CSIRO PUBLISHING

www.publish.csiro.au/journals/ajea *Australian Journal of Experimental Agriculture*, 2008, **48**, 335–341

Architectural modelling of maize under water stress

Colin J. Birch[A,F], *David Thornby*[A,E], *Steve Adkins*[B], *Bruno Andrieu*[C] *and Jim Hanan*[D]

[A]School of Land, Crop and Food Science, The University of Queensland, Gatton Campus, Gatton, Qld 4343, Australia.
[B]School of Land, Crop and Food Science, The University of Queensland, Qld 4072, Australia.
[C]Institut National de la Recherche Agronomique, Centre de Versailles-Grignon, Unité Environment et Grandes Cultures, 78850, Thierval-Grignon, France.
[D]ARC Centre of Excellence for Integrative Legume Research, ARC Centre for Complex Systems and Advanced Computational Modelling Centre, The University of Queensland, Qld 4072, Australia.
[E]Present address: Queensland Department of Primary Industries and Fisheries, Leslie Research Centre, Toowoomba, Qld 4350, Australia.
[F]Corresponding author. Email: c.birch@uq.edu.au

Abstract. Two field experiments using maize (Pioneer 31H50) and three watering regimes [(i) irrigated for the whole crop cycle, until anthesis, (ii) not at all (experiment 1) and (iii) fully irrigated and rain grown for the whole crop cycle (experiment 2)] were conducted at Gatton, Australia, during the 2003–04 season. Data on crop ontogeny, leaf, sheath and internode lengths and leaf width, and senescence were collected at 1- to 3-day intervals. A glasshouse experiment during 2003 quantified the responses of leaf shape and leaf presentation to various levels of water stress. Data from experiment 1 were used to modify and parameterise an architectural model of maize (ADEL-Maize) to incorporate the impact of water stress on maize canopy characteristics. The modified model produced accurate fitted values for experiment 1 for final leaf area and plant height, but values during development for leaf area were lower than observed data. Crop duration was reasonably well fitted and differences between the fully irrigated and rain-grown crops were accurately predicted. Final representations of maize crop canopies were realistic. Possible explanations for low values of leaf area are provided. The model requires further development using data from the glasshouse study and before being validated using data from experiment 2 and other independent data. It will then be used to extend functionality in architectural models of maize. With further research and development, the model should be particularly useful in examining the response of maize production to water stress including improved prediction of total biomass and grain yield. This will facilitate improved simulation of plant growth and development processes allowing investigation of genotype by environment interactions under conditions of suboptimal water supply.

Additional keywords: functional–structural plant modelling, internode extension, leaf extension, *Zea mays*.

Introduction

Key processes in the development of crop canopies are the extension of the stem, which affects vertical distribution of leaf area, leaf area index and light interception, and ultimately production and distribution of assimilate among vegetative and reproductive growth, thus influencing final yield of crops. Most models of crop canopy production do not consider the dynamics of vertical growth of plants and treat the canopy as a homogeneous entity, providing insufficient detail and resolution to account for plant and canopy architecture (Fournier and Andrieu 1998, 1999). Recently, considerable progress has been made in developing an architectural model of maize (ADEL-Maize; Fournier and Andrieu 1999) and in quantifying processes of internode and thus stem (Fournier and Andrieu 2000; Birch *et al*. 2002) and leaf extension in maize (Birch *et al*. 2007). These additional capabilities introduce functionality into the structural model and, therefore, ultimately to applications in simulation of the effect and efficiency of diverse agricultural inputs, e.g. fertilisers, sowing rates and pesticide application (Room *et al*. 1996, 2000). These studies have contributed important understanding of processes involved in canopy production in maize and provided an analytical framework capable of adaptation to other crops, e.g. wheat (Fournier *et al*. 2003; Evers *et al*. 2005) and rice (Watanabe *et al*. 2005). The capabilities being developed will be increasingly important as agricultural production adopts concepts of enhanced sustainability through site specific management with reduced or variable rate of inputs to accurately reflect local variability in resources and plant performance.

Much of the agricultural land currently or potentially useable for crop production receives inadequate rainfall to meet crop water requirements. Both short-term transient and longer-term water stress limits crop growth and yield. Short duration water

10.1071/EA06105 0816-1089/08/30335

stress events, especially around silking, may reduce maize yield from a potential 5–8 t/ha to 2 t/ha or even cause total crop loss (Westgate and Boyer 1985; Muchow 1989; Meyer *et al*. 1993) and are an important limitation to crop production in the semiarid tropical and subtropical regions of Asia, Africa and Australia. When this occurs during grain filling, crop failure in otherwise well-grown crops can result due to exhaustion of soil water reserves (Grant *et al*. 1989; Muchow 1989). This exhaustion is usually due to unsustainable leaf canopy production and thus transpiration during the vegetative stage coupled with low rainfall during grain filling. This combination of circumstances occurs widely in all semiarid tropical and subtropical regions. Consequently, crop production in these regions is highly variable and in areas of high population pressure (Africa and Asia) contributes to food shortages. Water stress limits crop yield and constrains the areas in which maize can be grown using current technology.

Water stress limits cell expansion and hence stem and leaf growth. The consequent reduction in leaf area (Muchow and Carberry 1989) reduces light interception and thus daily growth, ultimately lowering economic yield. These principles are well established from observation of the final size of organs and the yield of plants grown under water stress, but the dynamics of leaf initiation, appearance and extension, and sheath and internode extension in response to water stress have rarely been quantified. Plants also respond to water stress by changing leaf shape and/or inclination (Trenbath and Angus 1975). The curling of leaf edges reduces the leaf's presentation width (the width of the lamina that is exposed to radiation). Leaf angle of inclination (or presentation angle, the angle between a lamina and the stem) declines, and the rate of senescence increases (Muchow and Carberry 1989).

Study of the dynamics of organ extension will enable the relationship between rate of extension, timing of stress events, and final size and shape of organs to be quantified. This will lead to a better understanding of which organs are conserved (undergo preferential growth), and which are not, during water stress. Further, most crop models use empirically derived 'discount' factors to reduce leaf area production, canopy area, light interception and photosynthesis in response to water stress. Replacing 'discount factors' by functions derived from study of organ response to water stress may improve the accuracy of prediction by crop models making them more useful in research, as well as in strategic and tactical on-farm management.

Most modern-day crop models consider very few parameters or dynamic properties at the individual plant level and focus on the crop on a macro-scale. Such models are analogous to considering the whole crop as a single unit with inputs and outputs. In recent work, Hanan and Hearn (2003) followed a top-down approach, using a higher-level physiological crop model that captures reproductive structure initiation and abortion to drive apical development in a lower-level, individual-based, architectural model of cotton. The work reported here is a first step in extending this idea, investigating the provision of feedback from the individual plant model to the crop model (Hanan 1997), including those that contain water stress adjustments (McCown *et al*. 2002; Muchow and Sinclair 1991). Capturing the three-dimensional (3D) relationships between individual plants and their micro-environment over time, how stresses affect canopy architecture, photosynthetic efficiency, and therefore crop yield, can be investigated.

The aims of this research are to enhance our understanding of the impact of water stress on the production of maize canopy structure and to develop and test an individual-based, structural–functional model of a maize plant under water stress with a view to discovering the effect on dynamic canopy architecture and plant–plant interactions. This paper reports on aspects of the field experimentation and the consequent modification of the model, and indicates the direction of future research to enhance the utility of the modified model.

Materials and methods

The research consisted of a glasshouse experiment and two field trials and further development of an existing model for predicting canopy production using data from one field trial and some data from the glasshouse trial, with remaining data retained for subsequent validation of the modified model.

The glasshouse trial was conducted to obtain data on changes in leaf shape, presentation and inclination due to water stress. Maize plants were grown in 25 cm pots arranged in a 50 × 50 cm pattern with three levels of water supply: non-stressed, moderately stressed and severely stressed. Leaf length, width, shape and presentation angle were measured with a sonic digitiser (Freepoint 3D, Scientific Accessories Corporation/GTCO CalComp, Hertfort, CT) and Floradig software (Hanan and Room 1997).

The field experiments were conducted at Gatton, Australia, on a moderately fertile vertosol (Lawes series) soil (Schafer *et al*. 1986) that had 195 mm plant available water to 1.8 m (Dalgleish and Foale 1998). Populations of maize cultivar Pioneer 31H50 were sown on 10 November 2003 (experiment 1) and 27 January 2004 (experiment 2) into soils that were wet to 1.8 m and were fully irrigated from planting to physiological maturity (both experiments), irrigated until anthesis (experiment 1) and non-irrigated (both experiments). The populations were thinned to produce established plant populations of 7 plants/m^2. Nutrients were applied at rates to ensure non-limiting conditions, and weeds and pests rigorously controlled.

Detailed data on hourly average and daily maximum and minimum air temperatures, vapour pressure deficit, incident radiation, rainfall and evaporation, soil temperature at 5 cm and 1 cm deep, 5 cm above ground, and hourly average temperatures at the plant apex until the apex was 40 cm above ground were collected (as in Birch *et al*. 2002). Plant data were collected by a combination of destructive and non-destructive sampling for crop development stages at emergence (coleoptile visible above ground), establishment (three leaves visible on 75% of plants, tassel initiation as in Moncur 1981). Data included times of tasselling, silking, and physiological maturity, total and fully extended leaf number (including microscopic primordial leaves), leaf lamina and sheath status (extending, fully extended, senescing), visible length of laminae and sheaths, total and presentation leaf width (the latter allowing for rolling of leaves when water stressed), utilising manual and automated data collection as appropriate to the data being collected.

The modelling study used a plant modelling language (Prusinkiewicz *et al*. 2000) developed to provide the capability of simulating 3D structural growth based on L-system (Lindenmayer 1968) specifications at any required level of detail (Prusinkiewicz 1998; Watanabe *et al*. 2005). The first step was to extend the capability of an existing structural functional model of maize, ADEL-Maize (Fournier and Andrieu 1999) to accurately model the impact of water stress on maize canopy architecture. For this, data from experiment 1 was used for parameterisation of the model.

Results

Effective individual leaf area tended to be greater in fully irrigated than rain-grown conditions at 60 days after sowing (Fig. 1*a*). The differences though were not great, as the soil profile was wet to field capacity (plant available water capacity to 180 cm = 195 mm; Dalgleish and Foale 1998) at sowing, and rainfall during leaf production and stem extension. In experiment 1, 90.8 mm was received during emergence to 30 days after emergence (DAE). In experiment 2, the respective rainfall amounts were 140.4 mm and 66.4 mm. Lesser amounts (46.0 mm and 66.4 mm were received from 31 DAE to 60 DAE in experiments 1 and 2. Therefore, water stress only developed in the latter part of vegetative growth. Leaf lengths, except for those near the top of the plant, were mostly unaffected by water regime, though presentation widths of leaves were reduced in the rain-grown treatment, reducing effective leaf area. Internodes above leaf 10 that extended after water supply became limiting in the rain-grown treatment were consistently shorter in the irrigated crop (Fig. 1*b*). Below leaf 10, there was some evidence of unexpected variation in length of specific internodes, e.g. internodes 7–9 longer in rain-grown than irrigated. The reason for this is not clear, and is reflected in total plant height of the rain-grown treatment being slightly greater than irrigated treatments at the time that these internodes were extending. However, internodes higher on the plant and total plant height in data after internode 10 had extended were shorter in rain-grown plants.

Modifications to the model

The major changes were modifications to parameters that control the size of individual leaves and internodes, allowing the simulation of the rain-grown and irrigated plants as observed in the experimental data. At this stage of our research, we elected to take an empirical approach, defining organ lengths directly. Parameters for leaf laminae and sheath length and internode length are specified at the beginning of the model run, depending on which growing condition the user opts to simulate. ADEL-maize has the facility to use either data for each fully expanded organ length or to generate a set of organ lengths given a maximum lamina or internode length, with a relationship between these maximum lengths and the position of a given organ on the plant. Cardinal temperatures in the model for calculation of thermal time were retained. Thermal time is used for schedules of initiation and expansion of leaves and identification of phonological events in crop life.

The key parameters that differ from the original model are: lamina, sheath and internode lengths; maximum number of leaves per plant (and therefore the progressive and final length of the main stem); and the ratio of full lamina width to lamina length. These changes represent both cultivar-specific differences in, for example, parameters describing leaf initiation, appearance and expansion, between the original model and the current iteration, and developmental responses to the different growing conditions experienced at the Gatton field site in general, and between the water supply regimes in particular. Leaves above position 7 on the plant were found to present less than their full width once mature whether water stressed or not. To capture these differences from the original parameterisation of the model, a simple multiplier for width is applied to the calculation of lamina presentation width from lamina length: for irrigated plants, the multiplier is 0.84; for rain-grown plants the multiplier is 0.57, derived from the glasshouse and field experiments; the large difference being attributed to rolling of leaves in water stressed treatments.

An empirical representation of leaf senescence was added to the model. Data on the number of leaves that had senesced were collected from just before silking to physiological maturity. Senescence of leaves commencing near the base of the plant and progressing up the stem was modelled empirically by defining the number of leaves senescing per day for dates where data were collected for the irrigated and rain-grown treatments independently, but only to 80 days after sowing, during which no senescence of upper leaves occurs. The model uses the data

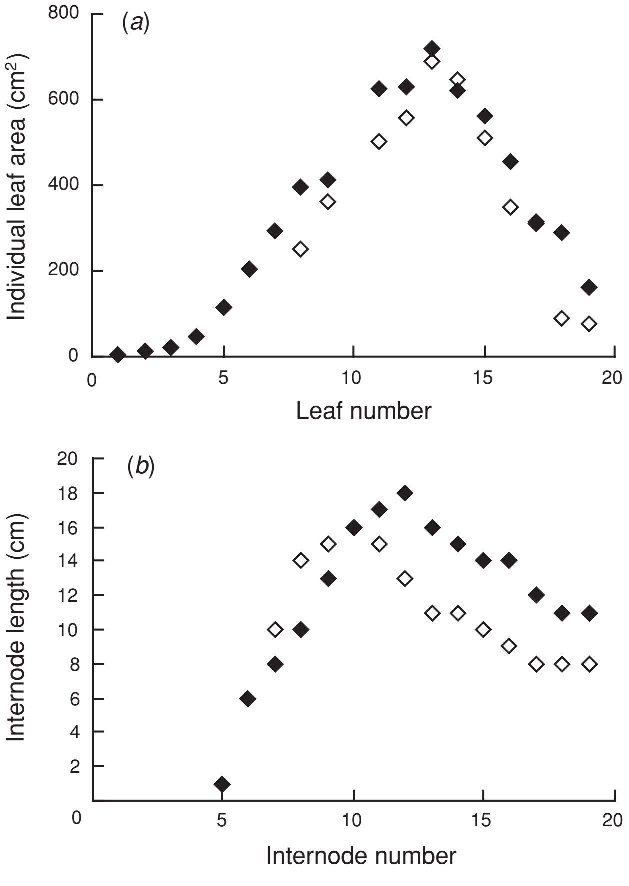

Fig. 1. Median (*a*) effective leaf area (cm^2) and (*b*) internode length (cm) at 60 days after sowing in maize grown under fully irrigated (solid symbols) and rain-grown (open symbols) conditions at 7 plants/m^2 at Gatton, Australia.

to determine which leaf should be removed from the plant on a day. It produces leaf laminae in three sections: a section with a parabolic curve, a section with an elliptical curve and a leaf tip. An angle of bending separates each section. Changes were made to the model to prevent unlikely leaf bend angles occurring by constraining the calculated angles to upper limits such that the angle of any leaf section did not recurve past vertical. The upper limit values were determined by assessment of simulation output.

Observed and fitted leaf area – field experiment

Observed total leaf area production (i.e. accounting for reduction due to senescence) followed the expected increase until anthesis 60 days after sowing in the two treatments that were fully irrigated until anthesis, but in the non-irrigated treatment, maximum leaf area occurred around 10 days earlier (Fig. 2). This was later than expected, as substantial rainfall was received in early December delaying the onset of water stress during the vegetative stage. Fitted leaf areas per plant follow a similar pattern, as they are derived directly from plant leaf area. These show that the model provides an expected pattern of increase in plant leaf area (Fig. 2). However, it has not indicated the earlier occurrence of maximum leaf area in the water stressed treatment evident in Fig. 2 and has expanded leaf area too slowly before 40 days after sowing and then too rapidly to produce final plant leaf areas and leaf area indices close to observed values in both treatments.

Plant height

Fig. 3 shows the progressive increase in observed and fitted plant height (cm), calculated as the sum of internode, peduncle and tassel lengths for the fully irrigated and rain-grown treatments. Plant height continued to increase for several days after full expansion of the flag leaf, as the final internodes and peduncle extended to their full length, and was similar in the fully irrigated and irrigated to anthesis treatment, but rain-grown plants were shorter. As with leaf area, final plant height is reasonably accurately fitted by the model. However, it does not increase sufficiently rapidly early in plant life, but increases very rapidly just before the end of leaf growth around 60 days after sowing to be close to observed values at this time. Subsequent increase in plant height, due to further extension of the upper internodes and peduncle and elevation of the tassel produce slightly taller plants than observed, and is an area of the model that requires attention to confine extension to a period that represents accurately the few days after full expansion of the final leaf during which stem extension continues.

Canopy prediction

The model produced predictions of the canopy at anthesis that were realistic representations of the canopy (Fig. 4*a*, *b*). The visualisations, as expected, are quite similar, as the LAI values in the experimental dataset at tasselling were 5.1 (irrigated) and 4.2 (non-irrigated), both being sufficient for near full light interception. Plant heights are correctly shown as shorter by around 25 cm for the rain-grown crop.

Discussion

This research is focussed on quantifying maize development and leaf area production under non-limiting and limiting conditions of water supply, with the intention of introducing functionality into structural models of maize. In order to introduce functionality into structural models, it is necessary to adequately document rates of processes of canopy production and senescence and quantify the response to water stress. Once these are adequately documented, inclusion of functionality such as light interception, dry matter production and distribution and final yield accumulation can be considered. To introduce functionality, the structural model could be used to analyse components of an existing crop model to assess its accuracy or inform a crop model of daily leaf area, for instance, and then utilise the routines in a crop model to predict dry matter

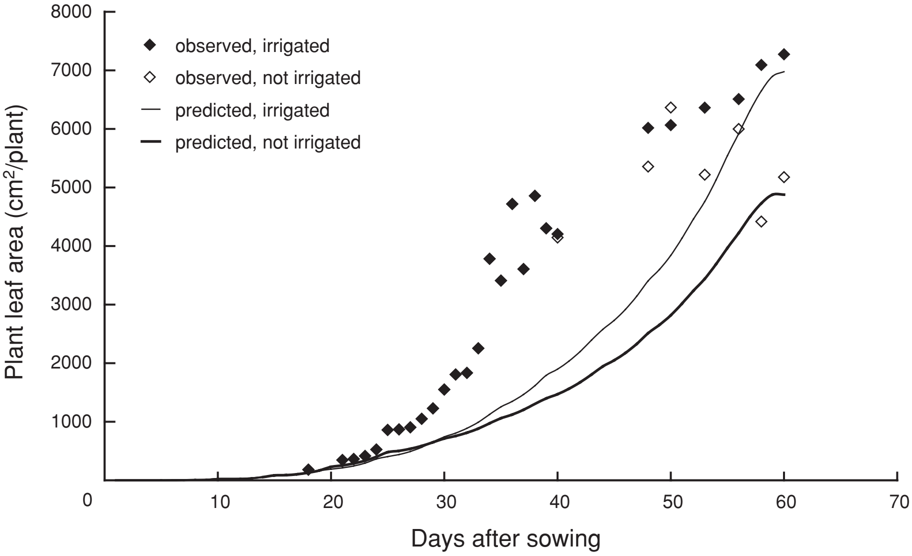

Fig. 2. Observed and fitted total plant leaf area (cm^2/plant) from sowing to the end of extension in maize grown under full irrigation and rain-grown conditions at 7 plants/m^2 at Gatton, Australia.

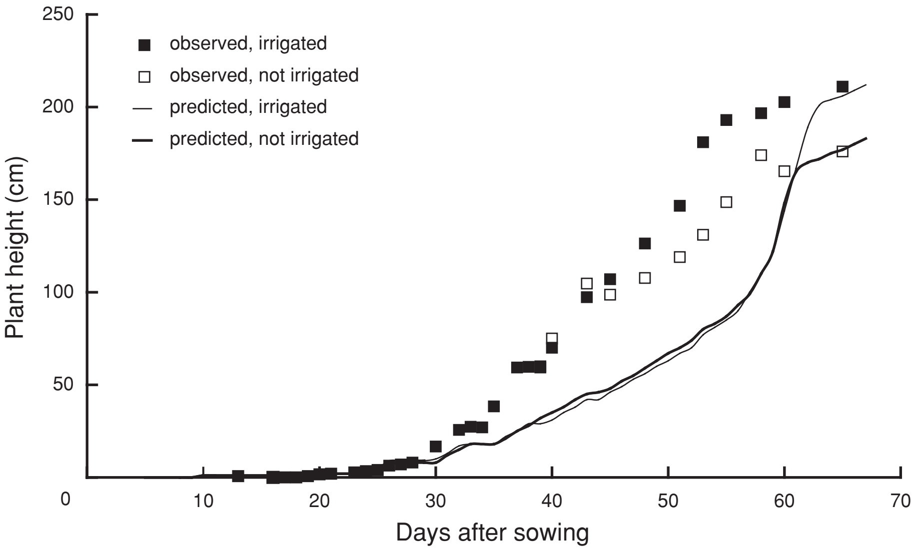

Fig. 3. Observed and fitted increase in plant heights (cm) from sowing in maize grown in irrigated and rain-grown conditions at Gatton, Australia.

accumulation and distribution. Alternatively, the structural model provides the temporal and final structure of plants and functionality, e.g. modelling of growth, calculated by running the model in inverse mode could be used. In inverse mode canopy, structure is modelled as the initial step and functionality imposed later, rather than concurrently (Yan *et al.* 2004). The approach selected will depend on the purposes to which the model is used – essentially analytical for process understanding or predictive for estimating plant productivity.

The virtue of the approach used here is detailed description of how water stress impacts on the structure of the canopy and decorrelation of the effect on light interception from that on leaf photosynthesis. It is evident that the model provides credible terminal predictions of leaf area and plant height, as it should have as final organ size data were provided empirically. Final 3D structure, which is also credible (Fig. 4), is predicted in the model from rates of processes of leaf production and stem extension using protocols for positional relationships of leaves around the stem. In our current research, data on the relative position of one leaf to another on the maize stem was not collected, so the protocols in the model were retained.

This approach makes it possible to simulate the time course of structural development from a final size dataset. In this way, we hope to explore the relationships by which water stress

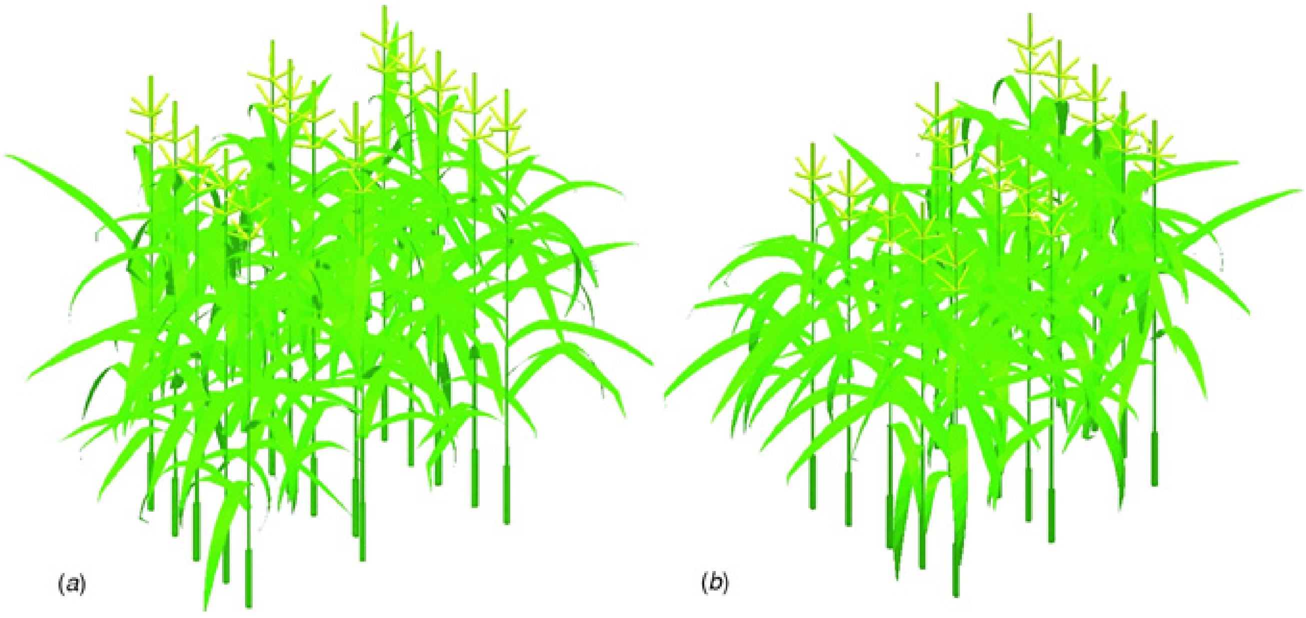

Fig. 4. Visualisation showing prediction of canopies for (*a*) fully irrigated and (*b*) rain-grown maize crop grown at Gatton, Australia (Scale: box height = 3.1 m).

impacts on productivity. However, temporal predictions are not sufficiently accurate to be used reliably in assessing requirements for and effects of agronomic inputs as proposed in Room *et al*. (2000) and Birch *et al*. (2003). It is likely then that one or more functions in the model are producing intermediate variables that are not applicable in environments represented by Gatton or that the mechanisms of the response to water stress are not included at a sufficient level of resolution. The challenge now is to locate the causes of low predictions of leaf area and plant height early in plant life and make the necessary modifications. Changes in rates of processes such as cell expansion and thus leaf and internode extension and leaf rolling will not be constant through the life of the crop, varying according to time of occurrence and severity of water stress. Therefore, it will be necessary to more accurately model these changes in a mechanistic way that accommodates physiological processes rather than take an empirical approach of applying constants as multipliers (as used here for calculation of lamina presentation width from lamina length) and parameter values that do not respond to timing and severity of the stress experienced by plants. For this purpose, crops grown with water stress of varying severity applied for specific periods to examine organ production, extension and expansion will be needed. In the field experiment used for parameterisation in this study, the impact of water stress was limited to later stages of canopy production and stem extension due to rainfall during these processes. Greater effects would be expected had the plants been subject to more severe water stress. Nevertheless, the approach used here has identified areas of the model that need modification – more severe water stress is unlikely to have led to different conclusions, but will be included in subsequent research to relate rates of processes of leaf and canopy production and stem extension to severity of water stress. This work is currently being undertaken under field and glasshouse conditions and will yield results that can be combined with data from experiment 1 to further develop the model. The model will then be validated using data from experiment 2. Also, inclusion of modelling of leaf senescence is necessary. This aspect will be developed and validated in a similar manner.

ADEL-Maize produced acceptable predictions of individual leaf area for maize plants with 16 leaves and a maximum leaf area of 600 cm^2 and provided sound fitted values for dry matter accumulation up to 50 days from emergence for differing populations in France (Fournier and Andrieu 1999). That predictions of cumulative leaf area and plant height early in crop life in the present study were inaccurate (low) while terminal values are close to observed values indicates that one or more plastochron, phyllochron and extension rate are inappropriate. Phyllochron varies with temperature and/or photosynthate supply (Birch *et al*. 1998; Hunt *et al*. 2001; Padilla and Ortegui 2005) and differences among cultivars in phyllochron and plastochron have been reported (Padilla and Ortegui 2005). Initial estimates of plastochron (24.3 and 25.9 degree days) and phyllochron (34.8 and 37.8 degree days) in experiments 1 and 2, respectively, are similar (plastochron) or lower (phyllochron) than those for other tropically adapted cultivars at Gatton (Birch 1996). Taken with the larger plants in this study [22 leaves and maximum individual leaf areas of 720 cm^2 (irrigated)] than in Fournier and Andrieu (1999) referred to above indicates that it is probable that differences in values of parameters describing plastochron, phyllochron and leaf expansion are responsible for trends in fitted values found here. These factors have been found important to the performance of canopy-based models, requiring either specific input or embedded predictive equations to accurately predict them (Muchow and Sinclair 1991; Birch *et al*. 1998) and findings here indicate that similar inclusions may be required in architectural models.

Unsatisfactory prediction of leaf area and plant height early in crop life suggests that constants and equations for leaf expansion and internode extension that are embedded in the model should be examined with more cultivars covering a range of maturity types. Higher linear extension rates for internodes (Birch *et al*. 2002) and phyllodes (laminae plus sheaths) (Birch *et al*. 2007) have been found for maize grown under non-limiting conditions of water supply in Australia (where higher temperatures prevail) than in France (Fournier and Andrieu 2000; Birch *et al*. 2002). Routines need to be incorporated in the model to accommodate these differences that are also related to ordinal and normalised leaf position and total leaf number. The simple procedures used for prediction of peduncle and tassel length need revision to be related to measures of water severity of stress and its duration so modelling can reflect physiological processes. To improve the fitted values and permit assessment of the performance of the model on independent datasets with final leaf numbers ranging from 18 to 24, sensitivity analyses of key constants, coefficients and variables in the model supported by additional analysis of existing data and further experimentation will be conducted in our continuing research. To further the capability of the model, data from the glasshouse trial will be used to provide initial parameters for modelling of the impact of water stress on effective (presentation) leaf width and leaf shape. Values for relative extension rates and linear extension rates of internodes and phyllodes for maize with 20 to 24 leaves grown under water non-limited conditions at Gatton (Birch *et al*. 2002; Birch *et al*. 2007) will also be incorporated in the model, along with daily weather data, including diurnal trends in temperature) rather than the single daily mean temperature currently used. Curvilinear equations for extension of peduncles and tassels will be developed from available and future experimental data. On completion of these steps, the performance of the revised model will be assessed on independent datasets for a wider range of cultivars grown under irrigated and non-irrigated conditions, including the second field experiment referred to here, and data in Madhiyazhagan (2005), Birch (1996), Birch (1991), Karanja (1993) and Birch *et al*. (2007).

References

Birch CJ (1991) Development and yield of selected maize cultivars in the sub–tropics. In 'Maize in Australia – food, forage and grain. Proceedings of the 1st Australian maize conference, Kyabram, Victoria'. (Ed. J. Moran) pp. 50–53.

Birch CJ (1996) Modelling crop ontogeny, leaf area, and dry matter accumulation and distribution in diverse cultivars of maize. Ph D Thesis, The University of Queensland. 258 pp.

Birch CJ, Rickert KG, Hammer GL (1998) Modelling leaf production and crop development in maize (*Zea mays* L.) after tassel initiation under diverse conditions of temperature and photoperiod. *Field Crops Research* **58**, 81–95. doi:10.1016/S0378-4290(98)00087-2

Birch CJ, Andrieu B, Fournier C (2002) Dynamics of internode and stem elongation in three cultivars of maize. *Agronomie* **22**, 511–524. doi:10.1051/agro:2002030

Birch CJ, Andrieu B, Fournier C, Vos J, Room P (2003) Modelling kinetics of plant canopy architecture – concepts and applications. *European Journal of Agronomy* **19**, 519–533. doi:10.1016/S1161-0301(02)00183-1

Birch CJ, Andrieu B, Fournier C (2007) Kinetics of leaf extension in maize: parameterization for two tropically adapted cultivars planted on two dates at Gatton. *European Journal of Agronomy* **27**, 215–224.

Dalgleish N, Foale M (1998) 'Soil matters – monitoring soil water and nutrients in rain-grown farming.' (Agricultural Production Systems Research Unit: Toowoomba, Australia)

Evers JB, Vos J, Fournier C, Andrieu B, Chelle M, Struik PC (2005) Towards a generic architectural model of tillering in Gramineae, as exemplified by spring wheat (*Tricitum aestivum*). *New Phytologist* **166**, 801–812. doi:10.1111/j.1469-8137.2005.01337.x

Fournier C, Andrieu B (1998) A 3D architectural and process-based model of maize development. *Annals of Botany* **81**, 233–250. doi:10.1006/anbo.1997.0549

Fournier C, Andrieu B (1999) ADEL-Maize: an L-System based model for the integration of growth processes from the organ to the canopy. Application to regulation of morphogenesis by light availability. *Agronomie* **19**, 313–327. doi:10.1051/agro:19990311

Fournier C, Andrieu B (2000) Dynamics of the elongation of internodes in maize *(Zea mays* L.): analysis of phases of elongation and their relationships to phytomer development. *Annals of Botany* **86**, 551–563. doi:10.1006/anbo.2000.1217

Fournier C, Andrieu B, Ljutovac S, Saint-Jean S (2003) ADEL-wheat: a 3D architectural model of wheat development. In 'International symposium on plant growth modeling, simulation, visualization, and their applications'. (Eds BG Hu, M Jaeger) pp. 54–63. (Tsinghua University Press/Springer: Beijing, China)

Grant RF, Jackson BS, Kiniry JR, Arkin GF (1989) Water deficit timing effects on yield components in maize. *Agronomy Journal* **81**, 61–65.

Hanan JS (1997) Virtual plants: integrating physiological and architectural models *Environmental Modelling & Software* **12**, 35–42. doi:10.1016/S1364-8152(96)00040-0

Hanan JS, Hearn AB (2003) Linking physiological and architectural models of cotton. *Agricultural Systems* **75**, 47–77. doi:10.1016/S0308-521X(01)00114-7

Hanan J, Room P (1997) Practical aspects of virtual plant research. In 'Plants to ecosystems. Advances in computational life sciences. Vol. 1'. (Ed. M Michalewicz) pp. 28–44. (CSIRO Publishing: Melbourne)

Hunt LA, Yan W, McMaster GS (2001) Simulating response to temperature. In 'Proceedings of a workshop: modeling temperature response in wheat and maize'. (Ed. JW White) pp. 23–29. (International Maize And Wheat Improvement Centre: Mexico)

Karanja DR (1993) The effect of planting date on growth and development of short, medium and long season maize (*Zea mays*) cultivars. MAgrSc Thesis, The University of Queensland. 186 pp.

Lindenmayer A (1968) Mathematical models for cellular interaction in development. Parts I and II. *Journal of Theoretical Biology* **18**, 280–315. doi:10.1016/0022-5193(68)90079-9

Madhiyazhagan R (2005) Modelling approach to assess the impact of high temperature and water stress on dry land maize. PhD Thesis, The University of Queensland, Australia.

Meyer SJ, Hubbard KG, Whittle DA (1993) A crop-specific drought index for corn: II Application in drought monitoring and assessment. *Agronomy Journal* **85**, 396–399.

McCown RL, Keating BA, Carberry PS, Hochman Z, Hargreaves D (2002) The co-evolution of the agricultural production systems simulator (APSIM) and its use in Australian rain-grown cropping research and farm management intervention. In 'Agricultural systems models in field research and technology transfer'. (Eds LR Ahuja, L Ma, TA Howell) pp. 149–176. (CRC Press: Florida)

Moncur MW (1981) 'Floral initiation in field crops. An atlas of scanning electron micrographs.' (CSIRO Division of Land Use Research: Canberra)

Muchow RC (1989) Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment. II Effects of water deficits. *Field Crops Research* **20**, 207–219. doi:10.1016/0378-4290(89)90080-4

Muchow RC, Carberry PS (1989) Environmental control of phenology and leaf growth in a tropically adapted maize. *Field Crops Research* **20**, 221–236. doi:10.1016/0378-4290(89)90081-6

Muchow RC, Sinclair TR (1991) Water deficit effects on maize yields modelled under current and 'greenhouse' climates. *Agronomy Journal* **83**, 1052–1059.

Padilla JM, Ortegui ME (2005) Co-ordination between leaf initiation and leaf appearance in field-grown maize (*Zea mays*): genotypic differences in response of rates to temperature. *Annals of Botany* **96**, 997–1007. doi:10.1093/aob/mci251

Prusinkiewicz P (1998) Modeling of spatial structure and development of plants. *Scientia Horticulturae* **74**, 113–149. doi:10.1016/S0304-4238(98)00084-3

Prusinkiewicz P, Hanan JS, Mêch R (2000) An L-system-based plant modeling language. In 'Applications of graph transformations with industrial relevance'. (Eds M Nagl, A. Schurr, M. Munch) pp. 395–410. (Springer-Verlag: Berlin)

Room PM, Hanan JS, Prusinkiewicz P (1996) Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. *Trends in Plant Science* **1**, 33–38. doi:10.1016/S1360-1385(96)80021-5

Room P, Hanan J, Nolan B, Battaglia R (2000) Pesticide targeting: measuring and simulating effects of plant architecture on pesticide deposition. Insect pest management in sweet corn. In 'Proceedings of workshop no. 3, Bowen Research Station'. pp. 20–25. (Queensland Department of Primary Industries: Brisbane)

Schafer BM, Ritchie AM, Strachan DB (1986) . Soils of the Queensland Agricultural College farm, Darbalara. Queensland Agricultural College Technical Report No. 7. Queensland Agricultural College, Lawes.

Trenbath BR, Angus JF (1975) Leaf inclination and crop production. *Field Crop Abstracts* **28**, 231–244.

Westgate ME, Boyer JS (1985) Carbohydrate reserves and reproductive development at low leaf water potentials in maize. *Crop Science* **25**, 762–769.

Watanabe T, Hanan J, Room P, Hasegawa T, Nakagawa H, Takahashi W (2005) Rice morphogenesis and plant architecture: measurement, specification and the reconstruction of structural development by 3D architectural modelling. *Annals of Botany* **95**, 1131–1143. doi:10.1093/aob/mci136

Yan HP, Kang MZ, deReffye P, Dingkuhn M (2004) A dynamic, architectural plant model simulating resource dependent growth. *Annals of Botany* **93**, 591–602. doi:10.1093/aob/mch078

Manuscript received 6 February 2006, accepted 15 May 2006