Plant Physiology

ASPECTS OF MODELLING SUGARCANE GROWTH BY COMPUTER SIMULATION

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ABSTRACT

Conventional procedures for increasing sugarcane productivity are providing only marginal increases in yield. Most research into aspects of plant growth has been reductionist and has had little impact on yield improvement programs because the necessary integration has proved too complex. Computer techniques offer a means of integrating basic physiological knowledge into models which simulate plant growth and are capable of highlighting the factors which limit yield.

A conceptual model of cane growth is outlined and the sub-model for photosynthetic production is presented in more detail. Preliminary validation of the sub-model indicates that it is functional and the effects of water stress are empirically simulated as an illustration.

INTRODUCTION

Sugarcane productivity per unit land area is tending to reach a ceiling in most areas of the world despite continued efforts by agronomists and allied scientists. The increased yields expected from breeding, fertilizer application, pest control, etc., are a part of history in most cane regions and future increases in productivity from the conventional approaches are likely to remain marginal. However, despite many hundreds of years of domestication, sugarcane yields remain below not only the theoretical maximum of some 280 tons cane hectare$^{-1}$ year$^{-1}$ (Bull and Glasziou3) but also the practical maximum for a particular region. It is not uncommon in most mill areas to find isolated fields which are capable of greatly exceeding the average yield for the district. Instead of dismissing these fields as freaks they should be accepted as a potential norm for the district. They should be examined in detail so that the factors restricting yields in other fields can be determined. Consideration of the major limiting factors will indicate whether they can be overcome by conventional procedures. It is this analysis of limiting factors which has led us into a program on computer simulation of crop growth to help define the most important factors involved.

Research into plant growth and plant behaviour has mainly been reductionist, that is, plant processes most likely to be important in yield determination are studied in ever-increasing detail. Consequently a great deal is known about photosynthetic pathways, metabolic processes, enzyme kinetics, modes of hormone action, etc., but very little is known about the interactions of these processes in relation to plant growth. The main problem in relating this detailed knowledge to overall plant growth is that the required integration usually exceeds the procedures available. However, the advent of computers has allowed the construction of elaborate models in which data from many levels of plant
organisation can be incorporated to provide an adequate simulation of plant growth.

The term model conjures up mental pictures of scale models of buildings, bridges, etc., used by engineers and architects to facilitate design procedures. Although these models are of little use in biology, the construction of more conceptual models is an integral part of investigations on plant behaviour. Probably the most widely used model in biology involves the statistical analysis of a large amount of data to produce a series of curves or regressions relating to plant responses. Such models are demonstrative in that they present relationships without providing an explanation of the processes involved, and this restricts their usefulness in depicting a dynamic process like crop growth. Analogue computer models, in which the real system is represented by electronic or hydraulic components, are too cumbersome for simulating the complexities of plant growth. The greatest impetus to simulation techniques has followed from the development of both systems analysis procedures for investigating non-linear systems and high-speed digital computers.

All plant growth models endeavour to simulate the production of photosynthate and its allocation to growth, storage and respiration. The research activity on photosynthesis is reflected in the sophisticated models which exist for predicting photosynthesis from data on solar elevation, leaf geometry, light penetration, individual leaf photosynthesis rates, etc. Far less attention appears to have been paid to the processes involved in partitioning photosynthate within the plant. The strategy adopted for model construction is dictated by the reasons for undertaking the model. Consequently, models may vary from the single level approach of Monsi and Murata, which is based on observed patterns of photosynthate distribution, to the multi-level approach of de Wit et al. and Fick and Loomis in which distribution is predicted from the integration of basic physiological data.

METHODS AND MATERIALS

Model construction was based largely on results obtained from our own studies. For this reason the experimental methods used to obtain the results will be briefly outlined. In most experiments plants were grown from single-eye cuttings planted in 9-litre containers of a 1:1 vermiculite-perlite mixture and supplied with a complete nutrient solution. Details of the procedure used for measuring photosynthesis in single leaves attached to the plant have been outlined elsewhere (Bull). In essence an infra-red gas analyser was used to monitor the difference in CO₂ level between the inlet and outlet air ducts of a perspex chamber containing the leaf. Throughout the year, measurements were made on top visible dewlap leaves of plants of different age and of several varieties to establish seasonal variations in the potential photosynthesis rate measured at an irradiance of 1,2 cal cm⁻² min⁻¹.

A similar technique was utilised to measure photosynthesis and respiration rates in whole plants. Plants were placed in a mobile, transparent chamber (90 x 90 x 450 cm high) with air passing through at 1000 l min⁻¹. The difference in CO₂ levels between inlet and outlet ducts was used to measure photosynthesis rates in an airconditioned glasshouse. Respiration rates were measured when the chamber was moved to a dark room at the same temperature. Leaf respiration rates in whole plants were determined by difference. When
whole plant respiration had been established the leaves were removed and respiration due to the remainder of the plant (including root medium) was measured.

Gross daily photosynthesis and overnight respiration were measured in field cane by enclosing 3 m of row in a transparent chamber (150 × 300 × 450 cm high) through which air was circulated at 6 000 ℓ min⁻¹. Measurements were made over days of differing radiation to establish the relationship between daily photosynthesis and nightly respiration.

Growth analysis data were obtained from 15 varieties grown in 9-litre containers placed to simulate field spacing and adequately supplied with nutrient and water. Three replicate plants of each variety were harvested at regular intervals and dry weights determined. Results were bulked to provide an estimate of average variety performance.

**MODEL CONSTRUCTION**

Our main reason for undertaking a model of sugarcane growth is to determine the primary factors limiting crop productivity. Naturally this also involves a recognition of secondary limiting factors which will achieve importance should the primary limitations be removed. It is envisaged that the crop growth model will ultimately be incorporated into an overall industry model capable of improving sugar production.

As a result of these considerations the initial approach to the sugarcane model has been primarily agronomic. This approach has allowed the com-

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**FIGURE 1.** Flow diagram for the conceptual model of sugarcane growth.
plexities of physiological systems to be treated as simply as possible; a procedure further dictated by the dearth of knowledge on many of the systems. The rationalisation necessary to develop the basic outline of a model exposes those areas in which knowledge is deficient and reveals any misconceptions on growth processes. In fact, this is one of the major benefits to be derived from the development of a simulation model. However, the model will often continue to operate if arbitrary functions are inserted at non-sensitive points pending more detailed experimentation.

An outline of the conceptual model is presented as a flow diagram in Fig. 1. This is not meant to be all-inclusive but to serve as a guide for model development based on current concepts. Undoubtedly modification will be required as the model develops. Since photosynthesis is the primary process determining growth the development of a sub-model for photosynthesis was considered first. The flow chart for photosynthesis and preliminary partitioning of dry matter is given in Fig. 2, and includes routines for the development and senescence of leaves. To illustrate the concepts behind this sub-model the components can be considered separately.

**P MAX (potential maximum photosynthesis rate)**

This parameter is derived from leaf chamber measurements of photosynthesis rates in top visible d\_2\_\_\_leaves irradiated at 1,2 calories cm\(^{-2}\) min\(^{-1}\).

![Flow diagram for the sub-model of photosynthetic production and preliminary partitioning of dry matter.](image-url)
FIGURE 3. (a) Seasonal fluctuation in solar irradiation (I) and potential maximum photosynthesis rates (P MAX) of single leaves measured at a radiation flux density of 1,2 cal cm⁻² min⁻¹. (b) Seasonal change in the light response curves of single leaves. (c) Light response for all seasons expressed as a percentage of the prevailing P MAX.
It is difficult to detect a difference in P MAX between varieties grown under non-limiting conditions (Bull⁹) so this value should function for all varieties. P MAX shows a seasonal decline in step with decreasing solar radiation (Fig. 3a). Consequently the current P MAX can be derived from the seasonal radiation regime.

**PHS (actual photosynthesis rate)**

The seasonal reduction in P MAX causes a reduction in photosynthesis at all levels of irradiation (Fig. 3b). However, the decline in photosynthesis at any one light level remains a constant proportion of the prevailing P MAX value (Fig. 3c). PHS can then be derived from P MAX according to the current light regime, degrees of shading in the developing canopy, and level of water and/or nutrient stress.

**P GROSS (gross photosynthate)**

The summation of the products of PHS and leaf area for layers in the canopy gives the gross photosynthetic production.

**R LOSS (respiratory losses)**

Measurements of dark respiration rates (RSP) in leaves of sugarcane have shown a close relation with the previous light regime and, presumably, with previous photosynthesis rates (Fig. 4a). Although the remainder of the plant does not exhibit such marked fluctuations in respiration the overriding influence of the leaves causes a similar response in total plant respiration rate. This is reflected in the general relationship between daily gross photosynthetic assimilation and total overnight respiration measured in field plants (Fig. 4b). McCree⁶ has derived a function for respiration rate in white clover which is dependent upon both gross photosynthetic rate and plant weight. Until more precise information is available to allow such a function to be developed for cane, the respiration rate (RSP) has been provisionally expressed as a constant proportion of the photosynthesis rate (PHS). At present only gross plant respiratory losses are calculated (plant weight × RSP) but it is recognised that this may require revision at a later date.

**P NETT (nett photosynthesis)**

This term indicates the remainder from P GROSS minus R LOSS and is used to bring plant and leaf weight up to date. Until this sub-model is functioning there has been no attempt to partition photosynthate for the separate organs of the plant with the exception of leaf and sheath. At present the partition function for leaf development (PTN) has been entered as a time-varying constant consistent with observed results. Further experimentation should allow this to be altered to a function consistent with leaf demand. Sheath production is envisaged as a constant proportion of leaf development since they are essentially one organ. Sheath photosynthesis is extremely low, usually less than compensation, and has been ignored in this model.

**SEN (senescence)**

Leaf and sheath production is also accompanied by leaf and sheath senescence (SEN) as growth continues. Since leaves and sheaths are components of the same organ a common senescence function is used for both and the nett losses to leaf and plant weight are calculated. During the preliminary stages
of model construction senescence rate has been taken as a function of leaf emergence rate. Although this is inappropriate immediately following germination the discrepancy appears very small.

RESULTS AND DISCUSSION

Perhaps the most pertinent fact emerging from this attempt to construct a model of sugarcane growth is just how little is known about growth processes. The present sub-model was conceived in the light of these deficiencies and was designed to utilize available data where possible. Such an approach has led to a simplistic model which will probably be inadequate in the long term.
Ultimately the detailed information will be available for a more sophisticated approach which will develop as the current concepts are discarded. In the short term, aspects of photosynthesis, assimilate partitioning, respiration, senescence, etc., will require a more detailed examination to validate, or invalidate, the functions adopted in the model.

The sub-model for photosynthesis was tested by comparing its output with harvest data from several varieties of cane grown in 9-litre containers with non-limiting water and nutrient supply. Actual solar radiation values measured during the growth period were utilised in the model and good agreement was obtained between model output and harvest results (Fig. 5). Although simulation of growth under non-limiting conditions appears adequate a further validation of the model will depend upon an accurate prediction of stress effects on growth.

The effect of stress (e.g. water restriction) was empirically examined by entering a 50% reduction in P MAX over 28 days at various stages of growth. Figure 6 illustrates the predicted influence of such a stress, when applied over the periods 42–70, 126–154 or 266–294 days from planting. Yield reduction due to a late season stress (266–294 days) is accompanied by a loss in leaf area and is of the magnitude expected from field results. The drastic decline in final yield predicted from stress during the early stages of growth (42–70 days) appears excessive in the absence of validating experimental data. This example shows that the model incorporates very little provision for "compensatory
FIGURE 6. Predicted effect of applying a 50% reduction in P MAX at three separate periods in the growth of (a) dry matter and (b) leaf area. The indicated stress periods were given at 42-70 (I), 126-154 (II) or 266-294 (III) days from planting.
FIGURE 7. (a) Comparison of leaf:plant and root:plant rates in control plants (O) and plants with half the leaf area or root volume removed (●). (b) Comparison of plant and leaf growth in control plants (O) and plants with half the leaf area removed (●). Plants were 2 months old when leaf or root removal was effected and were grown continually at 30 C with a non-limiting nutrient and water supply.
growth” following stress. Preliminary studies of root and leaf pruning effects on subsequent growth of young plants suggest that the model may be correct and that “compensatory growth” may not be a valid concept. Half the leaf area or root volume was removed from 2-month-old NC 310 plants growing at 30°C with water and nutrients non-limiting. Treated plants rapidly re-established leaf:plant and root:plant ratios similar to those of the control by adjusting the partitioning of photosynthate (Fig. 7a). However, dry matter losses incurred during the recovery period were not recouped and plant and leaf weight remained significantly below control (Fig. 7b).

Apparently the factors controlling partitioning of photosynthate within the plant reduce any significant overshoot in leaf or root growth during recovery from pruning. Consequently there is little opportunity for the pruning-induced deficit to be replaced by “compensatory growth”. Should the prediction of stress effects be valid it is evident that final yield may be far more sensitive to growth conditions early in crop establishment than it is to conditions later in the season.

Although only at a preliminary stage, the proposed model of sugarcane growth has clarified several misconceptions of the processes involved and offers promise in the detection and removal of factors limiting optimum productivity.

REFERENCES

MODELOS PARA LA SIMULACION ELECTRONICA DE CRECIMIENTO DE LA CAÑA DE AZUCAR

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RESUMEN

Los métodos convencionales para aumentar la productividad de la caña están proporcionando solamente los aumentos mínimos de rendimiento. La mayoría de los estudios dentro de los aspectos de crecimiento en las plantas...
fueron reduciendo y produjeron efectos mínimos en los programas para perfeccionar los rendimientos porque la integración fue demasiado compleja. Las técnicas electrónicas ofrecen un método para integrar las concepciones fisiológicas básicas dentro de modelos para la simulación de crecimiento de las plantas y tienen capacidad para acentuar los factores limitadores contra el crecimiento.

Un modelo concepcional para crecimiento en caña se presenta y el submodelo para producciones de fotosíntesis se presenta en mejores detalles. La validez del submodelo indica que es funcional y los efectos de deficiencia de agua se simulan empíricamente para ilustración.