

Modelling kinetics of plant canopy architecture – concepts and applications

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Abstract

Most crop models simulate the crop canopy as an homogeneous medium. This approach enables modelling of mass and energy transfer through relatively simple equations, and is useful for understanding crop production. However, schematisation of an homogeneous medium cannot address the heterogeneous nature of canopies and interactions between plants or plant organs, and errors in calculation of light interception may occur. Moreover, conventional crop models do not describe plant organs before they are visible externally e.g young leaves of grasses. The conditions during early growth of individual organs are important determinants of final organ size, causing difficulties in incorporating effects of environmental stresses in such models. Limited accuracy in describing temporal source-sink relationships also contributes to difficulty in modelling dry matter distribution and parameterisation of harvest indices.

Functional-architectural modelling overcomes these limitations by (i) representing crops as populations of individual plants specified in three dimensions and (ii) by modelling whole plant growth and development from the behaviour of individual organs, based on sound models of organs such as leaves and internodes. Since individual plants consist of numerous organs, generic models of organ growth applicable across species are desirable. Consequently, we are studying the development of individual organs, and parameterising it in terms of environmental variables and plant characteristics.

Models incorporating plant architecture are currently applied in education, using dynamic visual representation for teaching growth and development. In research, the 3D representation of plants addresses issues presented above and new applications including modelling of pesticide distribution, fungal spore dispersal through splashing and plant to plant heterogeneity.

Key words functional architectural modelling, plant architecture, modelling, virtual plants

Introduction

The mechanistic modelling of crop canopies aims to simulate plant growth and development as a function of microclimate (Whisler 1986, Weaver 1996). Such models consider the canopy functioning at the level of complexity that depends on the objectives for which the model was built. For example, sound prediction of whole crop canopy leaf area may be adequate for large scale estimation of crop productivity, but does not allow an accurate estimation of vertical distribution of light, photosynthesis or of spatial distribution of materials applied to the plant canopy. Such issues raise the question of canopy morphology, as well as canopy function as a medium to capture light, exchange gases, fix carbon and transpire water.

Canopy morphology and its dynamic (i.e. the kinetics of vertical extension and horizontal expansion of plant parts and the occupation of space between plants) is a significantly under-researched area (Hanan and Room 1996), and not included in most crop models. The vertical dimension may range from a few centimetres to tens of metres in the case of trees, while the interplant space may be occupied by aerial structures of crop plants, companion crop plants or weeds. Also, plant architecture both responds to and determines the physical, chemical and biotic factors to which the plant is exposed (Wilson and Chakrabarty 1998). For example, architectural and hydraulic features of root systems influence water uptake (Doussan et al. 1999), and consequently resources (nutrients) by plant roots, which finally influences root elongation itself.

Plant architectural models have mainly considered empirical laws to simulate 3D development of the structure (Bernston 1992, Prusinkiewicz 1998). That is, they did not consider the influence of plant functioning or environmental variables on the process of morphogenesis. Functional structural models of plant development (virtual plant models) aim to fill that gap, by including physiological processes of plant growth and development as well as the physical structure of plants. This modelling approach is a more recent activity, and can be applied to root systems as well as aerial plant parts

(Bernston, 1992, Hanan and Room 1996, Doussan et al. 1999, Pages 1999). This paper focuses on modelling of aerial plant structures on which most research has been concentrated. However important developments have been made in integrating structural and functional aspects of the root system (Pages 1999). Doussan et al. (1999) developed an 'Hydraulic Tree Model' of the root system and simulated water extraction patterns for plants with contrasting root systems – maize and peach tree, and Bidel et al. (2000) have developed a carbon transport and partitioning model for simulating the dynamics of the root system architecture.

This paper examines commonly used approaches to 'mechanistic' modelling of morphogenesis and functioning of crop canopies, and outlines some of the limitations of these approaches. It then explores some of the central concepts in plant architectural modelling and the application of kinetics of plant canopy production, but not roots, and concludes by outlining some of the applications in which plant architectural modelling is relevant. It does not address the computing aspects used in architectural modelling – comprehensive bibliographies have been provided, for example by Prusinkiewicz (1998, 1999), de Reffye and Houllier (1997) and Barczy et al. (1997). Briefly, L- system (Prusinkiewicz and Lindenmayer, 1991) appeared as the most widely used, apart for the simulation of tree architecture where the AMAP family of software have been used extensively in forestry and agronomy (de Reffye and Houllier 1997, de Reffye et al. 1999).

Existing Approaches

The conventional approach has been to treat the canopy as an expanding homogeneous mass, and to not address the heterogeneous and non – random structural properties of the canopy (de Reffye and Houllier 1997), or model spatial interactions with other organisms e.g. weeds, insects, companion crops. Production of leaf area is usually based on a thermal or real time schedules that consider leaf initiation, appearance and expansion as key processes. They generally do not consider extension of leaves before they are visible externally, or rates of extension after they become visible.

The schedules are usually controlled by constants for intervals for initiation, appearance and expansion of leaves. However, at least some of these ‘constants’ are known to vary with environment and/or genotype, and they are thus only constant within a limited range of conditions. For example, the interval of thermal time between the appearance of successive leaf tips in maize is shorter at low than at high temperatures (Kiniry and Bonhomme 1991, Bonhomme et al., 1991, Kiniry et al. 1991, Birch et al. 1998a). However, the thermal interval for leaf initiation appears constant across environments, at least in maize (Birch and Vos 2000).

Approaches to modelling the canopy include calculating individual leaf area, integrating to whole plant and canopy areas according to plant population density and introducing competition for light at a nominated LAI (CERES approach, Jones and Kiniry 1986). Canopy photosynthesis is calculated using constant radiation use efficiency, without adjustment for distribution of light through the canopy or changes in light spectral composition in the canopy. Further, such approaches rarely consider vertical growth and thus the height of the canopy, although empirical adjustments have been used (Kiniry et al. 1992, Kropff and van Laar 1993, Kropff et al. 1997).

Nevertheless, some adjustments have been made to expand the range of application of these models. For example, Goudriaan and van Laar (1994), calculated photosynthesis for depth intervals in a canopy from simulated irradiance and assumed changes in maximum rate of photosynthesis according to depth in the canopy. This approach provides some capacity to calculate photosynthesis according to local conditions in the canopy, but it does not use a ‘differentiated’ canopy, nor account for differences in maximum photosynthesis according to variations in nitrogen concentration in leaves. However, the effectiveness of adjustments is limited as individual leaves occupy a microenvironment that is variable and leaves are distributed in a non-random manner. Moreover leaf properties adapt to their local environment, for instance Drouet and Bonhomme (1999) found that variations in nitrogen concentration occur accordingly with local variations in

irradiance conditions in a heterogeneous canopy, thus resulting in correlations between photosynthesis capacity and light availability.

Adjustments to account for environmental effects on leaf appearance in maize (Birch et al. 1998a) or to change the basis for calculating leaf area and senescence in maize and sorghum have been made (Birch et al 1998b, Carberry et al 1993). Further, factors that modify photosynthesis according to water and nitrogen supply in the CERES models (e.g. CERES – Maize, Jones and Kiniry 1986), and models derived from them (Carberry and Abrecht 1991, Wafula 1989, Keating et al 1991, Birch 1996) can be refined. However, lack of application to organ growth e.g. of leaves in grasses before they are visible, and thus any effect that early stress may have on final organ size remains. It may, though, be possible to account for the effect of stresses in early growth affecting later canopy characteristics by using time-delayed functions but introducing stress functions without describing the organs they actually apply to can be but empirical. The limitations in describing the effects of stresses early in crop/organ life may explain some of the difficulty in parameterisation of source-sink relationships through concepts such as specific leaf weight, specific leaf area, or harvest index (Birch et al. 1998, 1999, Tardieu et al. 1999).

Most existing modelling approaches use a whole plant as the unit of modelling, and integrate to a full canopy through plant population and competition effects. While this simplification has proved acceptable for agro-ecological studies and yield prediction on an area basis, it does not accommodate plant-to-plant variation and thus is of limited applicability for modelling heterogeneous canopies, and especially multispecies canopies eg crop-weed interactions, companion and intercropping. It is worth noting that in conventional, high input agriculture, enough treatment (e.g. nutrients, water) is used to minimize plant to plant variability. However, emerging sustainable agriculture using reduced inputs will lead to more interest in spatial heterogeneity of soil, economic plants, weeds, plant-pest interaction and stress resulting from limited treatment.

The strength of such models is in advancing understanding of crop adaptation to the macro-environment, in assessing potential for crop production and in agricultural systems analysis. In these applications, processes that occur at the level of individual plants or organs are of secondary or no concern, provided sufficient compensations occur when integrating at the canopy level. These models are used in decision support systems such as WHEATMAN (Woodruff 1992, Cahill et al 1998), PERFECT (Littleboy et al. (1993), and in systems analysis packages such as APSIM (Mc Cown et al. 1996), SWAT (Arnold et al. 1996) EPIC (e. g. Cableguenne et al. 1993, 1995), and that proposed by Adiku (1998) for intercropping of maize and cowpeas. They have also been used for a wide variety of other applications including assessment of the impact of climate change or increased carbon dioxide concentration in the atmosphere (e.g. Stockle et al. 1992a,b, Easterling et al. 1992), and environmental pollution (e.g. Phillips et al. 1993). Further, they are used in education, for teaching plant physiology, crop agronomy and systems analysis (Birch and Rickert 1999).

Plant Architecture Modelling

Aims of plant architecture modelling

Architectural modelling aims to solve the problems of canopy structure and morphology, thus resource use efficiency, by representing crops as populations of individual plants whose structure and development is described in 3 dimensions to varying degrees of realism. At their most detailed resolution, they integrate biophysical processes from organ to canopy level, and provide a framework to model growth of individual plants according conditions at specific locations in the canopy and plant to plant interactions.

The aim of architectural (or morphogenetic) modelling is to produce models that accurately reflect botanical structure and development in both space and time. To do so the model must incorporate botanical 'laws' that explain and define plant growth and form (de Reffye et al. 1988, Kurth, 1994, Lewis 1997, Fournier and Andrieu 1998). When considering the canopy, there are two important and interacting components – the

plants that make up the canopy, and the microenvironment within it, since plants are made up of organs that may be located in quite different microenvironments. Thus, detailed knowledge of temperature and radiation (including light quality) profiles and humidity in the canopy is required, as each is likely to influence one or more processes of canopy production and function.

Requirements for organ initiation and expansion

The models need to describe the rate of production of organs (roots, leaves, internodes, leaf sheaths in grasses, lateral apices, flowers) and the processes that cause the plant to change from one form of growth (i.e. meristematic activity or cell expansion/extension) to another. It is taking plant modelling to a much greater level of detail than the crop models mentioned earlier. However, the detail represents the essentially repetitive modular structure of plants (Jaeger and de Reffye 1992), and specific characteristics of individual species. Thus, data are needed on the initiation of leaves, branches (dicots, trees) and tillers (grasses) and on the orientation, elongation, expansion and senescence of leaves (and sheaths in grasses), internodes and branches to build a three dimensional model of a plant canopy. An example showing the temporal detail of data necessary for describing the dynamics of internode extension is shown in Figure 1. These data have been analysed to describe four stages of internode extension. These are: Stage I, during which elongation is exponential; Stage II – which is short and during which extension rate increases rapidly; Stage III – extension rate is essentially constant and internode length increases linearly; and Stage IV, during which extension rate decreases as the internode approaches its final length (Fournier and Andrieu 2000).

INSERT FIGURE 1

Further, the factors or events that cause change from one form of growth to another (e.g. leaf to sheath to internode in grasses), initiate new organs and/or change organ behaviour need to be resolved. This requires an adequate representation of numerous factors and processes that influence canopy architecture and morphology - these include

physiological processes that lead to the production and growth of individual organs, termination of growth of individual organs, geometry of individual plants, effects of interplant competition on individual plant geometry and photomorphogenesis, and environmental factors that modify plant canopy structure. For example, they must explicitly describe the start, rate and termination of growth of the different organs and modules that comprise the plant. Thus, it is necessary to study in detail the production of individual organs from very early in their morphogenesis (as near as possible to initiation) to organ maturity, their response to micro-environmental factors, and inherent growth and development processes. Also, the pattern of development needs to be taken into account. For example, the fruiting branches of cotton follow sympodial development rather than the more common apical development on the main stem and vegetative branches. To model this phenomenon, it is necessary to specify that each apical bud in a fruiting branch develops into a terminal flower and that continuation of the branch results from development of the axillary bud at each successive node. This results in the characteristic zig-zag shape of fruiting branches (Figure 2).

INSERT FIGURE 2

These factors emphasise the need for having good models of the growth of individual organs such as leaves, internodes and leaf sheaths. Also, there are usually numerous organs that are actively growing at any time, models of organ growth will need to be sufficiently generic for application, if possible, across species. This issue is particularly important with, for example, non-determinate crops and trees that are likely to have numerous branches as well as leaves, and grasses that have tillers, stolons and rhizomes.

Canopy and microenvironment variation

Plant architectural modelling represents the canopy in both temporal and spatial domains, and thus include changes that occur constantly as a result of variations in environmental conditions during their growth (Room et al. 1996, Hanan and Room 1996, Room et al. 2000). Depending on planting pattern there may be substantial horizontal variability in

microclimate, as in row crops (Drouet and Bonhomme 1999). Moreover plants change the microenvironment within the canopy, particularly in the vertical dimension and with time. Plants also adapt to their environment during growth. Thus, it is necessary to consider the regulation of organ development by environmental variables. This has traditionally been by use of temperature, expressed as thermal time, but several other environmental variables also regulate plant behaviour. Among these are light intensity and spectral composition (Myneni 1991), light quality (red-far red ratio) and availability of water and nutrients.

Because plant architecture modelling requires modelling of individual organs, and from that 'growing' the virtual plant, the calculation of thermal time needs to be re-examined. The temperature actually experienced by organs rather than atmospheric (or soil) temperature will be required for assessing thermal duration of intervals in plant or organ ontogeny, thermal thresholds for events in plant development and thermal effects on growth and cell expansion. For example, in maize, a base temperature at the organ level of 9.8°C has been established (Durand et al. 1982, Ben Haj Salah and Tardieu 1996), whereas 6-8°C have been widely used in crop modelling. This emphasises the need to consider specific temperature conditions affecting specific organs, as average atmospheric temperature is unlikely to be accurate. For grasses, in which the growing point (apex) remains below ground for some time (e.g. in maize, until about 10 leaves are visible, Stone et al. 1999), soil temperature is likely to be more appropriate than air temperature, at least until after the apex emerges from the soil. After that, organ temperature will depend more on air temperature, but may differ from it because of canopy characteristics, thermal characteristics of plants and thermal conditions near the soil surface. As apex temperature or temperature of other organs is rarely measured directly, predicting them from environmental and plant variables may be possible. For example, Cellier et al (1993) and Guillioni et al. (2000) present detailed models of the apex temperature in maize, but such models are not as yet available for a wide range of species.

Considerable research effort has been directed towards understanding the microenvironment of the canopy of both single and mixed species canopies, the latter requiring understanding of both spatial structure and reaction of one plant to another (Kurth 1994). Examples include simulation of distribution and/or transfer of photosynthetically active radiation in a poplar stand (Myneni 1991), forest (Kurth 1994), maize (España et al. 1998, Drouet and Bonhomme 1999), soybean (Meyer et al. 1984), and faba bean (Diaz-Ambrona et al. 1998). Also, Chelle and Andrieu (1999) presented radiative models for architectural models of plant canopies, and explored their application to crop modelling, with particular reference to maize.

Given the diversity of information required to be integrated in functional architectural modelling, it is, of necessity, a multidisciplinary activity involving among others, environmental physicists, plant physiologists, agronomists, mathematicians and computer scientists to ensure the realism and applicability of architectural models (e.g. Barthelemy and Caraglio 1991 Jaeger and de Reffye 1992, Kurth 1995)

Some achievements in architectural modelling

Plant architectural modelling is most developed for tree/forest applications (e.g. example Host et al. 1990, Barthelemy and Caraglio 1991, Prusinkiewicz et al. 1994, Kaitaniemi and Honkanen 1996, Kurth 1994, 1995, de Reffye and Houllier 1997, Perttunen et al. 1998) but is being applied, at least at the analytical level, to herbaceous and low stature plants (e.g. peas – Gould et al 1992, kiwi fruit – Smith et al. 1992, cotton – Room et al. 1995, 1996, pasture legumes – Wilson et al. 1999, Gautier et al. 2000, faba bean - Diaz-Ambrona et al 1998, maize - España et al. 1998, Fournier and Andrieu 1998, 1999, sweet corn – Room et al. 2000) and agroforestry (Oldeman 1992). Oldeman (1992) argues that architectural modelling of agroforestry is the most complex, because of the potential number of species and rotations possible, and the concurrent presence of short and long term plants (e.g. annual crops and trees).

An example of a functional architectural model is ADEL-Maize (Fournier and Andrieu 1999), that has been successfully used to model interplant competition in maize (Fournier and Andrieu 1999) (Figures 3 a,b,c). Figure 3a shows the realism of the simulation, and Figures 3b and 3c respectively the simulated reduction in leaf area of individual leaves and the variability in individual plant dry weight that occur as plant population density increases. Also, significant progress has been made in developing a functional architectural model of sweet corn including application of pesticides (Figure 4 (later) Room et. al. 2000), and some aspects of grain sorghum (Kaitaniemi et al. 1999).

INSERT FIGURES 3a, b, c

Applications of Architectural Modelling

Though architectural modelling is relatively new concept, a diversity of applications has been identified (Room et al. 1996). In summary they relate to theoretical, research, educational and practical aspects of crop production that are affected by canopy geometry as well as crop physiology. This paper will not attempt to address all of the possible applications, but rather expand on a some examples.

1. Virtual plants as research tool

(a) generating hypotheses

Virtual plants are useful for generating hypotheses and thus focussing research onto the most important relationships. This is a generic attribute of all kinds of models (e.g. Penning de Vries and Rabbinge 1995, Bouman et al., 1996, Hanan and Room 1996). In the case of architectural models, it applies at a particular level of spatial resolution – that of organs within a canopy. Many more scenarios of for example, plant to plant variability, fate and impact of inputs such as pesticides applied within the canopy, can be examined at much reduced cost by modelling than is possible in real field, laboratory or controlled environment experiments. Plant recovery from the effects of grazing animals can also be examined. Research can be undertaken with 3-dimensional computer models that

otherwise is expensive or destructive, or even impossible (for example some aspects of tree or forest research) because of the very long life cycle of trees (Kurth 1994). The effects of pruning on the canopy and canopy recovery in forests or orchards and vineyards is an obvious example where architectural modelling would be helpful (Le Dizez et al. 1997).

(b) Modeling light microclimate and canopy reflectance

Architectural models provide an accurate description of the canopy structure through the geometric description of each plant organs using polygons. This geometric information enables accurate simulations of radiative transfer using either commonly used models based on the turbid medium (TM) (Myeni and Ross, 1991) or using more recent models called surface-based models. The TM models consider the vegetation as a continuous medium, where the foliage is statistically described by parameters, such as the leaf area density and the leaf angle distribution. These parameters may be calculated from the 3D structure generated by an architectural model. Surface-based models calculate directly the radiative exchange between the surfaces produced by an architectural model (Chelle and Andrieu, 1999).

As the surface-based models use an exact description of the canopy structure, they are interesting to study the physics of the light-vegetation interactions (Chelle et al. 1997, Espana et al, 1998). Results from such studies may be used to improve modeling using the TM approach (Kuusk et al, 1997, Shabanov et al, 2000). Also, they are helpful in studying ecophysiological processes. For example in photomorphogenesis, a good description of the light signal is needed so the plant response can be described. For remote sensing applications, the better understanding of the effect of the canopy structure on reflectance allowed assessment of the meaning, thus interpretation, of data gathered by satellites (Lewis, 1999, Espana et al, 1998).

The use of explicit canopy structures to simulate light enables estimation of light distribution. However new questions arise – for example (i) how detailed the geometric

description of organs needs to be, and (ii) the level of error arising from using static structures to simulate the behavior of a real canopy, where plant organs move mainly due to the wind or solar tracking. As an example, Espana et al (1999) showed that a crude description of the maize leaf by a small set of planar polygons is sufficient for light simulation.

2. Virtual plants as an educational tool

As education is becoming progressively more resource limited (Birch and Rickert 1999), more efficient means of teaching plant physiology, ecology and agronomy are required. Some progress has been made in this area through using decision support and crop simulation models, but these are not ‘purpose built’ for educational purposes. Students need exposure to sufficient examples to develop understanding of the underlying processes, and so ‘construct’ knowledge for themselves (Bouchard et al. 1995). This is most readily achieved by making the models interactive, and thus more interesting. Architectural models offer specific advantages as the model presents objects - plants, leaves, internodes. These are much more readily accessible than LAI, leaf angle and distribution. Visualisation by use of computer graphics makes learning more enjoyable, as well as assisting interpretation of results. Plant architectural modelling software is becoming very interactive, and thus it is easy to test the effect of changing parameters – an essential part of the learning process. Importantly, this software is now able to be run on lap-top computers, so learning is not constrained to formal sessions and fixed locations.

3. Plant production

Plant production is a complex activity involving many routine tactical decisions. These decisions are almost invariably made in an environment of considerable uncertainty, and thus methods for predicting the outcomes of alternative options are desirable. We now propose some areas where functional architectural modelling may be used to make such predictions.

(a) Population density, planting time and cultivar selection.

These three aspects of plant production interact to produce the canopy. From an architectural modelling perspective, population density is obviously important, but the optimum density depends in part on planting time and cultivar selected. The appropriate combination is needed to allow completion of the crop life cycle while conditions, especially temperature, are favourable, and to produce a canopy that optimises light interception. However, additional considerations are optimising water use and the control of competition from weeds. These issues often interact and give rise to many potential solutions to be assessed. Canopies function as a light intercepting volume and as a diffusion route for water. The functions are often difficult to reconcile – a large leaf area is desirable for light interception and to suppress competition from weeds, but a large leaf area can lead to exhaustion of limited water supplies. Architectural models could explore many more plant population densities, planting times and cultivar selections than is possible by field trials for a wider range of environments. They could be combined with long term rainfall data to examine risks of failure or risks of stress at specific time in plant development associated with particular options. This application is similar to that proposed by Muchow et al (1991) for crop models, but applies at a different level of resolution, and can conceivably assess local variation. However, success in this application will depend on accuracy of modelling the canopy, and this ultimately depends on accuracy in modelling leaf number, the temporal production of leaf area and its senescence. Further, for water limited environments, equally accurate models of water supply and extraction will be needed, implying the need for functional architectural models of root systems.

(b) Pest management

Functional architectural models have been identified as a tool for use in research and extension in pest management (Room et al. 1997, 2000). A key question in management of insects and diseases is the surface concentration of pesticides on leaves. The rate of

application per hectare is of little consequence, since much of the pesticide is delivered to non-target locations e.g. soil, off site, plant parts not affected by the target pest, is wasted and becomes an environmental contaminant (Pimentel et al. 1980). Further, as leaves bearing pesticide expand, the surface concentration declines, rapidly reaching sub-lethal levels. Also, new leaves that will have received no pesticide are quickly generated and are at risk of immediate attack by pest organisms. There is a dual problem here – attack of new leaves, and receipt of sub-lethal doses by pests that attack leaves expanding at the time of pesticide application. This latter situation must often result in selection for resistance, in which the most susceptible individuals in the pest population are killed, leaving the less susceptible to complete their life cycle, increasing the population-level of resistance in the next generation. It is here that architectural modelling, and the kinetics of canopy production in particular could be very useful for predicting surface concentrations of pesticide to assist planning of pesticide applications. This should reduce reliance on repeated population assessment and provide the opportunity for proactive rather than reactive decisions.

A second important aspect of pesticide application is canopy penetration, to control insects and diseases located within the canopy. Importantly, modification of the microclimate by the canopy influences disease outbreak and insect behaviour (Wilson et al. 1999). Specific examples include diseases that attack the lower part of the canopy where relative humidity is higher, insects that attack the silks and ears of maize and sweet corn, and insects and diseases that attack fruit located within the crown of a tree or the canopy of crops e.g. bolls of cotton. This aspect is currently being studied with sweet corn in Australia, with promising results being achieved (Figure 4).

INSERT FIGURE 4

(c) Nitrogen management. Nitrogen is a major input to the production of field and horticultural crops and pastures, and a potential environmental contaminant when used inefficiently by plants. For example, radiation use efficiency and thus plant growth is related to area nitrogen concentration (g/cm^2) in leaves of maize (Muchow and Davis

1988, Vos et al. 2000), which in turn is influenced by the local light environment (Drouet and Bonhomme 1999). Thus the dynamics of leaf area production become important to prediction of concentration of nitrogen in leaves. Limited nitrogen supply does not greatly affect leaf appearance rate or reduce leaf area until nitrogen supply is severely limiting but does reduce photosynthetic rate (Vos et al 2000). This behaviour could be incorporated in architectural crop models, to predict when nitrogen supply limits plant growth. Clearly, robust procedures to model soil nitrogen transformations and uptake are necessary involving architectural modelling of the root system (e.g. Doussan et al. 1999, Pages 1999).

(d) Fungal spore dispersal in a canopy

Fungal infections depend on the arrival of spores in the canopy, and subsequent redistribution within the canopy, and knowledge of canopy geometry will assist in predicting the severity of disease outbreaks. Further, it would assist in assessing the microclimate in the canopy, since it is microclimate that determines the survival of spores, and their germination and infection of plants. The presence of free water or the extent of raindrop or irrigation droplet splash, needed to disperse some spores could also be predicted from canopy geometry (St Jean et al. 2000).

Conclusion

This paper has provided an outline of the concepts of functional architectural modelling of the dynamics of plant canopies. It is clear that large quantities of data are required for successful architectural modelling, and incorporation of functionality, as distinct from the purely descriptive, in the models. To meet these needs, more extensive data that is more precise than usually collected is needed. Consequently, the development and evolution of architectural models depends on substantial additional data becoming available on the dynamics of production of individual organs of plants and canopy expansion. Inherent in this requirement is the need to provide data on plant interaction in single or multi-species stands. It is also evident that architectural modelling is a multidisciplinary activity,

involving at least environmental physicists, plant physiologists, agronomists, mathematicians and computer scientists that can be applied to all forms of plant production. Uses to which architectural models mirror those of widely used crop models, but at a greater level of resolution than possible with models that are designed to operate at population and canopy rather than individual plant level. Architectural models will be used to investigate aspects of plant production and management that involve detail of the vertical and horizontal characteristics and variability of the canopy. They will also be used for investigations and assessments of issues such as insect and disease status and management in a canopy.

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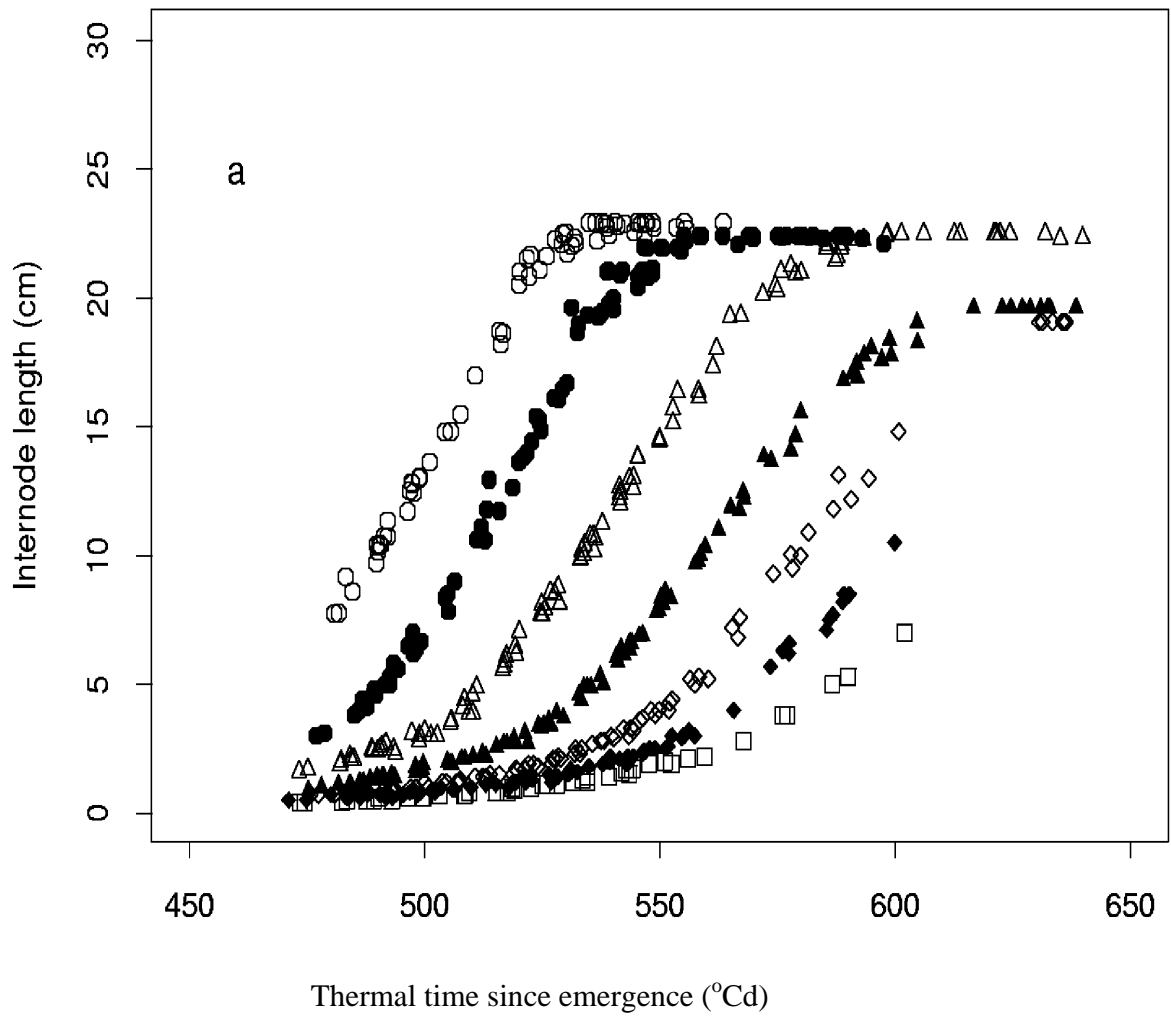


Figure 1. Thermal time course of internode lengths (cm) for internodes 9 to 15 of maize, cultivar Dea grown at Grignon, France (base temperature = 9.8°C) (Source: Fournier and Andrieu 2000).



Figure 2. Virtual cotton fruiting branch showing sympodial development and a flower bud, an open flower, and a developing boll.

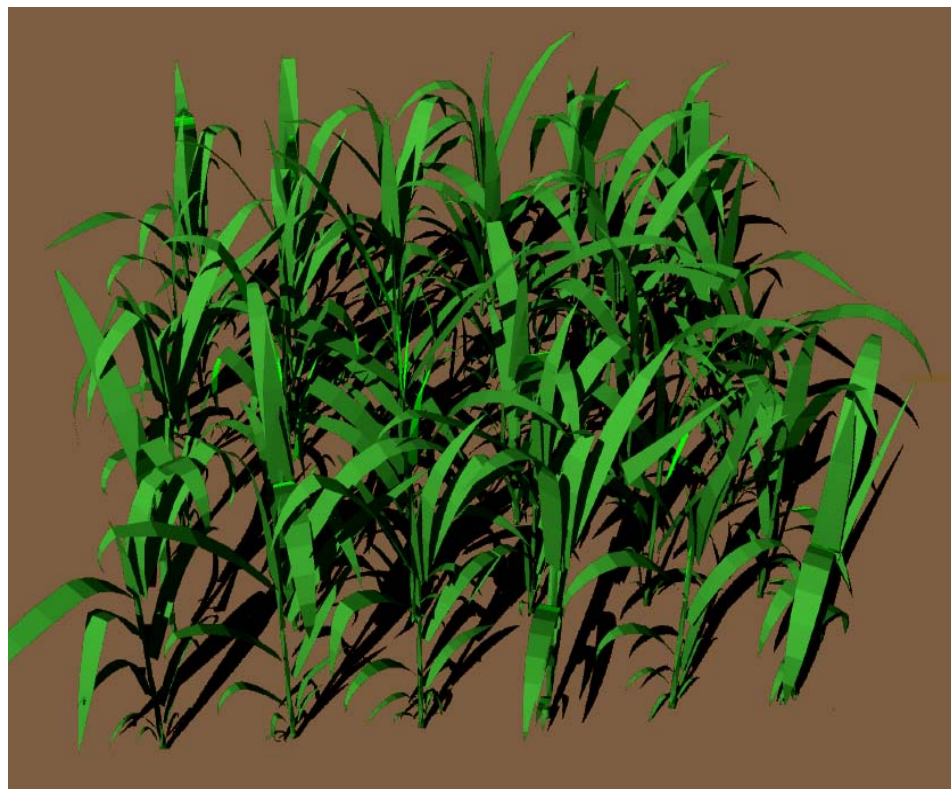


Figure 3a. Results of simulation studies with ADEL –Maize (a). pictorial representation of a simulated maize canopy using ADEL maize

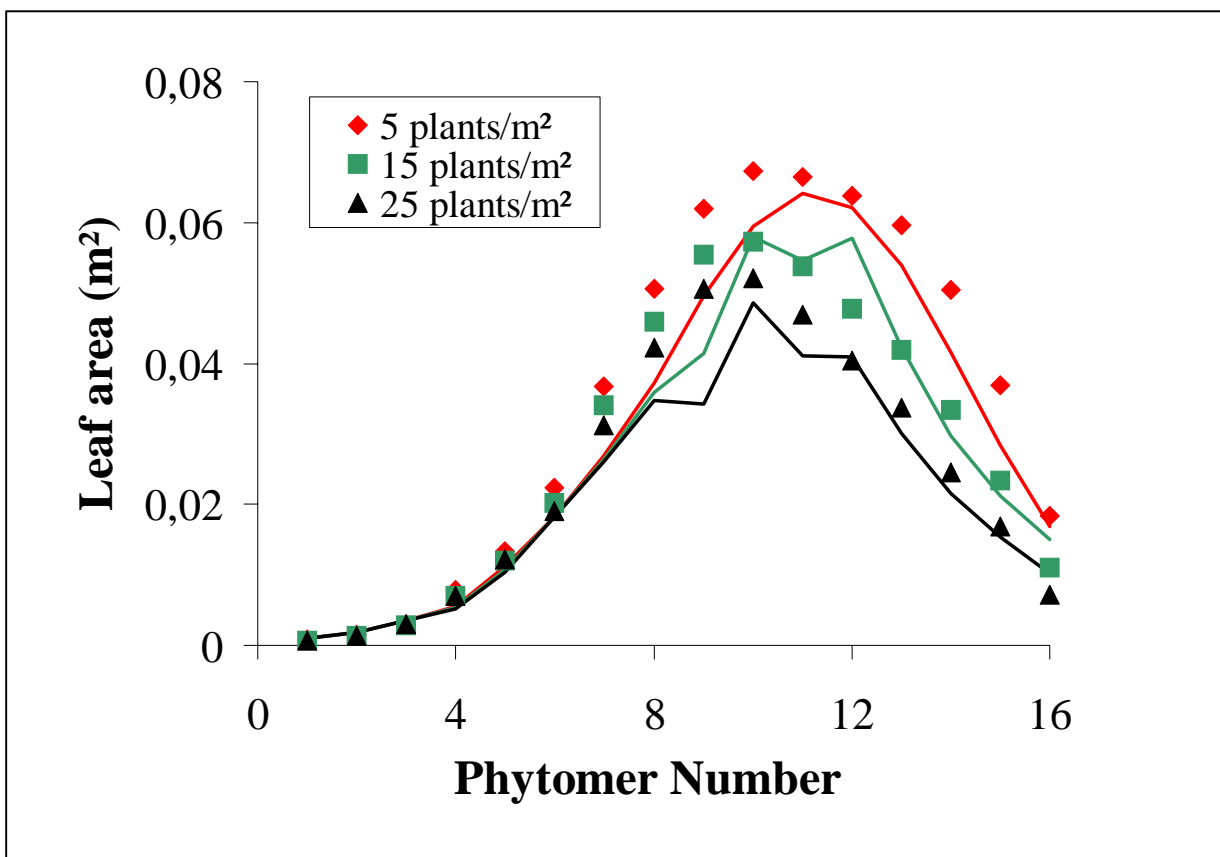
Figure 3b Simulated leaf area (lines) for maize at 5,15 and 25 plants m² (symbols)

Figure 3c Simulation of differing accumulation of plant dry matter by individual plants in a heterogeneous canopy.

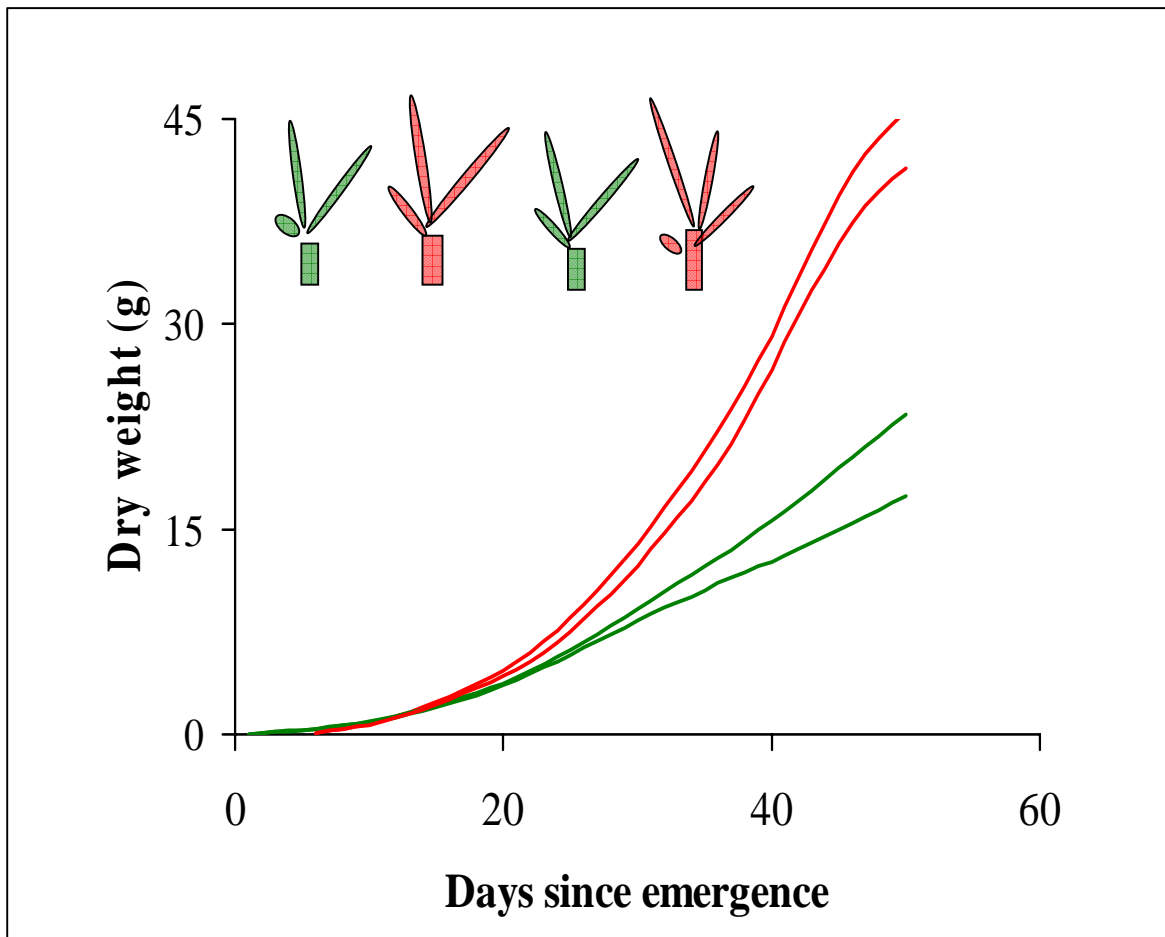




Figure 4. Virtual sweet corn canopy: views along furrows (left) and across rows (right) during a simulated pass of spray droppers having 2 nozzles each side. Spray is not shown beyond the midline of the nearest row of plants.