CHAPTER 13

IS PLANT GROWTH DRIVEN BY
SINK REGULATION?

Implications for crop models, phenotyping approaches and ideotypes

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Abstract. There is a new interest in plant morphogenesis and architecture because molecular genetics is providing new information on their genetic and physiological control. From a crop modeller's point of view, this requires particular attention paid to the regulation of sinks associated with organ development, as well as their interactions with assimilate sources. Existing agronomic and architectural crop models are not capable of simulating such interactions. A conceptual framework is presented for the analysis and simulation of crop growth driven by either assimilate source or sink dynamics, building on the assumption that meristems are the main sites in the plant architecture where sinks are initiated and adjusted to resources. Among the numerous sink–source feedbacks to be considered are sensing of the plant's resource and stress status by meristems (enabling adjustment of morphogenesis), as well as transitory reserves, organ senescence and end-product inhibition of photosynthesis (necessary for the plant to cope with acute imbalances). These feedbacks are to a large extent related to sugar metabolism and can be explained with recent molecular findings on the prominent place in plant development of sugar sensing and the regulation of sucrose cleavage at sink sites. A model integrating these phenomena in a simplified manner, called EcoMeristem, was developed and is being applied in phenotyping for functional-genomics studies on rice. Theoretical evidence and model sensitivity analyses suggested that sink regulation during vegetative growth has a strong effect on plant vigour and growth rate, even at given levels of leaf photosynthetic capacity. However, the usefulness of complex, whole-plant models such as EcoMeristem for heuristic phenotyping approaches remains to be demonstrated. Specific problems are related to the stability of process-based crop parameters across environments, as well as the measurement of such crop parameters that are inaccessible to direct observation. But it is argued that integrated, structural-functional models may be the only means to quantify complex traits, such as those governing adaptive morphology (phenotypic plasticity). Furthermore, such models may be well suited to develop improved plant type concepts *in silico*.

INTRODUCTION

In recent years crop physiology has received a considerable boost from molecular genetics, and in particular from functional genomics. New advances in physiological theory are largely due to emerging information on causal linkages between processes at the molecular scale and at the plant scale. These linkages were inherently inaccessible to physiological research methodology, and are now being exposed by the identification of genes that are involved in them.

The clues provided by molecular genetics are redirecting the attention of physiologists to new or previously sidelined aspects. The physiology of phytohormones, which had exhausted its means of analysing ever smaller compartments and ever-increasing system complexity, is currently experiencing a revival through knowledge on direct causalities established by molecular genetics. On the other hand, the importance of developmental aspects, including the ontogenesis of architectural and morphological structure, has been emphasized by molecular findings and is receiving a prominent place in physiological research (Seki et al. 2002; Gazzarrini and McCourt 2003; Liu et al. 2005). The latter observation should not come as a surprise because genes, through physiological processes, build the plant apparatus in a continuous process of physical and biochemical differentiation. Plant functioning can therefore not be understood without the study of its (onto)genesis, and consequently, processes that happen in meristems – the tissues that are probably the least accessible to physiological study because of small cell size and hidden location within the plant.

Crop models have inadvertently reflected contemporary, physiological research priorities and accorded little attention to developmental biology. They generally give emphasis to environmental effects on source processes, such as photosynthesis, and mostly consider the size of sinks as perfectly adjusted 'slaves' of the incremental source. The type and relative weight of different sinks (e.g., leaves, roots, stems or inflorescences) is thereby commonly forced by empirical, phenology-dependent partitioning functions or tables (ORYZA2000: Bouman et al. 2001; APSIM: Wang et al. 2002; STICS: Brisson et al. 1998). The sometimes large discrepancy between predicted (potential) and observed growth is attributed (correctly or not but this cannot be ascertained) to biotic or abiotic constraints not simulated by the model. Generally, however, the possibility of sub-optimal regulation of developmental processes determining sink dynamics in the plant's architecture is not considered (with the notable exception of reproductive sinks in cereals, which are frequently simulated through a resource-dependent, pre-dimensioning process after their initiation).

The present study, to a large extent conceptual, explores the hypothesis that sink dimensioning, as part of plant development, may act as a major driving force of plant growth. Furthermore, we will explore potential consequences of this hypothesis for model-assisted phenotyping, crop ideotype development and eventually, crop improvement strategies.

EVIDENCE FOR SINK-LIMITED VEGETATIVE GROWTH IN PLANTS

Any significant impact of sink dynamics on crop growth requires that growth is sink-limited in a significant range of situations and genotypes. Sink-limited growth, or excess production of assimilates, is a frequent phenomenon in perennial plants, which constitutionally have long lag phases between assimilate production and re-investment in growth processes. This involves large reserve compartments that buffer the asynchrony between supply and demand, particularly in temperate perennials that produce their foliage in spring with assimilates produced in autumn. Such asynchronies are also observed in tropical, seasonally defoliating perennials such as rubber tree (www.ppi-ppic.org/ppiweb/swchina.nsf/), as well as tropical orchard crops (Mango: Lechaudel et al. 2005). In oil palm, seasonal peaks of oil production probably draw from glucose and sucrose reserves stored in the trunk (Mialet, CIRAD, Montpellier 2005, unpublished); coconut trunks were found to maintain throughout the year a large reservoir of sucrose, little of which is utilized to buffer seasonal fluctuations in supply of, and demand for, assimilates (Mialet-Serra et al. 2005). Instead, it appears that assimilate production in coconut is down-regulated during periods of low demand (Mialet-Serra 2005).

It seems that the positive feedback of sink activity on leaf photosynthetic rates sometimes reported (Franck 2005) is probably due to the restitution of sub-maximal photosynthetic rates when the plant turns from sink-limited to source-limited conditions. Reductions of leaf photosynthesis by end-product inhibition (Sawada et al. 2001), associated with increased reserve storage, has been described for coffee (Franck 2005) and many other species. End-product inhibition of photosynthesis is under genetic control in *Arabidopsis thaliana*, and mutants were selected that show no such inhibition (Van Oosten et al. 1997). In other annual plants, such as cabbage, end-product inhibition of photosynthesis was caused by elevated ambient CO_2 concentration, but was less pronounced in genotypes that had greater assimilate storage capacity (Bunce and Sicher 2003). The same authors reported that end-product inhibitions could be predicted from weather, indicating that plants had a limited capacity to utilize assimilates exhaustively on sunny days.

Annual crops bred for rapid growth and maximal production, such as modern cereal varieties, probably have minimal lag periods between assimilate acquisition and their re-investment in structural growth. They are therefore unlikely to exhibit end-product inhibition of photosynthesis under stress-free conditions and 'normal' atmospheric CO_2 levels, although this may merit further investigation (Geigenberger et al. 2005). If such inhibitions exist, they are likely to occur in the afternoon on sunny days, and in fact stomatal conductance tends to decline during that time of day. To what extent this decline is caused by higher VPD (vapour pressure deficit) and/or saturation of carbon demand has not been studied explicitly. Leaves accumulate not only transitory starch but also soluble sugars in the afternoon (Munns et al. 1979). Furthermore, sugar concentrations in vegetative storage tissues, for example in leaf sheaths of rice, can be significant even during exponential growth (Luquet et al. 2005), and large quantities of non-structural carbohydrates are accumulated in stems during the month preceding heading (Samonte et al. 2001). Whether or not these phenomena indicate a general sink limitation of growth

remains open. It is also possible that some of these reserves are not of short-term, transitory nature (spill-over reservoirs), but instead are the result of a specific storage sink located in stems.

As a last piece of (rather anecdotal) evidence, we would like to point out that hybrid vigour in rice, which is associated with both greater biomass and harvest index compared with high-yielding inbred lines of similar architecture, cannot be explained by higher leaf photosynthetic rates and its physiological determinants (such as N concentration or specific leaf area (SLA)), nor by different partitioning patterns among organs (Laza et al. 2001). The physiological basis of hybrid vigour remains a mystery, and open to the alternative hypothesis of a general stimulation of structural sinks. (If this hypothesis were true, hybrid vigour should be associated with low levels of transitory reserves during vegetative development.)

DIFFERENT WAYS OF MODELLING SINK DYNAMICS

In quantitative terms, the process of morphogenesis in plants may depend on carbon assimilation, but in terms of the resulting structure it is driven by the organogenetic activity of meristems. Organogenesis can thus be seen as the successive initiation of new structures that act as sinks during their expansion phase, and may eventually turn into sources in the case of leaves (Figure 1: organ development). If we assume that 'fresh' assimilates form a common pool available to all its sinks (an assumption made in most crop models, but wrong in the case of large, complex tree structures (Franck 2005)), it follows that many sinks compete with each other at any given time for the incremental pool of assimilates. The simplest possible model of this process attributes a fixed, relative sink force to each organ type at any given developmental stage (e.g., ORYZA2000, www.knowledgebank.irri.org). A slightly more complex model representing architectural detail would attribute such a relative value to each individual organ and provide it with an empirical temporal profile (e.g., GREENLAB: Yan et al. 2004; Guo et al. 2006). The latter solution already involves the notion of meristems providing organogenetic rhythms and initiating different organ types that represent metamorphoses of a basic entity. Both types of models, however, do not simulate resource or environment feedbacks on the organogenetic process because they assume a perfect match between demand and supply at all times. In other words, they do not allow for sink-limited, vegetative growth, with the exception of secondary forcing, such as temperature-limited leaf expansion (e.g., ORYZA2000). Both types of models also suppose that final organ weight remains open, or responsive to supply, until the end of organ growth.

In fact, final (potential) organ size is for many species and types of organs determined at an early stage of organ development, not only for fruits but also for leaves (*Arabidopsis* leaves: Cookson et al. 2005; maize leaves: Tardieu et al. 2000; grass leaves in general: Fiorani et al. 2000; seed of rice: Kobayasi et al. 2002). This point is crucial: if organ size is determined early on, the plant has to regulate its potential sink size before the sink becomes effective. This can be described as a physiological commitment on the basis of a 'best bet', or early assessment of available resources.

Development of an organ
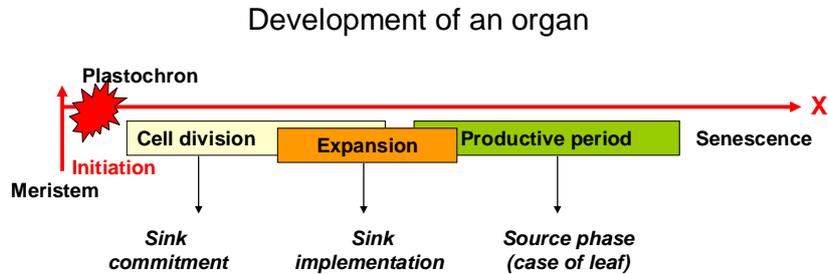
Figure 1. Schematic diagram of functional phases of plant organ development, illustrating the hypothesis that sinks are initiated and pre-dimensioned ('committed') before becoming effective

A model was recently reported that simulates such resource feedbacks on meristem behaviour (EcoMeristem: Dingkuhn et al. 2005; Luquet et al. 2006). According to this model, an index of internal competition (Ic) is calculated at each time step by dividing aggregate assimilate sources (supply) by aggregate sink activity (demand) (Figure 2). Via Ic, resources feed back on the rate of production of new organs (e.g., tillers, using a critical, genotypic value of Ic called Ict) and their potential size (down-sizing of sink if $Ic<1$). Since such adjustments of sinks involve a certain lag (time elapsing between organ initiation and expansion), temporary source/sink imbalances are inevitable, which result in reserve formation or mobilization or even organ death and recycling if Ic is very low.

SINK REGULATION VERSUS GROWTH AND PHENOTYPIC PLASTICITY

EcoMeristem demonstrates on a theoretical basis two phenomena that have so far received little attention in crop modelling. First, genotypes are conceivable that produce predominantly sink- or source-limited phenotypes, depending on whether organogenetic commitments made by the meristem are bold or rather conservative.
The bold (or source-limited) types would tend to use all available assimilates and frequently experience deficit situations, leading to low transitory reserve levels, large organ number and low organ longevity. The conservative (or sink-limited) types would tend to under-utilize available assimilates, produce fewer organs with greater longevity and accumulate more reserves. Interestingly, the conservative types show smaller biomass production even at given photosynthetic capacity (or radiation use efficiency (RUE)) because assimilates are not rapidly re-invested in new leaf area, and because of frequent end product inhibition of photosynthesis. This is illustrated in the sensitivity analysis of EcoMeristem to two crop parameters shown in Figure 3. The potential meristem growth rate (MGR), which sets the maximal rate of organ weight increase from one phytomer to the next, strongly increases not only plant height (which is evidently a function of organ size), but also plant biomass and leaf area. The increased organ size, however, is associated with
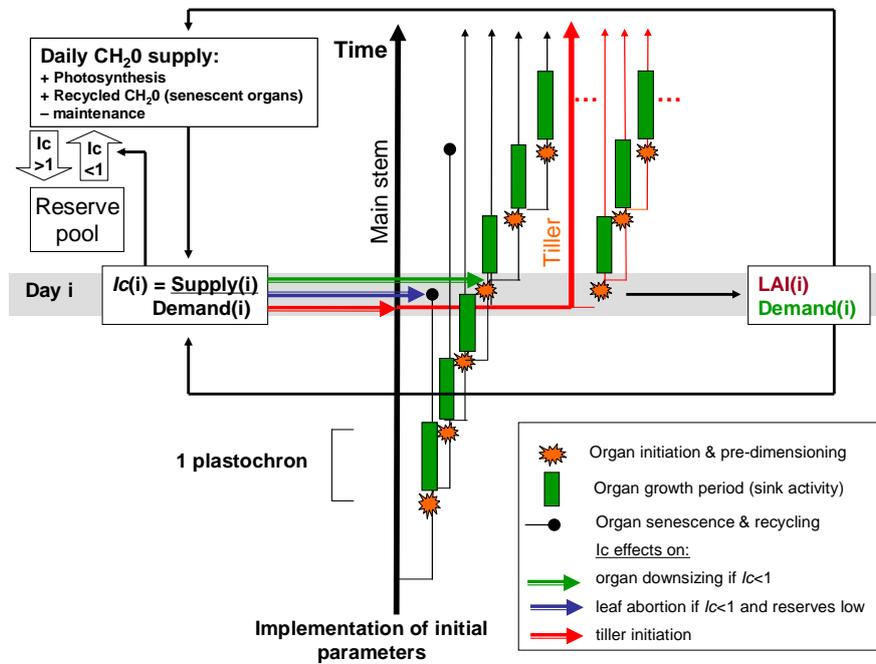
Figure 2. Schematic diagram of the model EcoMeristem implementing feedbacks of an index of internal competition for assimilates (Ic) on transitory reserve dynamics and potential organ size, number and longevity. Adapted from Luquet et al. (2006)

reduced tiller number and green-leaf number, whereas the fraction of dead leaves increases. In fact, if *MGR* is too high it results in excessive senescence and thus, reduced growth.

The critical *Ic* for tiller initiation (*Ict*), another morphogenetic crop parameter, has somewhat opposite effects. Increased Ict directly inhibits tiller production, and thus, number of leaves. Indirect effects include a slight, initial increase in leaf area (because reduced competition among tillers reduces leaf senescence), but a significant drop in leaf area at higher *Ict* (because the number of initiated leaves becomes limiting). Both *MGR* and *Ict* have previously been shown to differ strongly among genotypes (Dingkuhn et al. 2005) under given environmental conditions.

The predictions from sensitivity analyses should not be taken as quantitative but rather as trend information because the parameter variations tested exceed the ranges observed in true phenotypes. Also, not all possible combinations of parameter values will occur in reality. A real-world genotype producing large organs (high *MGR*) would probably have low tillering ability (high *Ict*), thus avoiding excessive organ senescence resulting from over-commitments (too many, too large sinks). As the sensitivity analysis of EcoMeristem shows, strongly over- or under-committing genotypes would still be able to thrive because of internal adjustments of organ size,
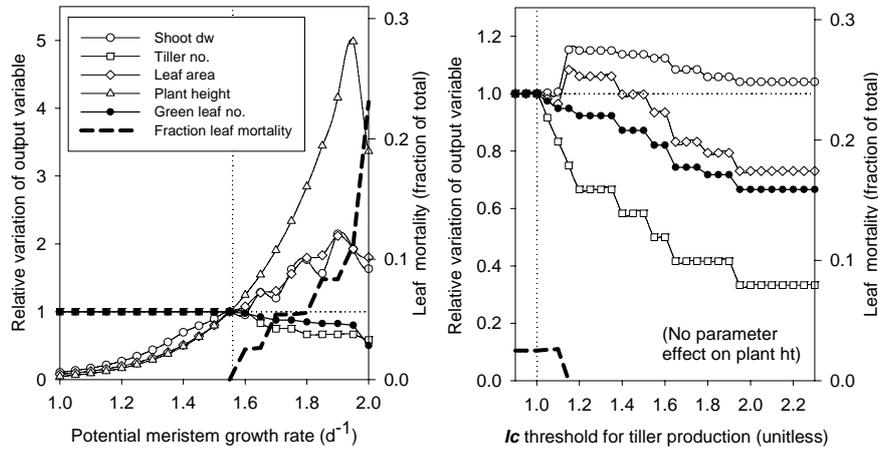
Figure 3. Sensitivity analysis of EcoMeristem model output variables (vertical axes) to variation of two crop parameters. Dotted lines indicate reference values for IR64 rice. Adapted from Luquet et al. (2006)

number and longevity; but they would not be efficient, and would probably not have survived any natural or man-made selection pressure.

The second biological phenomenon highlighted by EcoMeristem is resource-dependent, phenotypic plasticity (definition of term: Dewitt and Scheiner 2004). According to the model, branching rate (tillering), leaf appearance rate, organ size and assimilate-partitioning patterns are affected by internal competition for resources, and thereby lead to different plant architectures (Luquet et al. 2006). This type of phenotypic plasticity is of compensatory nature: it adjusts organ number and size on the plant, through modified rates of organogenesis and organ longevity, to variable carbon resources. The model was also used to interpret more specific effects of stresses, such as phosphorus deficiency, on rice plant morphology (Dingkuhn et al. 2006).

Phosphorus deficiency reduced shoot growth and stimulated, in relative terms, root growth. It thereby did not reduce RUE, but strongly reduced overall demand for carbon, resulting in sink-limited growth. The sink limitation, which led to a significant increase in carbohydrate reserves in leaf sheaths (Figure 4), was brought about by an inhibition of tillering and leaf extension rates (Dingkuhn et al. 2006). The lower leaf extension rates, combined with unaltered final leaf length, resulted in longer leaf extension duration and in reduced leaf appearance rates, probably by feedback. Root growth was stimulated by spill-over of excess assimilates from shoot to root, as evidenced by observations on sugar concentration levels and gradients within the plant.

This example of stress-induced phenotypic plasticity suggests that sink-limited growth situations, induced by the inhibition of specific, growth-related sinks, may
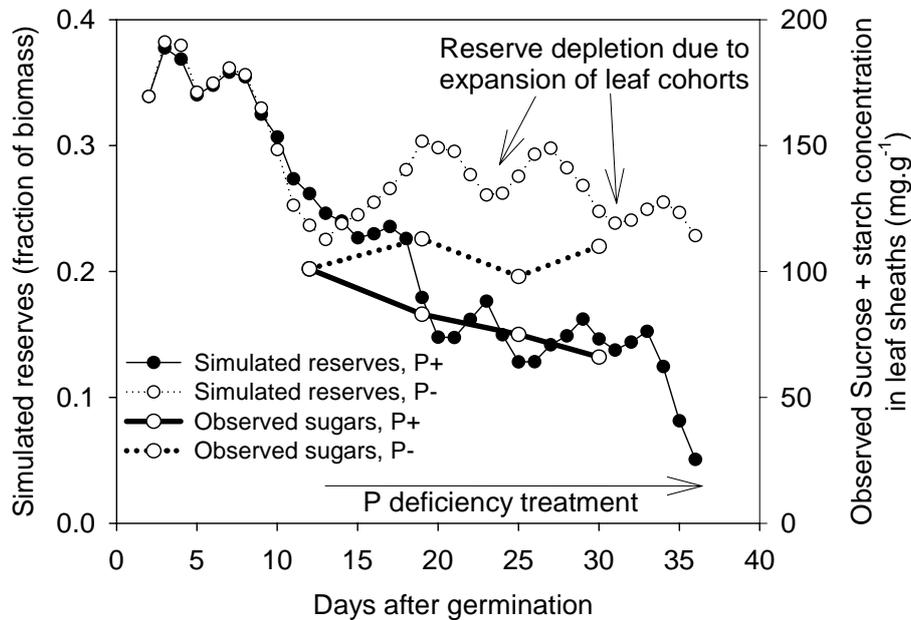
Figure 4. Kinetics of observed and simulated carbohydrate reserve concentrations in Aucena rice during vegetative growth under control and P-deficient conditions in controlled hydroculture environments. Initial reserve concentrations are high due to remains of seed reserves. Simulated oscillations of reserves are due to regular appearances of new organs (sinks). Adapted from Dingkuhn et al. (2006)

represent one possible strategy of plants to achieve adaptive changes in morphology and architecture.

PROCESSES INVOLVED IN THE REGULATION OF STRUCTURAL SINKS

A growing body of evidence points at a pivotal role of two types of acid invertases in source–sink relationships. The vacuolar invertase (Inv-V) is involved in tissue growth, including cell extension and reserve accumulation, whereas the apoplastic cell-wall invertase (Inv-CW) is involved in whole-plant sucrose partitioning, probably by controlling hexose supply to juvenile tissues such as meristems (Roitsch et al. 2000; Hirose et al. 2002). The Inv-CW is probably of particular significance for morphogenetic processes and phenotypic plasticity because it is controlled by both hormonal and sugar signalling (Black et al. 1995; Ji et al. 2005, Figure 5). Furthermore, tissue- or organ-specific control of Inv-CW activity is enabled by a family of genes coding essentially the same enzyme, called OsCIN 1 through 9 in rice (Ji et al. 2005; Cho et al. 2005). For example, OsCINx genes respond differentially to drought stress in flag leaves, panicles, anthers and peduncles of rice (Ji et al. 2005). Because of the close association of organ specific OsCINx

expression with growth processes such as peduncle elongation under drought, the reversibility of its drought response and its sensitivity to GA (gibberellic acid) and ABA (abscisic acid) treatment, Ji et al. (2005) suggested that the hormonal regulation of OsCINx genes may be a promising intervention point for breeding strategies.

Sink adjustment through sugar signalling
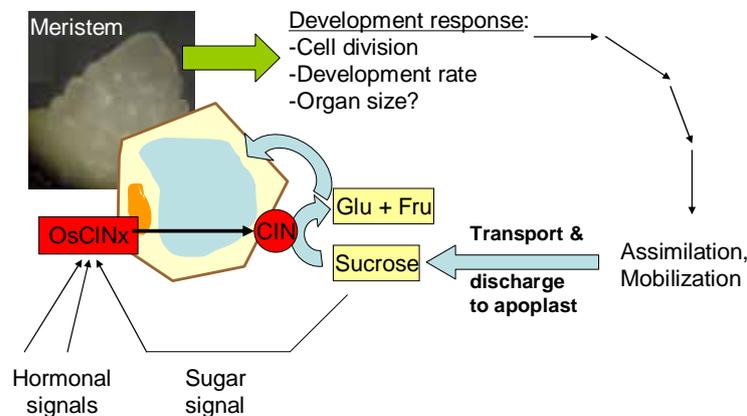
Figure 5. Schematic diagram illustrating the theory of sugar signalling of plant assimilate resources to meristems via cell-wall invertases (Inv-CW) and their coding genes (OsCINx) in rice

It is too early to conclude that cell-wall invertase genes are a generic, regulatory node linking hormonal with sugar sensing in developing tissues of the plant. However, if this should be the case, great scientific opportunities will arise for crop-physiological research and modelling (because Inv-CW regulation is pivotal for developmental biology, stress physiology and physiology of production), as well as for crop improvement (because Inv-CW regulation may hold the key for plant type traits and their phenotypic plasticity).

INCORPORATING SUGAR SENSING INTO CROP MODELS

It is evident that any crop model simulating sugar sensing by developing tissues (such as meristems) and the resulting effects on sink dynamics must include an explicit representation of organogenesis. This is the case for EcoMeristem (Dingkuhn et al. 2006; Luquet et al. 2006) and Greenlab (Yan et al. 2004; Guo et al. 2006), as well as for a number of other dynamic architectural models (e.g., GRAAL: Drouet and Pages 2003). Furthermore, the model must simulate carbon assimilation

(including its dependency on key environmental and morphological variables) and conversion (including respiration) with sufficient detail to predict incremental sugar supply. This is the case for most agronomic models and EcoMeristem, but not for the architectural models currently available. Finally, simulation of both source- and sink-limited growth requires the consideration of transitory reserve compartments, provision for deficit-driven senescence (notion of recycling), and end-product inhibition of photosynthesis.

On the basis of this minimum set of processes, incremental, quantitative assimilate sink and source assessments can be done and the degree of sink or source limitation diagnosed. This is essentially what the plant seems to be doing via sugar sensing, although physiological reality may be far more complex than this model, for example because of sugar concentration gradients within the plant apoplast. (The notion of a single assimilate pool equally accessible to all sinks is convenient but ignores proximity effects and transport processes.)

It would be complicated to simulate at the scale of the whole plant the fluxes and local concentrations of inter-convertible sugars such as starch, sucrose and hexoses. As a possible simplification, one may assume that sugar sensing by meristem cells (which in itself remains a black box) effectively amounts to sensing of available assimilate resources (analogous to the Ic state variable in EcoMeristem). If this hypothesis is true, we can use the ratio of daily demand (aggregate sinks) and supply (aggregate sources) as indicator variable and define empirical sensitivity coefficients relating meristem response to this variable. A major difficulty, however, resides in the fact that these coefficients, or crop parameters, cannot be measured directly and thus need to be fitted statistically by optimization. This approach has been adopted for the EcoMeristem model. Proof of concept was provided by Luquet et al. (2006), but Dingkuhn et al. (2006) demonstrated that crop parameter values change when a physiological stress is applied, such as P deficiency. Similar observations were made under drought and low light stress (Luquet, Montpellier 2005, unpublished data), indicating that physiological stresses induce modified reaction norms in the plant. In fact, it is known that hormonal stress signals affect the expression of cell-wall invertase genes (Roitsch et al. 2000; Ji et al. 2005), and thus re-calibrate sugar-sensing mechanisms. More physiological information is needed to formulate a model whose morphogenetic parameters related to sugar sensing are sufficiently robust to be considered genotypic, or genetic – particularly in .the case of studies involving stresses.

HEURISTIC APPLICATIONS OF CROP MODELS FOR GENOMICS

What is the scientific and practical usefulness of models such as EcoMeristem – supposing their genotypic parameters can be stabilized in future versions? In terms of scientific gain, this modelling approach integrates emerging knowledge on the plant's developmental biology with established paradigms of crop physiology, thus explaining the genotype- and environment-dependent plasticity of morphology and productivity. Phenotypic plasticity of crops is poorly understood, and it is likely that

much of the crop's capacity to adapt to variable environments is related to adaptive morphology, and not only tolerance mechanisms to physiological stresses.

In terms of practical applications, Dingkuhn et al. (2005) suggested that models of phenotypic plasticity can be used to assist phenotyping procedures, particularly with regard to process-based traits (or behavioural traits) that cannot be measured directly on the plant. Two recent examples show that model-assisted phenotyping by heuristics (Hammer et al. 2002) can provide quantitative trait loci (QTLs) that would be difficult to obtain with established phenotyping methods. First, Reymond et al. (2003; 2004) used a simple regression model to extract genotypic parameters from leaf elongation kinetics observed on maize. The experiment was designed to isolate soil water deficit, temperature and VPD as environmental variables while minimizing other sources of variation such as leaf rank, plant age or nutrition. The approach proved objectively superior to its conventional equivalent, namely, static measurements of leaf dimensions. In the second example, a simple phenological model was used to correct specific leaf area (SLA) observations on barley for bias caused by developmental stage (Yin et al. 1999; 2003). Here again, model-assisted phenotyping removed some genotype $\times$ environment (G$\times$E) 'noise' from observations and, thus, gave more specific and significant information on QTLs.

In the two examples cited, extremely simple models were used that transformed observations on the basis of existing knowledge (heuristics), in order to remove unwanted bias from measurements. This may not be enough if behavioural traits involved in phenotypic plasticity are the target. As we have argued, such traits are expressed within a complex system of phenological and trophic interactions at the whole-plant level, and can only be extracted using a more holistic modelling approach. The principle, however, remains the same: the model is parameterized by adjusting its parameters to observation. The parameters are then considered species traits (ideally, genes) and the genotypic parameter values are considered varietal traits (ideally, alleles). The parameter values are then correlated with molecular-genetic information using either a QTL approach (multiple recombinants of 2 genotypes, infinite number of possible loci) or an association-mapping approach (polymorphisms of few candidate genes (=loci), infinite number of genotypes). The technical difficulty of measuring plasticity parameters must thereby be overcome by means of statistical parameter optimization against target files containing information on directly measurable traits. In the case of Ecomeristem, such parameterization methods are currently being tested with the objective to achieve high-throughput methodologies for phenotyping purposes.

Model-assisted phenotyping for complex traits is a new field of research. An attempt was made to calibrate some parameters of an agronomic yield model of barley with known QTL effects (Yin et al. 2000). Thus parameterized, the model was to some extent predictive of yield and biomass of recombinants, but errors remained large. Improved versions of Ecomeristem are currently being used for model-assisted phenotyping of rice populations using both QTL and association-mapping approaches, but results are not yet available. This applies also to an ongoing, model-assisted study on a rice KO mutant having modified architecture (Luquet et al. unpublished).

CONCLUSION

We tried to develop a conceptual framework for the analysis and simulation of crop growth driven by either assimilate source or sink capacity, depending on environmental conditions and morphogenetic processes at the plant scale. We found that such a framework needs to take into account feedback effects of the plant's resource status on meristem behaviour, as well as mechanisms to cope with temporary imbalances. These mechanisms include the management of transitory reserves, organ senescence and end-product inhibition of photosynthesis, and are generally related to sugar metabolism. This conclusion is in line with recent molecular findings on the prominent place of sugar sensing and the regulation of sucrose cleavage at sink sites. A model integrating these phenomena in a simplified manner, called EcoMeristem, was developed and is being applied to phenotyping objectives in the area of functional genomics of rice.

The effective usefulness of complex, whole-plant models in heuristic phenotyping approaches remains to be demonstrated. Specific problems are related to the stability of process-based crop parameters across environments, as well as the measurement of such crop parameters that are inaccessible to direct observation. On the other hand, models of the proposed type may be the only means to analyse quantitatively the traits governing phenotypic plasticity and to relate them to the behaviour of the tissues that are at their origin, the meristems. Furthermore, models of phenotypic plasticity may be much better suited than the available, agronomic models to develop *in silico* improved plant type concepts.

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