SHORT COMMUNICATION

# PHYTOMER LEVEL SOURCE-SINK MODEL OF BIOMASS PRODUCTION AND PARTITIONING IN SUGARCANE

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## Abstract

A framework for above-ground biomass partitioning between competing sinks is proposed where partitioning depends on temperature, water status, the physiological age of the leaf and associated internode (phytomer), and on the structural demands imposed by the phenological development of leaves and tillers. This hypothesis was tested by comparing simulations from a model with observations from two glasshouse experiments. In these experiments, net photosynthesis, expansive growth, biomass production (at a plant level) and partitioning (at plant and internode levels) were measured for four genetically diverse sugarcane clones grown in two water and two temperature regimes. Although whole plant assimilation was simulated accurately for most treatments, the model did not provide for the observed clonal differences in response to low temperature. Whole plant partitioning response to water stress and temperature was simulated well when simulated assimilation was forced to measured values. Internode profiles of stalk fibre and sugar storage were adequately mimicked with functions that accounted for growth and development at internode level. A useful platform has been created for testing theories of genetic and environmental control of assimilate production and partitioning at whole plant and phytomer level.

*Keywords:* biomass, expansive growth, internode, model, sink, source, sugar, temperature, water

## Introduction

A simulation model of source-sink processes and biomass partitioning at a phytomer (leaf and associated internode) level could provide a useful link between cell level biochemical models and crop level growth models. This could advance understanding of genetic and environmental control of sucrose accumulation.

A framework for aboveground biomass partitioning between competing sinks (leaf growth, stalk structural growth and stalk sugar storage) is proposed where partitioning depends on temperature, water status and on the physiological age of the phytomer. Also proposed is that these relationships are strongly dependent on genotype through the structural demands (sinks) imposed by the phenological development of leaves and tillers. This hypothesis was translated into a mathematical model and then tested by comparing simulations with observations from two glasshouse experiments.

## Experiments

Net photosynthesis, plant elongation, biomass production (at a plant level) and partitioning (at plant and internode levels) were measured for four sugarcane clones in two glasshouse experiments conducted in the CSIRO Davies Lab tall plant facility (TPF) in Townsville,

Australia. Two water regimes (wet and dry) were imposed in the TPFFEB07 experiment (Inman-Bamber *et al*., 2009), and two temperature regimes (cool - about 19$^{o}$C; hot - about 25$^{o}$C) were imposed in the unpublished TPFDEC07 experiment.

## Model description and calibration

Daily above-ground assimilation was simulated using the radiation use efficiency (RUE) approach, where intercepted radiation is calculated from leaf area (interpolated from measurements) using Beer's law. RUE was taken as a product of a genetically determined maximum value (estimated from TPFFEB07 data), and zero to unity control factors for temperature (derived from Liu and Bull, 2001) and for water status (calibrated on TPFFEB07 data).

Whole plant partition fractions for structural sinks were calculated using a cultivar specific reference value (at optimal temperature and water status) and a cultivar specific response value to water status and temperature deviations from the optima. The cultivar reference values for stalk and leaf structure partitioning were estimated from experimental data and trends. For example, high sucrose (HS) clones partitioned less to leaf than low sucrose (LS) clones, while partitioning to stalk structure did not differ between clones. Temperature control functions were derived from the literature (Robertson *et al.*, 1998; Inman-Bamber, 1994) while water status functions were calibrated using TPFFEB07 data.

Sugar storage in the stalk is calculated as the difference between net assimilation and leaf and stalk structural growth. Whole plant hexoses to total sugars ratio is calculated assuming a linear relationship with the ratio of structural (stalk and leaf) mass to total mass derived from TPFFEB07 data.

Whole plant daily increments of the various pools were divided between the primary shoot and all the other shoots based on the measured ratio in biomass between primary and secondary shoots. Daily primary shoot increments are distributed to individual internodes according to carbon demands for leaf and stalk expansion (cell wall elongation) and stalk densification (cell wall thickening) based on the physiological age of internodes (Rae *et al*., 2005; Lingle, 1999). Carbon demands for these processes are calculated using a Weibull function, which is then normalised relative to the total calculated demand for the stalk.

Distribution of sugar storage to internodes is calculated from storage capacity and current sucrose content. Storage capacity is calculated from the genetic maximum (taken as the highest observed sugar to stalk fibre ratio measured in TPFFEB07), and current fibre mass and physiological age. Maximum sugar storage capacity was assumed independent of genetic and environmental factors. Whole plant hexoses mass is allocated to internodes in proportion to the relative respiration demands of each internode (Bindon and Botha, 2002), with upper and lower bounds of hexoses to sugars ratios of 0.85 and 0.03, respectively.

## Comparison between simulated and observed values

*Whole plant level*

Net assimilation was simulated accurately for most treatments, but was under-estimated for clone 2 (cool and hot treatments) and clone 3 (cool treatment) in TPFDEC07. This suggests that clones responded differently to temperature changes, a feature not accommodated in the model.

The performance of the model in simulating partitioning was investigated by forcing the simulation of assimilation to measured values to enable meaningful analysis.

In TPFFEB07, LS clones partitioned more assimilate to leaf than HS clones in both treatments (Figure 1). Although mean leaf size was smaller and mean leaf appearance rates slower, the higher shoot number presumably led to a bigger demand for leaf structural growth. More partitioning to leaf in LS clones resulted in less partitioning to sugar storage. Partitioning of sugars to sucrose was less, and to hexoses more, in LS clones in both treatments. The model was able to mimic these trends well, as it was semi-calibrated on the data.

In TPFDEC07, partitioning was simulated remarkably well, given that temperature functions were based on past literature. The model gave a good account of how high temperature increased partitioning to structural sinks. Increasing temperature enhanced stalk fibre growth more than leaf growth, resulting in a partitioning shift. This trend was more pronounced in LS clones than in HS clones. The model mimicked this response well for LS clones but could not mimic the distinction between clone types. Sucrose storage responses were clone specific and could be explained by partitioning shifts and assimilation responses to temperature.

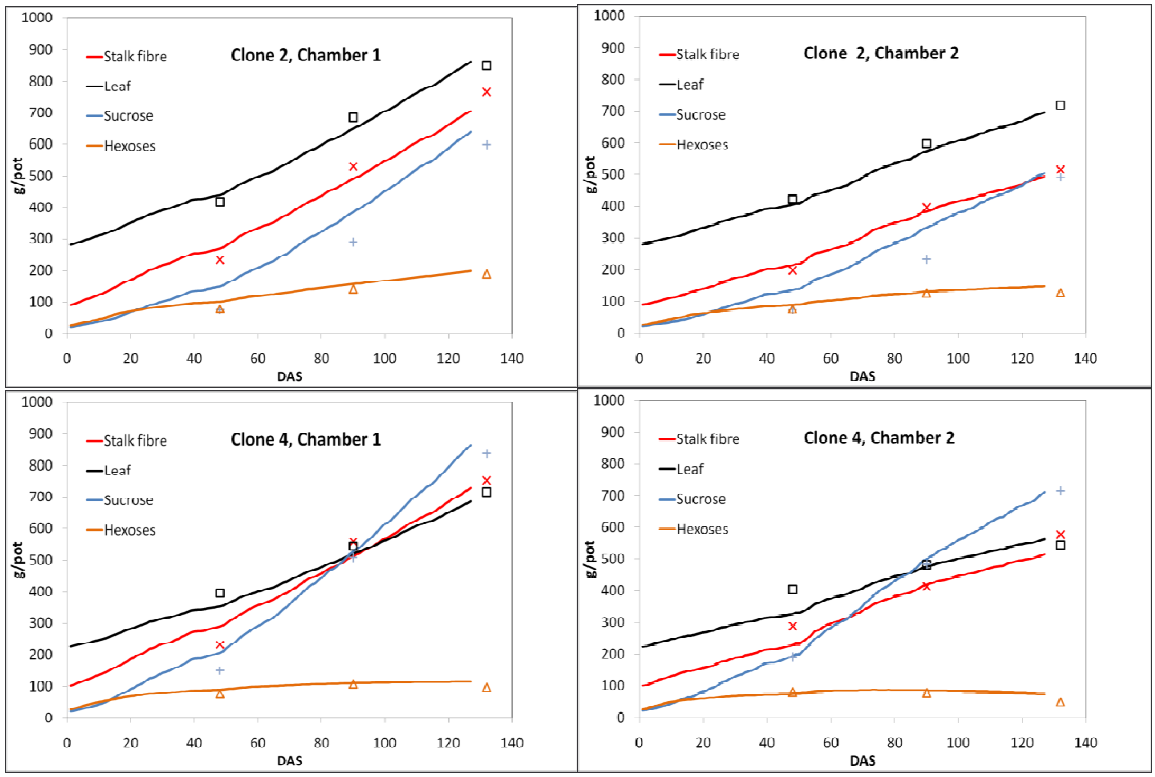


**Figure 1. Simulated (lines) and observed (symbols) leaf mass (□), stalk fibre (X), stalk sucrose (+) and stalk hexoses (△) as a function of days after the start of the treatments (DAS) for clone 2 (low sucrose) and clone 4 (high sucrose) in chamber 1 (wet) and chamber 2 (dry) in experiment TPFFEB07.**

*Internode level*

Simulated values of stalk fibre, sugar, sucrose and hexoses amounts per internode compared well with values observed at the final sampling of TPFFEB07. The model mimicked the unstressed sucrose content profile of the stalk well (Figure 2) and demonstrated the impact of faster maturity rates of HS clones, compared to LS clones. The model was unable to mimic the observed increase in sucrose content of top internodes due to water stress. The partitioning response coefficients therefore need further investigation.

In TPFDEC07, sucrose content of all internodes was over-estimated for LS clones, especially in the hot treatment. This was because of the overestimation of the sucrose pool at whole plant level.

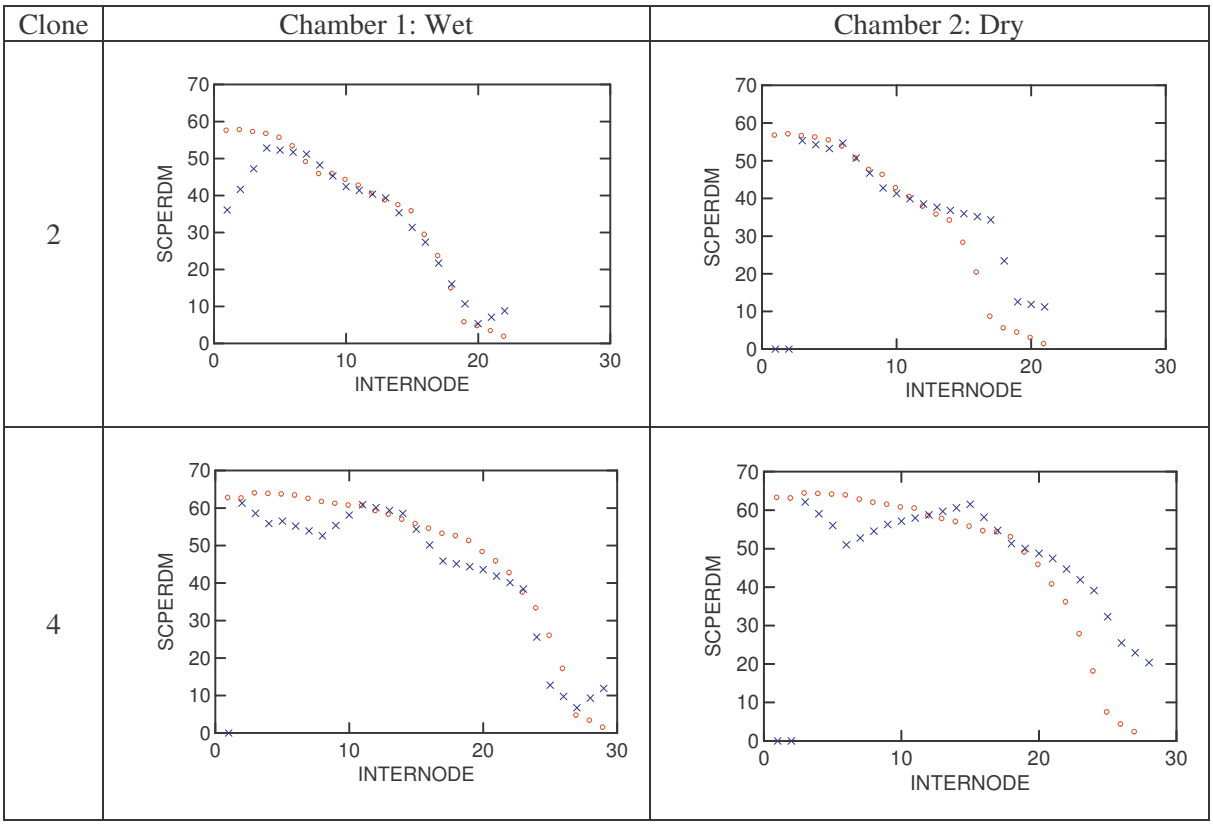


**Figure 2. Simulated (O) and observed (X) sucrose content (dry mass basis) per internode (numbered from the base of the stalk) for a low (2) and high (4) sucrose clone in the wet and dry treatments of the TPFFEB07 experiment.**

## Conclusions

Whole plant net assimilation was simulated well for most treatments. However, the model was unable to simulate the clonal difference in response to low temperature. Whole plant partitioning response to water stress and temperature was simulated well when simulation of assimilation was forced to measured values. Increased sucrose storage was linked to genetic differences in leaf partitioning and hexoses fraction of total sugars. Internode profiles of stalk fibre and sugar storage were adequately mimicked with functions that simulated the processes of cell wall expansion and thickening, and accounted for genotypic differences in rate of maturation. A useful platform has been created for further testing of theories of genetic and

environmental control of assimilate production and partitioning at whole plant and phytomer level.

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