Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists

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Abstract

A new phase is under way in the study of how plants interact with their physical and biotic environments. Tools are becoming available for handling three−dimensional (3−D) information on the development and growth of individual plants and activities of the organisms which live on them. These tools will lead to in−depth understanding at the level of plant architecture, intermediate between what goes on at the level of plant cells and physiology and the level of plant stands and biomass. Existing fields of study will be enhanced and new fields opened. Here, we explain why these developments are important and how they are taking place.

Reference

Peter Room, Jim Hanan, and Przemyslaw Prusinkiewicz: Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. *Trends in Plant Science* vol. 1, pp. 33−38.

software reviews

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A new phase is under way in the study of how plants interact with their physical and biotic environments. Tools are becoming available for handling three-dimensional (3-D) information on the development and growth of individual plants and activities of the organisms which live on them. These tools will lead to in-depth understanding at the level of plant architecture, intermediate between what goes on at the level of plant cells and physiology and the level of plant stands and biomass. Existing fields of study will be enhanced and new fields opened. Here, we explain why these developments are important and how they are taking place.

Structural dynamics of plants

Plants are modular organisms adapted for gathering the diffuse resources of light, CO_2, water and nutrients from 3-D space. The constantly changing architecture of a plant is crucial in determining the outcome of interactions with its environment. In addition, the architecture of a plant at any time constrains future development by defining the numbers and positions of meristems[1]. Despite such obvious significance, and although considerable progress has been made in understanding the temporal dynamics of plant parts largely stimulated by Harper[2] and White[3], the spatial dynamics of plant parts remain comparatively unexplored[4]. The main reason has been great difficulty in obtaining and manipulating information on 3-D positions while the numbers and positions of plant parts are constantly changing.

These constraints have been overcome by recent advances in computer technology. Now, 3-D positions can be measured easily and the rules of morphogenesis which generate plant architectures can be determined. These rules can be used to create 'virtual plants' – computer simulations of the structural dynamics of individual plants in 3-D space. Virtual plants will have many uses (Box 1) and should be especially valuable when interfaced with models of plant physiology and models of herbivores and plant pathogen activity. Animated examples of virtual plants can be seen on the World Wide Web (http://www.cpsc.ucalgary.ca/projects/bmv/vmm/animations.html).

The nature of virtual plants

A virtual plant is generated from a model which consists of explicit rules for structural dynamics. The rules may be restricted to the dynamics observed in a constant environment or may be more comprehensive and incorporate conditional responses triggered by environmental variations. As well as structural development and growth, the rules may represent such processes as wilting, compensation for damage, etiolation, tropisms, physical degeneration, senescence and abscission. A virtual plant may simulate a whole plant or parts of a shoot or root system. It may represent a single real plant whose morphogenetic rules have been derived from measurements, the average of several real plants, or a hypothetical plant. Multiple virtual plants may be generated simultaneously to explore 3-D spatial phenomena involving members of a stand.

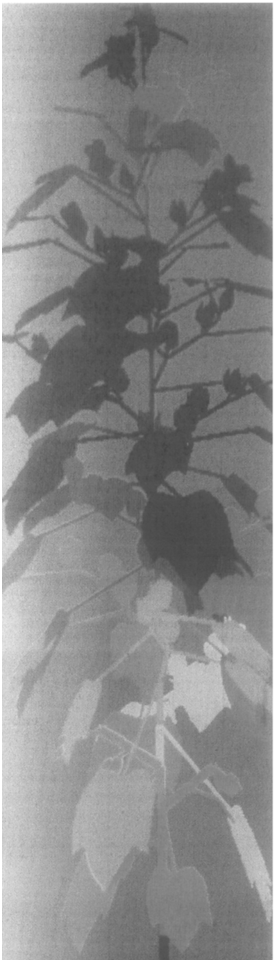
The architectural attributes of a virtual plant can be output as numbers, positions, sizes, surface areas, angles of attachment, ages and topological connections etc. of different plant parts. If the host computer has the necessary graphics capability, these attributes can also be summarized as images (Figs 1, 2) but a virtual plant is *not* just a computer-generated image. Such an image is 'a' model in the sense of being a representation of a plant at a particular instant but it is not 'the' model in the sense of the set of rules which generates a sequence of developmental stages and responses to environmental conditions.

Virtual plants are not restricted to simulating what can be seen from the outside of real plants. They can incorporate any measured or hypothetical process which is influenced by the topology or geometry of plant architecture. For example, movements of metabolites, hormones, induced defensive chemicals, systemic pathogens or systemic pesticides can be simulated in relation to morphogenesis and visualized as false colours or symbols. Independent simulations of external processes can be interfaced with virtual plants to represent the arrival of light, pathogens, damage, pesticides or the movement of insects over plant surfaces.

Rules of morphogenesis

The architecture of a plant can be considered as the product of repeated application of rules that control the appearance of new parts and the growth, senescence and shedding of existing parts. For example, the following rules might be implemented in each time-step:

(1) Each apical bud becomes an internode one unit in length bearing a leaf one unit in length, an axillary bud and an apical bud; the phyllotactic angle is 180°, the



Box 1. Practical uses

Virtual plants are expected to have applications in research, education/extension and decision-support in connection with:

Management of crop pests: Improved definition of action thresholds through simulation of interactions between plant architecture, pesticide deposition, insect movement and feeding, and plant compensatory growth.
Biological control of weeds: Identification of combinations of weed architecture and types of damage caused by herbivores and pathogens that interact effectively to limit weed populations.
Management of pathogens: Improved understanding of disease dynamics through simulation of pathogen deposition and growth on plants whose growth modifies microclimates.
Plant breeding/genetic engineering: Specification of target 'designer plants' by identification of architectures optimal for interception of light, lodging resistance, harvestability, damage compensation etc.
Agronomy: Exploration of competition for space/resources at the level of single shoots, roots and individual plants, both intraspecific and interspecific (relevant to intercropping, sowing rates, control of weeds).
Horticulture and forestry: Identification of optimal pruning strategies through simulation of compensatory growth responses.
Grazing: Identification of optimal strategies for the timing and intensity of grazing to maximize compensatory growth by pasture plants.
Insect behaviour: Improved understanding through simulation of insect movement, feeding etc. on dynamically growing plants.
Developmental biology: Exploration of how information in genes gives rise to integrated 3-D structures (emergent properties of simple rules).
Fire: Predictions of 3-D arrangement of fuel and combustibility; pruning strategies to minimize tree contact with power lines.
Remote sensing: Improved interpretation of images through exploration of effects of architecture and leaf orientation on reflectance.
Landscape architecture: Simulations of the interactions between plants and buildings.
Entertainment: As components of games, films and educational software.
Art: Exploration of the aesthetics of growth forms, realistic and imaginary.

angle between successive internodes is 10° and the branching angle is 25°.

(2) Each axillary bud becomes an apical bud.

(3) The length of each internode and leaf increases by 0.5 units until they reach an age of 4 time-steps.

(4) Each leaf is shed when it is 4 time-steps old.

This set of rules will give rise to an alternately branched structure (Fig. 3) when starting from a single apical bud. Continued elongation of internodes when they are no longer at the apex of a shoot causes the geometrical positions of distal nodes to change in each time-step. In nature, it is common for some rules to have priority over others under certain conditions. This allows major transitions to occur, such as from vegetative to reproductive growth when a plant experiences a particular photoperiod or reaches a specific age. Some rules seem to be deterministic while others appear to be stochastic within limits.

The architecture of a plant is an emergent property of its morphogenetic rules, and the complexity which can be generated by simple rules is at first surprising. Conversely, it is very satisfying that complex behaviour and structure can be condensed into a relatively small set of rules and it is in this idea that the major value of virtual plants probably lies. By collapsing apparently diverse 3-D dynamics to their underlying rules, we may be able to identify patterns which have broad theoretical and practical significance.

Visualization

People are best at detecting patterns in complex information when it is presented in visual form. Virtual plants can be regarded as part of the current revolution in scientific visualization made possible by the increasing power and decreasing cost of computers[5]. Visualization combined with simulation is particularly appropriate for plant morphogenesis because of the repeated application of rules: a small error in a rule becomes magnified by repetition, causing visualizations of a virtual plant to look increasingly 'wrong' as a simulation progresses.

It is very difficult to predict and understand the architectural consequences of particular rules by any technique other than simulation combined with visualization. This is even more true for processes superimposed on dynamic plant architecture, such as movement and feeding of herbivorous insects and their natural enemies, or invasion by plant pathogens.

Obtaining rules of morphogenesis

Morphogenetic rules are worked out by inspection and measurement of real plants. An initial approximation of the rules is usually made by retrospective analysis of the structure of mature or well developed plants. Feedback from inspection of images of virtual plants generated from preliminary rules often leads to rapid improvements. More detail is then obtained from time-series measurements of real plants receiving different experimental treatments. The frequency of measurement and levels of detail measured and simulated depend on the questions it is hoped to answer. As in any experimental study, preliminary work is needed to decide such things as treatment levels and numbers of replicates. If the behaviour of plants in stands is of interest, growth must be measured in stands. This ensures that the resulting morphogenetic rules incorporate shoot responses to light reflected from nearby shoots[6] and root responses to resource depletion by nearby roots[7].

The practical use of virtual plants in research has been made possible by 3-D digitizers developed for the film and engineering industries. Rather than attempting to measure lengths and angles of plant parts with callipers and protractors, the 3-D coordinates of significant points can now be determined to accuracies of less than 1 mm by any of several types of digitizer. Some have an articulated arm that incorporates potentiometers to measure angles between arm segments. The position of a pointer at the end of the arm is calculated from these angles and the lengths of arm segments. Other digitizers use magnetism, sound (Fig. 4) or light to determine the position of the end of a probe.

We have written software which runs on a personal computer to facilitate efficient digitizing of plants of many different architectural types followed by calculation of the lengths and orientations of plant parts. Morphogenetic rules for rates of growth, maximum sizes, changes in orientation, longevity and other parameters are then obtained by grouping results according to the type, position and age of parts in a database and performing analyses with a commercially available statistics package.

Building virtual plants

Morphogenetic rules may be expressed directly as computer code in a unique program written for each plant[8] and flexibility can be enhanced by allowing implementation of the rules to be controlled by input parameters[9]. Alternatively, the rules may be formulated in a plant modelling language and used as input for an interpreter program. We express rules as L-system[10] productions (Box 2) which are read and interpreted by the program pfg (plant and fractal generator[11]). This program can simulate morphogenesis of shoots and roots of single or multiple individuals of any plant from an alga to a tree so long as it is given the appropriate L-systems. The program can also simultaneously interpret L-systems representing processes or organisms moving through or over the structure of virtual plants and can make the interpretation of any rule dependent on environmental conditions being modelled separately.

A virtual plant exists as a string (Box 2), an array[12] or other data structure which is updated at each time-step of a simulation according to morphogenetic rules. The data can be further processed in a variety of ways to produce output which can be summarized in tables or graphs or used to construct images. Images can be produced by pfg which are schematic or as detailed and realistic as the information in a simulation allows (Fig. 1). The images may be viewed from any angle by manipulating them using a mouse and a series of images can be displayed to give the impression of time-lapse photography.

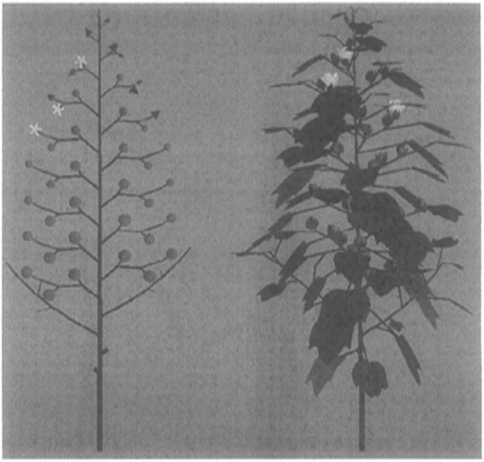


Fig. 1. Virtual cotton: schematic and realistic images.

Performing virtual experiments

As with any simulation modelling, a virtual plant can be used to predict performance under circumstances not represented in the data on which it was based. Prudent users will first verify that models can reproduce the observations from which they were derived and will validate performance against observations made under some different sets of conditions. Some of the infinite number of sets of other conditions can then be explored through simulation by manipulating parameter values. If the results look interesting for a particular set of values, real experiments can be used to investigate further. This is a powerful way of homing-in on critical questions and minimizing the amount of costly, real experimentation.

To take a simple example, it might be of interest to know if the lengths of petioles found in a real plant are those which result in the most efficient interception of light. Virtual experiments could be used to investigate whether longer or shorter petioles might result in reduced self-shading, perhaps leading to a new target ideotype for plant breeders. More complex scenarios might involve searching for better timing of sprays to minimize use of pesticides. Attack by pests results in altered plant architecture which modifies in turn the probability of future attack, the searching efficiencies of natural enemies and the way pesticide droplets will be distributed. Many more permutations of spray timings, patterns of insect activity and expressions of genetically engineered resistance could be explored by simulation than would be feasible with real experiments.

Virtual experimentation can be made particularly easy by running plant models in an appropriate software environment such as the virtual laboratory in botany (**vlab**[11]). A user of vlab can change parameters such as growth rate, branching angle

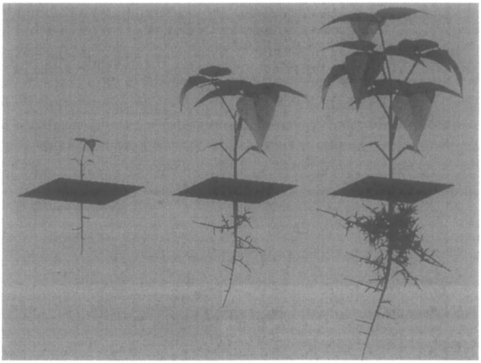


Fig. 2. Virtual bean: three stages of growth showing roots and shoots.

Fig. 3. Results in time-steps (1), (3) and (5) of implementing the four morphogenetic rules given in the text.

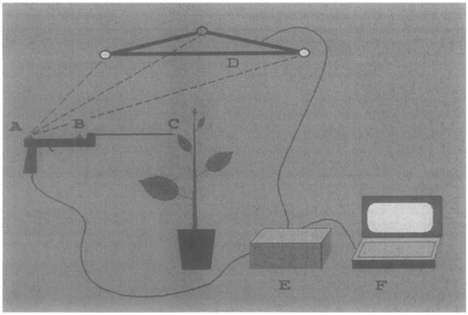


Fig. 4. Sonic digitizing: when the trigger of the gun is pulled, the processor (E) fires sound emitter A followed by emitter B. The processor converts into distances the time taken by sound to travel to each of the three microphones (D). These distances and the lengths AB and BC are used to calculate three-dimensional coordinates for the end of the pointer (C) whose line of sight to a microphone may be obscured by parts of the plant. The coordinates are recorded by the portable computer (F).

or leaf longevity and see the effects by simply clicking on sliders displayed on the screen (Fig. 5). The vlab also facilitates construction of plant models by allowing easy access to all the necessary software tools; it maintains a filing system of virtual plant models based on how they are related to one another through progressive modification and it files hypertext notes with each model. If required, multiple simulations to investigate numerous permutations of parameters can be run as batch jobs.

Examples of virtual plants

As early as 1971, the static 3-D structure of branched trees had been simulated and images of top- and side-views produced[13] but the structures did not develop and grow. Perhaps the first, true, virtual plants were models of *Aster novae-angliae* produced in 1974 (Ref. 14).

Once more sophisticated software had been developed in the 1980s for simulating branching growth and visualizing the results, virtual plants ranging from grasses to herbs, cotton and coffee bushes, palms and trees were produced[9,11,15]. Generic root simulators were created[16] and evolutionary contests between different branching patterns of shoots were played out[17]. Most of the underlying models were built by trial-and-error until images produced from them bore a close visual resemblance to real plants. Few were based on extensive measurements until 3-D digitizers became available[18–20].

Most of the work to date has focussed on the development of simulation techniques and on simulating morphogenesis observed under a single set of environmental conditions. Now, significant effort is going into allowing virtual plants to respond to changes in environmental conditions[21]. An important step will be to interface virtual plant models with existing crop models which calculate durations of developmental stages and rates of growth from environmental inputs. A generic interface is being constructed to allow appropriate parameter values to be passed between crop and virtual plant models with minimal reconfiguration of the models (R. Sosic and J.S. Hanan, pers. commun.). To facilitate this, it has been necessary to enable virtual plants to operate in condensed real time rather than the more usual physiological time scales based on units of development[22]. A number of issues remain to be resolved, most of them relating to spatial resolution. For instance, although most crop models simulate partitioning amongst different types of plant parts, they do not specify allocations according to topological or geometrical positions. Virtual plant models will complement crop models by allowing visualization of simulation results and by allowing resource acquisition to be adjusted for changes in plant architecture.

Box 2. L-Systems

L-systems allow specification of how an object transforms from one state to another, sometimes adding new parts, during an interval of time. Particular plant parts in particular states are represented by symbols and the process of transformation is expressed as morphonenetic rules or 'productions' which resemble equations except that an arrow is used instead of an equals sign. For example, some of the rules used to generate Fig. 3 can be expressed as follows when 'A' represents an apical bud, 'B' an axillary bud, 'L' a leaf, 'F' a unit length of internode and '[]' enclose a branch:

We start with an apical bud: A.
The following productions are then implemented in each time-step:

A → FL[B]A	(each apical bud becomes an internode + leaf + axillary bud + apical bud).
B → A	(each axillary bud becomes an apical bud).
F → FF	(each internode doubles in length).

In successive time-steps, the virtual plant is represented by:
Step (1) FLA
Step (2) FFLFL[B]A
Step (3) FFFFLFFL[A]FL[B]A
Step (4) FFFFFFFFFFFFFL[FL[B]A]FFL[A]FL[B]A
Other symbols, not shown for the sake of clarity, are used to represent angles and line widths, while another production controls leaf shedding. The basic concepts described here have been extended considerably to allow representation of phenomena such as continuous rather than discrete-stepped growth and control of rates by external influences such as temperature. These extensions are beyond the scope of this article and have been described elsewhwere[11,24,25].

The future

Even using digitizers, measurement of real shoot systems is labour-intensive. Happily, several technologies hold the promise of much quicker and easier data acquisition. An inertial guidance microchip mounted at the tip of a probe could eliminate the current requirement for fixed sensors and unimpeded line of sight to sensors from emitters on a probe. A more significant advance will be the development of systems which use 3-D scanning, tomography and image analysis to identify key points and measure their 3-D coordinates. These systems will need to use lasers, X-rays, micro-radar, confocal optics or similar approaches to 'see' right through a plant canopy without significantly affecting the physiologies of target plants and organisms living on them. Nondestructive measurement of root systems presents considerably greater difficulty, though it is possible that nuclear magnetic resonance scanning might provide a solution[23].

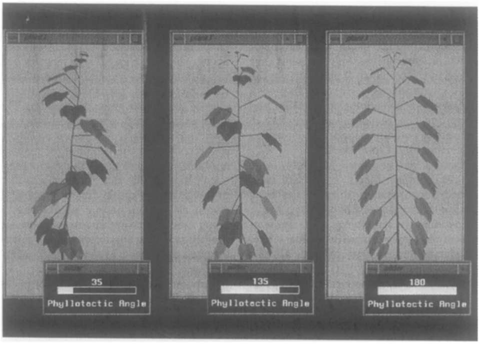


Fig. 5. A virtual experiment: the spiral angle between successive leaves was changed by clicking in different places on the slider bar.

Another constraint is the need for manual derivation of morphogenetic rules from measurements of real plants, and research is under way into automating this process. For example, it should be possible to develop software that generates L-system productions from statistics calculated from measurement data. It might also be possible to use genetic algorithms to derive by iteration L-systems that generate virtual plants that fit measurement data.

If a virtual plant accumulates many parts, is a member of a stand of virtual plants or is interfaced with simulations of insect movement, very large numbers of calculations must be performed in each time-step. Such simulations take a long time to run on small computers or a shorter time on large computers. If visualizations are desired, graphical projections from a 3-D virtual plant to a 2-D screen take even more time. Today, virtual-plant software having a high degree of biological realism needs the power of a workstation to run simulations in seconds rather than minutes, but this is about to change. Advances in hardware and 3-D graphics environments suggest that personal computers are likely to be on sale from about 1998 at a combination of price and power to give most plant scientists access to virtual plants. Further into the future, parallel processing should result in very significant improvements in performance because, as in real plants, much of the activity in virtual plants takes place in parallel.

Beyond research, virtual plants will become very valuable tools for teaching students, farmers and others how plants react to environmental conditions. Video sequences or interactive simulations will be included in computer aided learning (CAL) packages to illustrate plant dynamics, such as responses to pruning, which are very difficult to convey in any other way. Similarly, decision-support packages will be enhanced so that farm managers can see how their plants will develop if alternative agronomic or grazing practices are applied.

To stimulate international collaboration in virtual plant modelling, we intend to make our digitizing, pfg and vlab software available through the Internet early in 1996. We have a vision of scientists in many countries accessing each other's models through the Internet, making improvements or cultivar-specific adjustments, followed by making new versions of the models available to the international community. In such a scenario, the vlab will become a global virtual laboratory in botany.

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book reviews

Metabolic plasticity

Environment and Plant Metabolism: Flexibility and Acclimation
edited by N. Smirnoff
Bios Scientific Publishers, 1995. £60.00 hbk (270 pages) ISBN 1 872748 93 7

This book, with 13 chapters authored by a total of 29 individuals, covers topics concerning the responses of aspects of metabolism to experimentally manipulated changes in environmental factors. Included among the topics are: different aspects of photosynthesis (five chapters, including responses to water stress, temperature and UV-B radiation, the relationship between carbon and nitrogen assimilation, and the regulation of malate synthesis); the major classes of compatible solutes that are involved in the response of plants to physiological water-stress (three chapters); adaptations to phosphate deprivation and anoxia; and the responses of enzymes to temperature and antioxidants under different environmental conditions.

Whereas, as the editor suggests, large areas of photosynthesis have not been included, more than a third of the book directly concerns aspects of photosynthesis. For instance, it struck me that the syntheses of the major compatible solutes, proline, glycinebetaine and polyols, all use reducing power (NADPH) from photosynthetic electron transport – the synthesis of any of these compounds might therefore serve as a sink for electrons under conditions of water or salinity stress, when carbon dioxide availability is greatly reduced.

The book is, by and large, a very readable and up-to-date treatment of plant adaptation and acclimation to different environmental factors in the areas listed above. One of its greatest strengths lies in the numerous references to recent studies that have used transgenic plants with altered levels of gene expression. These studies have led to progress in our understanding of the role of different metabolites and enzymes in the acclimatory responses of plants, although many questions remain open. It is likely that further significant progress will be made during the next few years, as the numerous plants that are being modified using antisense constructs, greatly reducing the expression of particular gene sequences, are employed in future studies.

Advanced students of plant physiology and plant ecophysiology, as well as researchers and teachers in these areas, should find the book to be of great value. My knowledge in some of these areas has already benefited considerably, and I have shared information with students in my class. Furthermore, results discussed in several of the chapters have stimulated