conditions was validated with field data for the same cultivar published previously (Schnier et al. 1990). The model was run with climate data from the field site in the Philippines and the respective plant population density, which was much greater than that in the growth chamber (180 plants m\(^{-2}\), as opposed to 30 plants m\(^{-2}\)). None of the original crop parameters was modified.

Since the model does not consider the nitrogen status of the crop, and the field experiment consisted of six levels of N input, we compared simulations with all N treatments in the field for the initial 36 d of growth (Fig. 7). Simulated shoot

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**Fig. 5.** Observed dynamics of sugars in bulk leaf blade, sheath and root samples taken from IR64 rice at four sampling dates. Vertical bars represent standard error of three replications.

**Fig. 6.** Relationship of simulated carbohydrate reserves and internal competition index \( I_c \) vs. observed reserve (starch + sucrose) concentration in leaf sheaths for IR64 rice during vegetative growth.
dry weight per plant gave an excellent fit with observed values for the treatments having high N inputs, which is consistent with the fact that the model was calibrated on plants grown with non-limiting N supply. The same was observed for plant height. Predictions of tiller number were good until 30 d after germination but were followed by an over-estimation on day 36. In fact, the authors of the field data reported a slump in tillering at this stage, which was subsequently corrected with a second application of N, shortly before panicle initiation (Schnier et al. 1990). Consequently, the slump in tiller production was due to a temporary exhaustion of soil N supply and thus, not simulated by the model. Lastly, observed plant leaf area (calculated from LAI and population density) increased earlier than the corresponding, simulated values, but the two were similar at 36 DAT.

In summary, the model parameterised under growth chamber conditions gave a reasonably good prediction of field observations for the same genotype. It can thus be considered acceptable for non-water- and –nitrogen-limited conditions during vegetative development.

**Sensitivity analysis**

The model was extensively tested for its sensitivity to input variables and crop parameters, in order to explore its behaviour and evaluate the biological coherence of its responses. We present here examples of the effect on model outputs of variations of PAR (input variable) and three crop parameters that govern organo- and morphogenesis, and thus, plant type ($MGR$, $PLAS$ and $Ict$). These parameters affect not only the rate of increase of the size of consecutively appearing leaves ($MGR$), the rate of leaf appearance ($PLAS$) and the sensitivity of tillering to assimilate supply ($Ict$), but also, by way of feedback, most other morphological properties of the plant. The sensitivity analyses were limited to the initial 36 d
of plant development in order to stay within the limits of the available experimental evidence. The parameter values used as basic setting were the ones for IR64 grown under growth chamber conditions (Table 1).

(i) Effects of environment input parameters

PAR levels ranging from 5 to 20 MJ m\(^{-2}\) d\(^{-1}\) affected shoot DW approximately linearly up to 12 MJ m\(^{-2}\) d\(^{-1}\) and then did not increase dry weight any further (Fig. 8). The insensitivity of growth to higher radiation levels was not due to light saturation (which is not to be expected at this level of PAR because of the strong leaf inclination of rice; Dingkuhn et al. 1999) but to limited demand for assimilates. A higher value for MGR (enabling potentially larger leaves) or a lower \(\textit{Ic}t\) (enabling more responsive tiller production) would be necessary to provide positive growth responses to higher PAR levels, but it is not certain that the plants would indeed respond in this manner. When applied to dense crop stands in the field (where competition among plants for light is more severe than in our growth chamber experiment), the model predicts positive growth responses for the full range of naturally occurring light levels (data not presented).

It is characteristic of this model that simulated growth responses to parameters and input variables show oscillations, both in time and in response to parameter values, as observed for example for lower PAR ranges in Fig. 8. These oscillations are due to the impact of facilitative development events such as initiations of tillers and leaf cohorts, which temporarily increase demand for assimilates and thus reduce the size and/or rate of appearance of leaves. This phenomenon is more pronounced at low PAR levels because of severe competition among organs for assimilates, associated with increased leaf mortality (broken line in Fig. 8).

(ii) Effects of genotypic parameters

The empirical value of MGR for IR64 was 1.6, indicating that successively appearing leaves on the main stem are up to 1.6-fold larger (in weight terms) if carbon resources are not limiting their size. MGR values below this value led to lower shoot dry weight, plant height and leaf area, but did not affect tiller and leaf number (Fig. 9, top). Under these conditions, leaves remained small, thus limiting both production of assimilates (through poor light interception) and demand for assimilates. Increasing MGR above 1.6, however, led to greatly increased plant height, and to a lesser extent SDW and leaf area, while reducing tiller number. Green leaf number was also reduced by high MGR, partly because of lower tillering and partly because of increased leaf mortality. Death of old leaves was, in this case, caused by excessive demand for assimilates by large, new leaves during expansion. At extremely high values for MGR (e.g. 2.0), competition for assimilates was such that plant height decreased. Increasing MGR further killed the plant because of senescence of all leaves (data not presented).

Reducing plastochron below the empirical value for IR64 (60 °C) increased biomass, leaf area and plant height because of rapid succession of new phytomers (Fig. 9, centre). It also reduced tiller number and led to increased leaf senescence because of severe competition for assimilates among sinks. Conversely, increasing the plastochron (thus, slowing down organogenesis) reduced all aspects of plant growth.

The critical value of \(\textit{Ic}\) for tillering (\(\textit{Ic}t\)) had no effect on growth parameters when it was reduced below the empirical value for IR64 (\(\textit{Ic}t = 1.0\) ) (Fig. 9, bottom). At this level of \(\textit{Ic}\), assimilate supply and demand are equal; permitting the plant to tiller in such situations would mostly lead to deficit situations and would thus cause further decreases of \(\textit{Ic}\). Consequently, \(\textit{Ic}\) values below 1 were ineffective. Values higher than 1, however, strongly reduced tiller number, and consequently, leaf number. Leaf area, however, increased slightly as tillering was moderately inhibited (\(\textit{Ic}t\) between 1.1 and 1.3) because in this interval, reduced leaf mortality set off the effect of reduction in tillering. Larger values of \(\textit{Ic}\) decreased leaf area. Lastly, shoot biomass was generally, although moderately, increased by higher values for \(\textit{Ic}\). Note that leaf area and shoot dry weight behaved almost identically when MGR and plastochron were varied (Fig. 9, top and centre), but behaved differently under variable \(\textit{Ic}\) (Fig. 9, bottom). This was due to accumulation of assimilate reserves in the shoot (up to 33% of dry weight) when tillering was inhibited by high \(\textit{Ic}\), thus decreasing specific leaf area (or increase leaf thickness for a same structural area).

Overall, the strong effect of organogenetic parameters on shoot dry weight simulated by this model is surprising because RUE was constant and partitioning of assimilates...
Fig. 9. Sensitivity of various model outputs to variation in values of morphogenetic crop parameters [(top) meristem growth rate; (centre) plastochron; (bottom) Ic threshold for tiller production], based on model calibration for IR64 rice and 36-d simulation runs. As in Fig. 8, crop parameter variation, all model outputs except leaf mortality (left axis) were normalised as fraction of the model output with original IR64 settings at 8 MJ m\(^{-2}\) d\(^{-1}\) (phytotron conditions), with the respective reference values presented in the legend. Leaf mortality is presented as fraction of total leaf number produced (right axis).

among organs varied little. This apparent paradox was due to the model assumption that assimilates are not necessarily immediately used for growth, but pass through storage pools before the tissues use them for growth. The resulting delays in leaf area production under low-demand conditions, although small, have a strong effect on growth during its exponential phase. The most significant result of this modelling exercise is thus that plant growth is probably not only driven by assimilate supply, but also by demand for assimilates. We will focus the discussion section of this paper on this hypothesis.

Discussion

The model described here makes use of two well-established concepts, that of growth driven by carbon assimilation (which is at the basis of all agronomic crop models) and that of structural growth, resulting in a tree-type topology (realised in numerous other plant-architectural models). Since emphasis here was on combining the two in order to model interactions between growth and structural development, both complementary concepts were implemented in the simplest possible way. For example, light interception and photosynthesis were calculated at the canopy scale, thereby assuming that Lambert-Beer’s law of light extinction and the concept of RUE (proportionality between light interception and carbon assimilation) are sufficiently accurate to feed into a physiological model of sink-source relationships. In fact, we borrowed these modules from an existing, agronomic crop model (SARRA-H, Dingkuhn et al. 2003; Sultan et al. 2005), with the result that feedbacks of morphological change on assimilation are essentially mediated by LAI. We acknowledge that the EcoMeristem model’s potential would be more fully exploited if plant photosynthesis were also sensitive to changes and distribution within the canopy of SLA, leaf age, nitrogen content (Dingkuhn et al. 1992) and leaf orientation and distribution in space (Dauzat 1994; Dauzat et al. 2001). Most of these feedbacks are under study for the next version of EcoMeristem, but the simplifications and compromises made in the present model bear little on the main result, which is that crop growth depends as much on assimilate supply as it does on internal demand for assimilates.

We hypothesise that the concept guiding most agronomic crop models, namely, that plants generally convert into biomass all resources available to them in the most efficient way, is in many cases wrong. There are numerous examples to the contrary, such as the case of hybrid vigour, which is mostly not related to higher leaf photosynthetic rates, nor to different crop architecture when compared to similar, high-yielding inbred lines (Laza et al. 2001). Another, more extreme example is the physiology of temperate, perennial plants, which constitutionally have long lag phases between assimilate production and their reinvestment in growth processes, involving large reserve compartments to buffer the asynchrony between supply and demand (Lechaudel et al. 2005). Evidently, annual crops bred for rapid growth and maximal production, such as modern cereals, probably have minimal lag periods between assimilate acquisition and their re-investment in resource uptake (including carbon, but also
et al. (1995) of sinks. Further research is needed to confirm our hypotheses. We justified the development of EcoMeristem with the need for models that are capable of linking crop phenotypic plasticity in the field to genomic or genetic information. No evidence can be provided at this stage that this model is better suited to this purpose than classical, agronomic models of cereals, which are generally resource driven during vegetative growth. EcoMeristem operates with a new type of crop parameters governing morphogenetic reaction norms to internal resources (in addition to classical crop parameters such as $Th$, $RUE$, $K_{df}$/, or seed size). These new parameters characterise meristem behaviour and are sensitive to sugar signalling, and are thus in line with recent findings on the genetic control (e.g. expression of cell wall invertase genes; 3s et al. 2005) and physiological regulation (sugar and hormonal signalling; Black et al. 1995) of sinks. Further research is in progress to explore the relationships of genotypic model parameters with the expression of candidate genes and the activity of key enzymes encoded by them, such as cell wall invertases.

Conclusion

This paper presented a new model, EcoMeristem, which simulates interactions between development and growth processes in vegetative rice plants. The underlying hypothesis was that supply of assimilates feeds back on demand for assimilates resulting from the production of new organs and conversely, organ production feeds back on supply (assimilation). Imbalances between instantaneous supply and demand levels are buffered by reserve storage and mobilisation, as well as facultative organ initiation or senescence. Sensitivity analysis of the model suggests that biomass growth may be as much driven by internal demand as by supply. This finding requires further validation. Once the capability of the model to accurately simulate the plant type and phenotypic plasticity of contrasting genotypes has been demonstrated, it will be used to associate model parameters with genetic information.

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