Self-assembling Plants and Integration across Ecological Scales

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• *Background and Aims* Although individual plants exhibit much complex behaviour in response to environmental stimuli, they appear to do so without any identifiable centres of organization. We review a special class of model with the aim of testing whether plants can effectively be self-assembling, modular-driven organisms, in the sense that whole-plant organization and behaviour emerges solely from the interactions of much smaller structural elements. We also review evidence that still higher-level behaviour, at the population and community levels of organization, can emerge from this same source.

• *Methods* In previous work we devised a special cellular automaton (CA) model of plant growth. This comprises a section depicting a two-dimensional plant in its above- and below-ground environments. The whole plant is represented by branching structures made up from identical 'modules'. The activity of these modules is driven by morphological, physiological and reproductive rulesets derived from comparative plant ecology, a feature which lends itself to experimentation at several ecological scales.

• *Key Results* From real experiments using virtual plants we show that the model can reproduce a very wide range of whole-plant-, population- and community-level behaviour. All of these properties emerge successfully from a ruleset acting only at the level of the CA module.

• *Conclusions* The CA model can, with advantage, be driven by C-S-R plant strategy theory. As this theory can ascribe a functional classification to any temperate angiosperm on the basis of a few simple tests, any community of such plants can be redescribed in terms of its 'functional signature' and the net environment that it experiences. To a valuable first approximation, therefore, a C-S-R version of the CA model can simulate the most essential properties both of natural vegetation and of its environment. We have thus achieved a position from which we can test a plethora of high-level community processes, such as diversity, vulnerability, resistance, resilience, stability, and habitat-community heterogeneity – processes which, if investigated on the scales truly required for a full understanding, would fall beyond the practical scope of even the largest real-life investigation.

Key words: Self-assembling plants, cellular automata, vegetation dynamics, L-system, population, community, emergent properties, biodiversity.

INTRODUCTION

Although individual plants are distinct entities exhibiting behaviour typical of all complex organisms (preferential placement of food-gathering organs, differential distribution of biomass as a consequence of environment, interactions with other organisms at their own and higher levels of organization), they have no identifiable centres of tactical, as opposed to strategic, control. Within the strategic limits set by its genetics, it appears possible that a plant's tactical behaviour is emergent solely from the resource-handling properties of its constituent organs. A new class of model, the self-assembling cellular automaton (CA), now makes this hypothesis testable.

Preceding investigations into emergent topology have been in the domain of L-system models. These can produce topographically correct images (Lindenmayer, 1968; Room *et al.*, 1994; Room and Prusinkiewicz, 1996) that are photo-realistic and three-dimensional. Their spatial rules of growth are based upon 'real' plant morphology. L-systems can be made environmentally sensitive, such that the structure of the plant is influenced by the space that it occupies; these models are referred to as 'sighted' (Borchert and Honda, 1984; Bell, 1986; Ford, 1987; Sutherland and Stillman, 1988). Other types of virtual plant models can simulate population dynamics but usually ignore explicit plant–plant interactions (Mech and Prusinkiewicz, 1996). These mathematical representations of individual plants interact with one another under the control of a further, supervisor model.

Unlike CA, L-systems need complicated rulesets in order to generate realistic plant topologies. However, the botanical and ecological processes included in these rulesets serve purely to create the desired endpoint, a photo-realistic image. Topology and form are at the heart of L-system rule-bases; botanical, and certainly ecological, issues play a secondary role to visual ones.

In order to use CA to investigate our premise that individual plants exhibit no identifiable centre of organization, we needed to model at the same modular level as that addressed by L-systems. Simpler, 'chequerboard' spatial CA modelling (e.g. Colasanti and Grime, 1993) would not do. However, the emphasis of our methodology had

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to be the opposite to that of L-systems–it had to be led by botanical rather than by topological features.

The model which has delivered the results reviewed in this paper is a self-assembling plant CA that incorporates such a combination of methodologies. Our modelling (Colasanti and Hunt, 1997*a*, *b*; Colasanti *et al.*, 2001) is grounded in the extensive experimental observations on real plants reported by Grime *et al.* (1997). The models are thus well placed to examine whether the individual-, population- and community-level behaviour observed in real plants could be due solely to patterns resource acquisition and utilization at the modular level, thus determining the ecological status of the plant. The test for success of the self-assembling plant model is, of course, to compare the behaviour of real and 'virtual' plants. If the self-assembling plants are able to reproduce natural plant behaviour from simple, 'bottom-up' rulesets equally well, or even better, than assumptions involving complex, 'top-down' rulesets, then we should consider applying the much older principle of greatest parsimony and suggest that the self-assembling rulesets are the ones which more closely represent natural processes.

HOW THE MODEL WORKS

As our central assumption is that whole-plant behaviour could emerge solely from modular action and interaction, our model mimics the form and function of a whole, individual plant through the behaviour of fundamental, indivisible, subcomponents. Each of these subcomponents is a binary branching module. Within the simulation there is

thus no such thing as a 'whole plant' that is engaged in whole-plant processes, there is simply an interconnected collection of plant modules. In the same way that ecological behaviour emerges out of the actions of individual plants, we provide the opportunity for 'whole plant' behaviour to emerge solely from the interconnections and interactions of individual modules (Fig. 1).

As in other CA models, the spatial area within the simulation is divided into an array of cells. In our case, these represent a vertical section through the two-dimensional plant and its environment. The plant modules (if any) within each cell are linked into two branched networks, the 'root' and 'shoot' systems. This structure represents the plant as a collection of linked branching units seen through a vertical plane. The way in which the binary tree is structured, the way in which its internal relations are managed, and the way in which its external relations with its environment and with neighbouring modules are managed, are all described in outline by Colasanti and Hunt (1997*a*) and in detail by Colasanti and Hunt (2007). A pseudo-code listing of the model is given here in Table 1.

SIMULATIONS OF INDIVIDUAL GROWTH

Normal growth

The CA simulations supply the virtual plants with four resources, two from above ground and two from below. When these are presented in an abundant and balanced manner (Colasanti and Hunt, 1997*a*), a normal well-grown plant results (Fig. 2). In this vertical profile the different
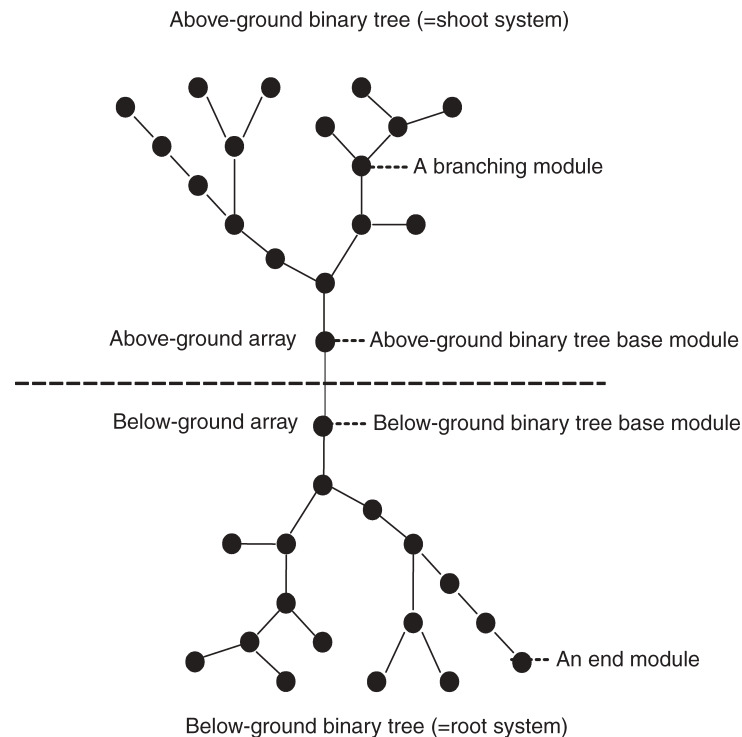

Fig. 1. The main components of the self-assembling, modular, cellular automaton model described in this paper (from Colasanti and Hunt, 1997*a*).

TABLE 1. *A pseudo-code listing of the Java code for the self-assembling model*

```
Cell object
  // properties
  resource (integer)
  neighbours[8] (Cells)
  occupant (Module)
Plant Module object
  // properties
  photosynthate (integer)
  nutrients (integer)
  parent (Module)
  offspring[2] (Module)
  home (Cell)
Experiment object
  // properties
  grid [64][64] Cell
  plantModules (arrayList)Modules
// iterative code
For each cell of the array:
  If below ground cell:
    randomly distribute resources between self and eight
      neighbours.
  If above ground cell:
    move light resource to cell immediately below self.
For each plant module:
  // Resource uptake
  If resource is available from within occupied (home) cell
    take up unit of resource from occupied cell
      if below ground resource
        add to nutrient variable
      if above ground resource
        add to photosynthate variable
  Randomly redistribute nutrient and photosynthate between
    self, parent and potential offspring modules
  // Growth
  If an offspring node is empty
    If a unit of nutrient and photosynthate available
      If more than one cell neighbouring the occupying
        cell is empty
      choose most resource rich
      create new plant module
      reduce nutrient and photosynthate values by one
      set the offspring node to newly created module
      set parent node of newly created module to current
        module
      set occupancy of chosen neighbouring cell to be
        newly created module
      set the occupied cell of newly created module to
        that of chosen neighbouring cell
```
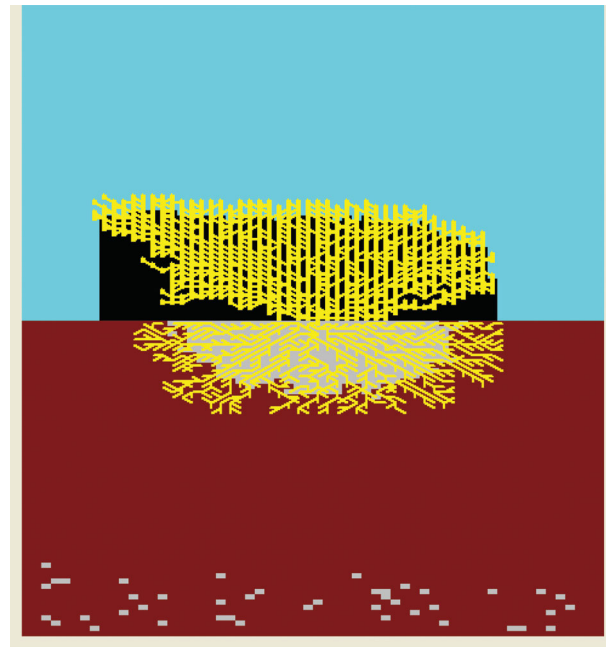

FIG. 2. A typical image at 150 iterations showing a simulation of growth in an individual CA plant. Each cell in the top row of the above-ground array was replenished with one unit of light at each iteration and each cell of the below-ground array was initially supplied with an average of six units of nutrient. In the above-ground array, the darker tone represents wholly light-depleted cells and in the below-ground array the lighter tone represents cells containing two or fewer units of nutrient (from Colasanti and Hunt, 1997*a*).

allocation (Fig. 5) that accords with Davidson's 'functional equilibrium' hypothesis (Davidson, 1969) (Fig. 6).

Varying plant physiology: a modification for active foraging

In natural plant communities, species of unequal form and function co-exist. A second model 'species' was created by mutating one of the resource-handling rules of the standard module. This modified 'species' had a competitive advantage over the standard one, but this came at a price (in the world of real plants, the evolutionary trade-offs that are necessary for such mutations to persist are well known; for example, see the discussion by Grime *et al.*, 1997). So we created a version of the plant in which the persistence of end modules was made dependent upon continued resource uptake: a grow or die imperative. Figure 7 shows the outcome of competition between standard and modified plants. A process of 'active foraging' has appeared within the resource-rich environment: the modified plant is rewarded by an enhanced capacity for physical exploration and the standard plant is penalized by its relative stasis. The shoots of the standard plant exhibit the densely packed morphology often associated with long-lived plants, whereas those of the modified plant exhibit a sparse under-layer and a highly branched upper layer. The latter feature, a 'rapidly ascending monolayer', is a well-established feature in populations of fast-growing, herbaceous competitors (Grime *et al.*, 1997). Under conditions of low resource (not shown), the modified plant was

colours indicate different resource concentrations. The morphology that has emerged within the above- and below-ground binary trees resembles that of the shoot and root structures of real dicotyledonous plants. Under these particular conditions, both binary trees are very similar in size, and both show approximately bilateral (left–right) symmetry. The above-ground binary tree exhibits the property of self-shading within the canopy (the darker area depicts a reduction in level of a resource originally presented from above in the manner of light) and the below-ground binary tree has produced a region of environmental 'nutrient' depletion (lighter area).

The time-course of the accumulation of biomass (total number of modules, Fig. 3) follows the usual S-shaped curve (Hunt, 1982). The curve is sensitive to different levels of resource supply, both above and below ground. The virtual plants can also forage for resources (Campbell and Grime, 1989*a,b*) in heterogeneous environments (Fig. 4) and they exhibit a plasticity in root–shoot
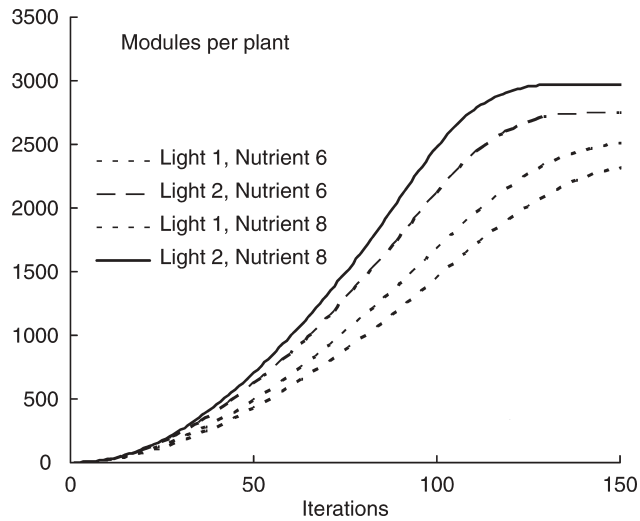
FIG. 3. The S-shaped time-course of individual growth. Each simulation began with the grid width, above-ground height and below-ground depth all set at 120 cells. Into this environment was planted a single, self-assembling plant of the standard specification. The total number of modules was recorded at every iteration and these smooth curves join the data means obtained from 20 replicate runs. Curves are shown for two different levels of light flux (number of units of light resource supplied to each cell in the topmost above-ground row of the CA). These levels are combined factorially with two different levels of initial nutrient supply, average units per below-ground cell of the CA (from Colasanti and Hunt, 1997a).

strongly disadvantaged because the costs associated with its explorations were insufficiently rewarded.

Varying plant morphology: a hormone for tap-rooting

We also looked at an internally driven flexing of the root's topology and search characteristics in the form of a modification which allowed the plant to forage for water
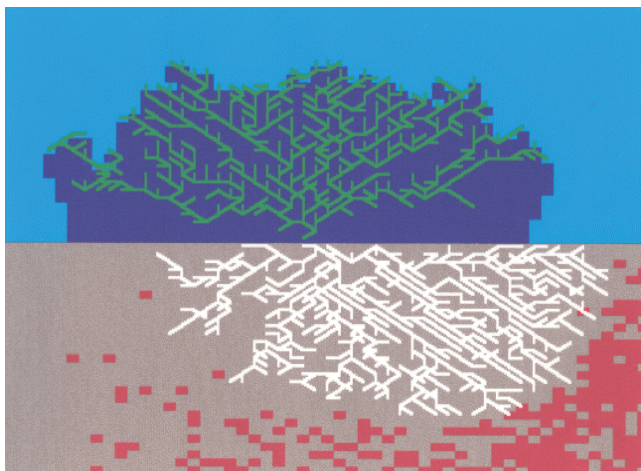

FIG. 4. An typical image at 150 iterations of an individual plant grown in an environment replenished at every iteration with one unit of light per cell in the topmost above-ground row of the CA. The initial supply of nutrients in the below-ground array of the CA averaged six units per cell but was biased positively towards the right-hand side of the environment (see also Fig. 2) (from Colasanti and Hunt, 1997a).
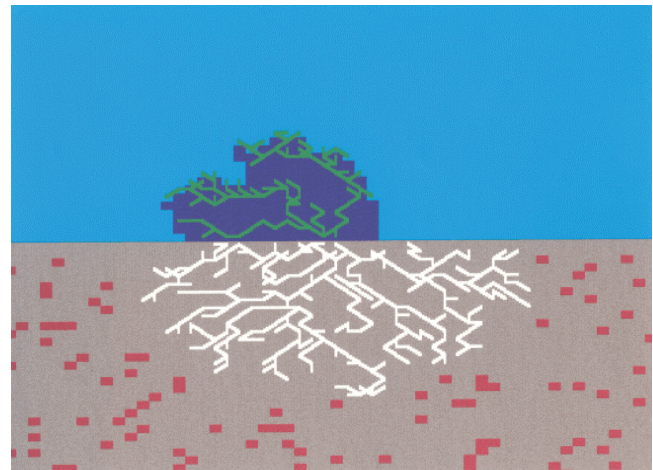

FIG. 5. A typical image of an individual plant grown for 150 iterations in an environment replenished with one unit of light per topmost cell of the CA at each iteration, but with an initial level of nutrients in the below-ground array averaging only two units per cell (see also Figs 2 and 4) (from Colasanti and Hunt, 1997a).

in situations of restricted availability. An extra 'hormone field' was added to the ruleset of below-ground modules, such that the stronger the hormone's influence the longer the interval that had to elapse before a new branch could be produced. High hormone strength generated long, lightly branched 'tap roots' (Fig. 8C) and a low hormone strength the more usual 'bushy' structure (Fig. 8B).

The resulting topology can be described in terms of the 'architectural' index used by Fitter (1993) in his analysis of real root structures. In this index, minimally branched
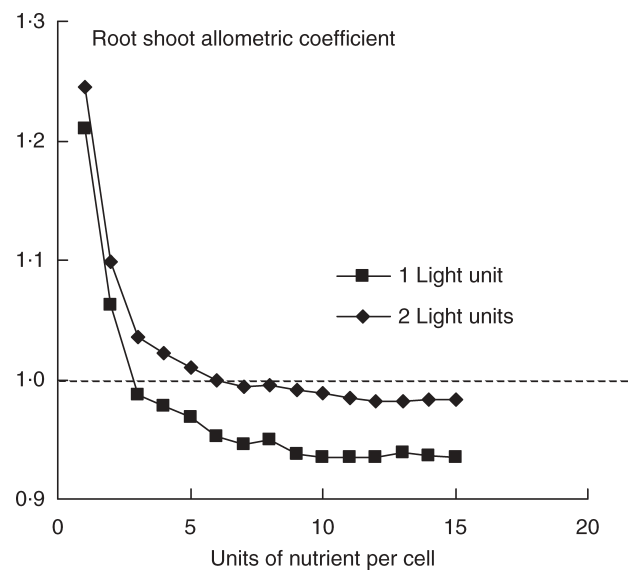

FIG. 6. Simulations of individual growth demonstrating flexibility in root–shoot partitioning. The root-shoot allometric coefficient, defined as $(\ln R - \ln c)/\ln S$ (where R is number of root modules, S is number of shoot modules and c is a constant), is shown after 150 iterations and averaged across ten simulations for each of two different levels of light flux combined factorially with fifteen different levels of initial nutrient supply (from Colasanti and Hunt, 1997a).
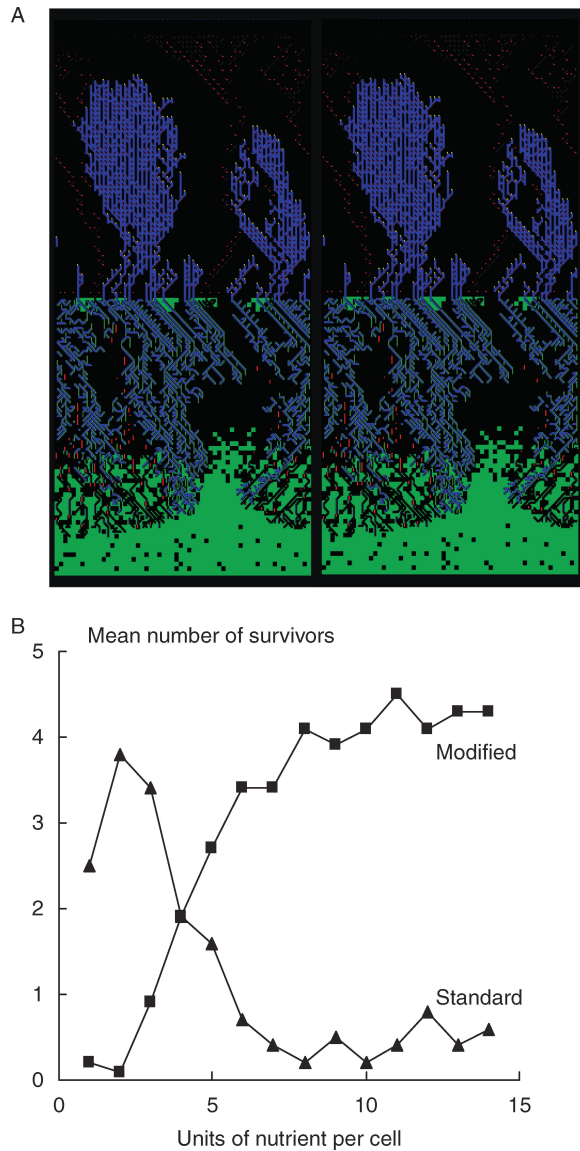
FIG. 7. The standard model (yellow plant in view A, triangular symbols in graph B) was given a modification (red plant in A, square symbols in B) which affected the uptake of resources by its end modules. In the standard plant, continued existence of an end module was independent of resource uptake, but in the modified plant, existence became dependent upon *continued* resource uptake (from Colasanti and Hunt, 1997*a*).

structures, described here as 'herringbone', produce a value approaching 1·0, whereas random or 'bushy' structures produce a value closer to 0·5. With a below-ground vertical gradient in our 'water' resource and the level of the 'virtual hormone' flexed in a geometric series, the modified plant (Fig. 8A) delivered a root shape index that increased asymptotically towards the herringbone shape as hormone strength increased. Here, the highest value of the index lay very near to its upper limit of 1·0 (the perfect herring-bone), whereas the index for the standard plant remained below 0·65 throughout. Like the 'active foraging' feature previously described, this potential for tap-rooting would be advantageous under certain conditions only, specifically
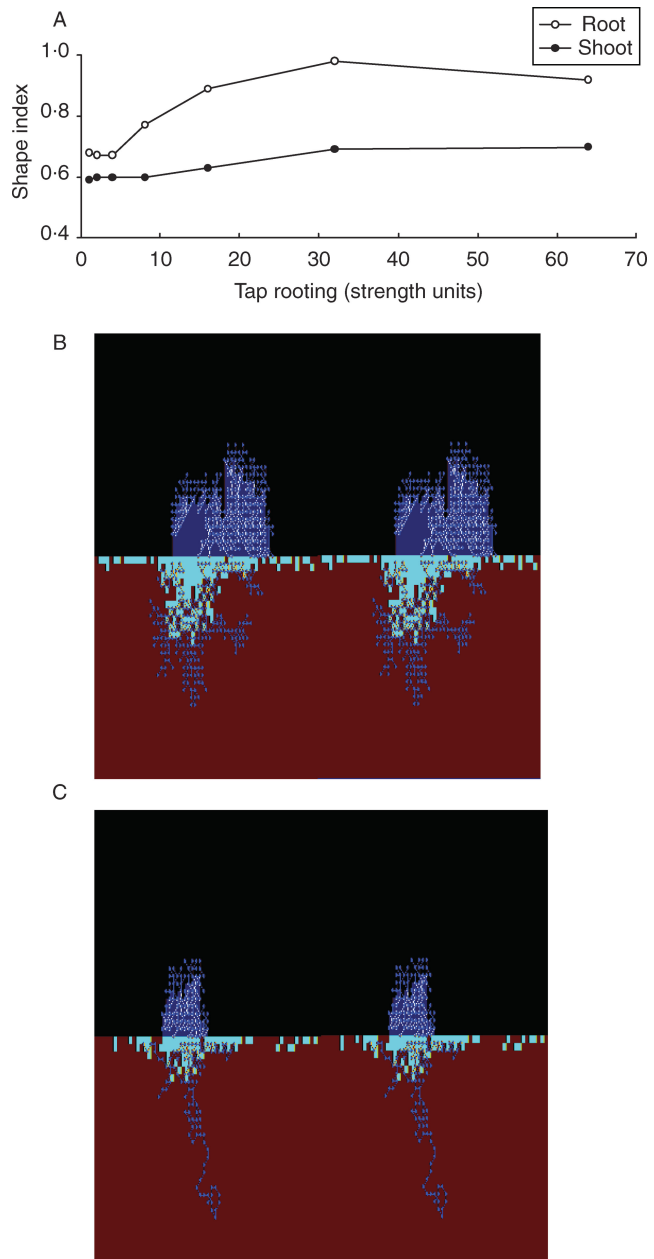

FIG. 8. Showing the effect of varying tap rooting strength in a bottom-replenished system with uniform distribution of water. The standard plant (data with closed symbols in A, typical image in B) has both a lower level of the tap-rooting 'hormone' and a lower root shape index than the modified plant (data with open symbols in A, and typical image in C) (from Colasanti *et al.*, 2007)

in the case of water being available only deep in the soil profile. Under conditions of plentiful surface water, this feature would be disadvantageous.

SIMULATIONS OF POPULATION GROWTH

The population density of equally spaced, identical plants can be varied within different runs of the model and, eventually, the denser populations will undergo self-thinning.
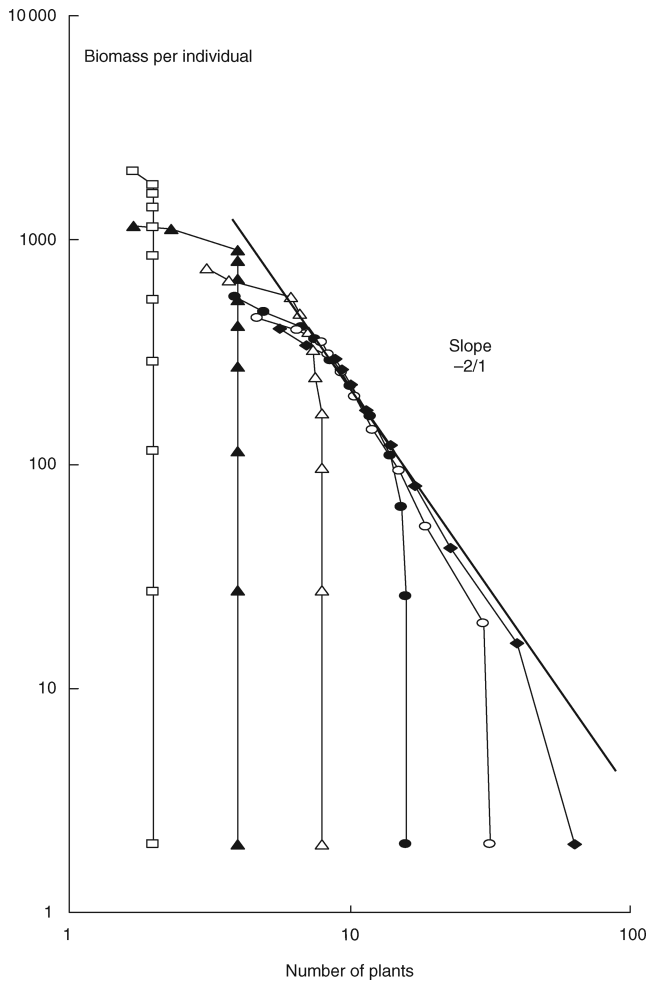
SIMULATIONS OF SIMPLE COMMUNITIES

Four functional types

The modification, described above, of the standard model plant into an actively foraging or a tap-rooting form allowed us to investigate the consequences of these modifications both individually and in combination. Four different 'functional types' (standard, actively foraging, tap-rooting, and actively foraging with tap-rooting) were grown together in all possible pairings, and in mixtures of all four types, in a series of replicated competition experiments.

One-on-one competition

In the pairwise simulations, the level of 'water' resource was flexed in a vertical gradient throughout the below-ground environment. The outputs (Fig. 10) show the numbers of survivors of each plant type in the six comparisons.

In competition with the standard plant, the plant with the tap-rooting feature was better at capturing water resources when these were scarce. However, the standard plant was more effective when resources were less scarce because its greater root surface area permitted higher resource uptake. The restriction on node formation in the tap-rooting plant also had the effect of reducing total growth, even under favourable conditions, in comparison with the standard plant. This result was similar to that observed when the standard type was paired with either of the two types having the active foraging feature. At low resource levels, where the tap-rooting feature was most effective, the active foraging feature already had a restrictive effect on the plants that possessed it, so the addition of the tap-rooting feature had little additional effect. In the three remaining comparisons, where only one of the plants had the foraging feature this was again the predominant factor in determining relative success in resource-poor environments. The foraging feature always had a deleterious effect at low resource levels. Finally, when the foraging feature was present in both plants, the addition of the tap-rooting feature had comparatively little effect. It did confer a slight additional advantage when water was replenished from below but, of course, this slim advantage was eliminated at high resource levels.

The tap-rooting and the active-foraging mechanisms again demonstrate the consequences of trait trade-offs: features which are advantageous in otherwise deleterious external conditions can only exist at the cost of reduced performance when such conditions do not obtain. These two specialisms thus resemble one another in this respect. However, when tap-rooting plants were in pair-wise competition with any type of plant with the active foraging feature, it was the tap-rooting feature that was the more dominant attribute at low resource levels.

Competition in simple mixtures

With all four plant types equally present from the beginning, the resulting four curves (Fig. 11) fell into two similar

Fɪɢ. 9. A simulation of population growth starting from initial densities of 2, 4, 8, … 64 equally spaced plants per simulation. Results are plotted on a double logarithmic scale. Each simulation began with grid width, above-ground height and below-ground depth all set at 120 cells. Into this was planted a population at the specified initial density which was allowed to grow for 150 iterations. All of this activity was replicated 20 times and the points shown are means of final module numbers per individual. On reaching full interaction between individuals, the denser populations underwent self-thinning along a line of slope −2/1 (from Colasanti and Hunt, 1997*a*).

The self-thinning of real plant populations (e.g. Kays and Harper, 1974) generally follows the so-called −3/2 power law (Yoda *et al.*, 1963; Hutchings, 1979; Westoby, 1984; Sackville Hamilton *et al.*, 1995), meaning that the logarithm of individual size is related to the logarithm of population density by a line of slope −3/2. This line arises ultimately from the underlying geometry of the growth process, the 'income' obtained by a real, three-dimensional plant being an approximate function of its surface area (a squared term) and its 'expenditure' being an approximate function of its volume (a cubic term). In the two-dimensional, self-assembling plant (Fig. 9), the self-thinning line has a slope of −2/1 because of the reduced dimensionality of the model system relative to that of the real world.
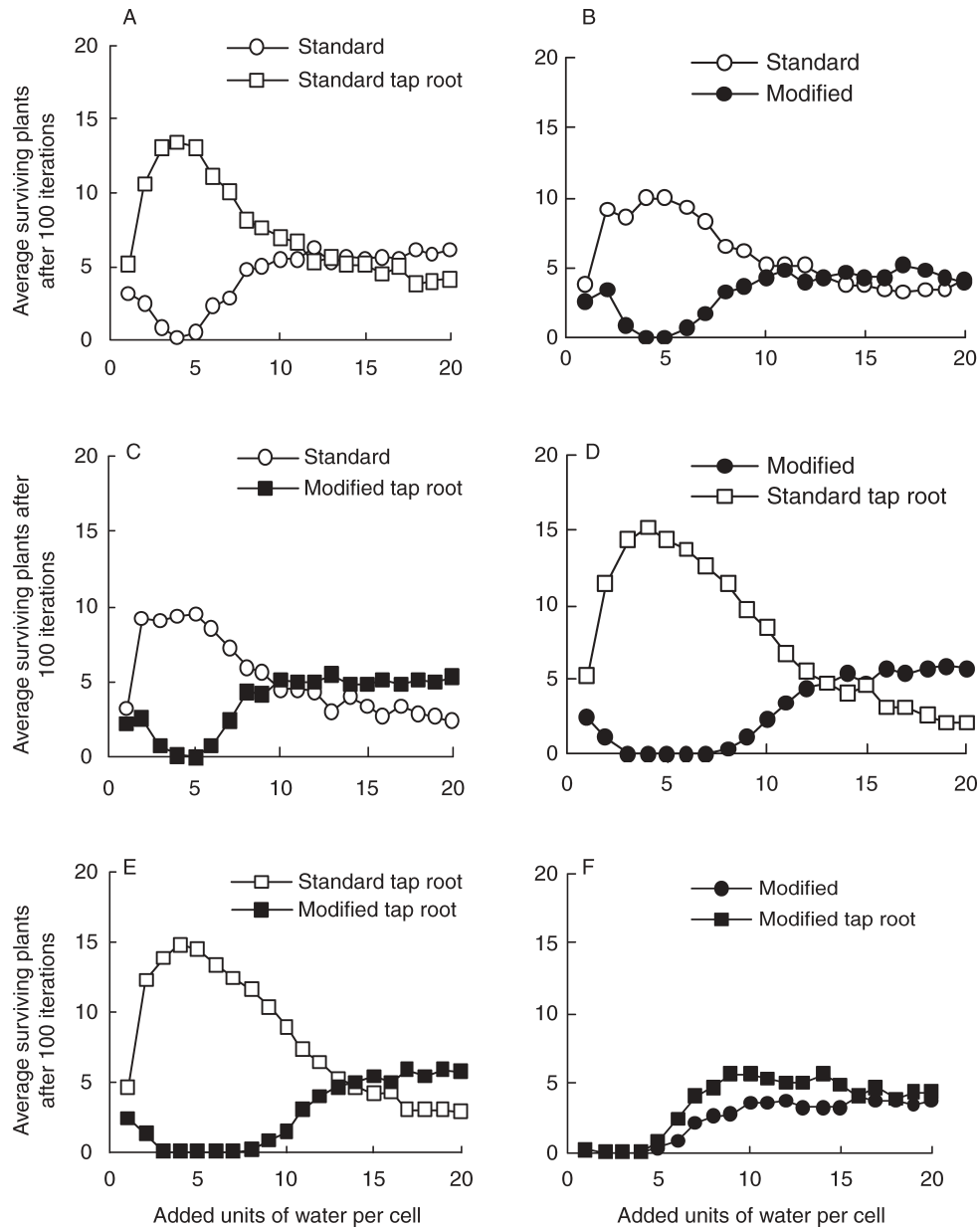
FIG. 10. Showing pair-wise competition between plants under conditions of constant nutrients, with varying levels of water all supplied from below. Plants having two different rulesets are compared in each part of this figure: (A) standard plant versus a plant with the tap rooting feature; (B) standard plant versus a 'modified' plant (with the foraging feature); (C) standard plant versus a plant with both tap rooting and foraging features; (D) a plant with foraging feature versus a plant with tap rooting feature; (E) a plant with tap rooting feature versus a plant with both tap rooting and foraging features; (F) a plant with a foraging feature versus a plant with both tap rooting and foraging features. Each simulation began with grid width, above-ground height and below-ground depth all set at 120 cells. All plants grew for 100 iterations and runs were replicated 20 times, the points shown being means (from Colasanti *et al.*, 2007).

pairs: those without the active foraging feature and those with it. The relative behaviour of these two pairs again demonstrates both the advantages and the disadvantages of the active foraging feature under conditions of varying water supply. Beyond this primary effect, a secondary one can be discerned due to the presence or otherwise of the tap-rooting feature. What was predicted by the pairwise comparisons had survived into this multi-type comparison.

SIMULATIONS OF COMPLEX COMMUNITIES

Seven functional types

It is a truism that in ecology 'there are many more actors on the stage than roles that can be played' (Colasanti *et al.*, 2001). Replacing species with plant functional types can, therefore, reduce the complexity of vascular plant communities without suffering important losses of process.
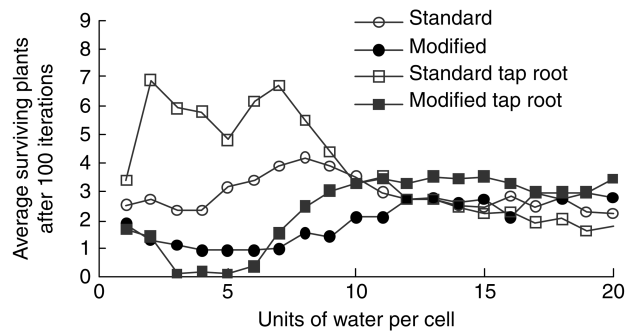
Fig. 11. Showing competition between equal mixtures of all the four functional types from Fig. 10, i.e. plants with or without the active foraging feature and with or without the tap-root feature (from Colasanti *et al.*, 2007).

Viewing plant communities as collections not of species but of functional types thus has many advantages: processes are clarified and modelling is, of course, greatly facilitated.

The C-S-R system of plant functional types (Grime, 1974, 1977, 1979, 2001) is a particularly powerful framework for CA modelling because the ratio between how much it explains and how much it needs to assume (Dawkins, 2006) is very high indeed. The theory and practice of this system have been reviewed by Hodgson *et al.* (1999). In essence, it is held that plant life has evolved three trait-combinations ('competitive', 'stress-tolerant' or 'ruderal') which allow it deal with the opposing capacity of the environment to destroy plant biomass either pre-growth or post-growth ('stress' and 'disturbance' respectively). Plant and environment states can both display many intermediates.

For maximum concision, we drove our virtual plants by means of a very compact plant attribute set: (*a*) size per module, (*b*) longevity of the module in the absence of resources, (*c*) propensity to flowering by the module (Colasanti *et al.*, 2001). Table 2 shows how three levels

TABLE 2. *Combinations of plant attributes* used to create seven C-S-R functional types within the self-assembling model*

Type	Morphology	Physiology	Reproduction
C	Large	Fast	Slow
S	Small	Slow	Slow
R	Small	Fast	Fast
SC	Medium	Medium	Slow
SR	Small	Medium	Medium
CR	Medium	Fast	Medium
CSR	Medium	Medium	Medium

*Three levels per attribute were determined by experiment. The following arbitrary and unexceptional values proved sufficient to demonstrate the desired plant qualities. For the morphology attribute, the three levels comprised 3, 2 or 1 CA cells per module, with the same unit quantities of each resource being needed for growth to occur at any iteration. For the physiology attribute, 24, 12 or 6 iterations in the absence of resource uptake were permitted before death of the module was demanded. For the reproduction attribute, in which all terminal, above-ground, modules detached themselves from their branches and re-located at random on the 'soil surface', these events were triggered after 100, 50 or 25 iterations.

in each of these three attributes were combined to produce the seven functional types necessary for a C-S-R implementation of the CA model. Again, evolutionary tradeoffs played an important part in this design: out of a maximum of 27 types that could have been created, only the seven combinations known from nature were used.

Community simulations

To simulate environmental stress, 'nutrient' resource availability was manipulated. To simulate environmental disturbance, a destructive external force in the form of a 'trampling' event was created at appropriately defined widths, locations and frequencies. When 'trampled', all above-ground plant material was destroyed and its former resources liberated appropriately. By creating graduated series of such disturbance events, and by combining these events with manipulations of environmental resource, we could explore the simultaneous roles of stress and disturbance in determining the relative performance of all seven functional types in any manner of simple or complex community. In most of these community experiments, an end-point of 150 iterations was chosen. In ecological terms this is a long period, sufficient to support 150 consecutive generations of the fastest-reproducing type.

Community simulations under single gradients

Simple community experiments involving just three functional types were able to reproduce the predicted distribution of C-S-R types in all the environmental combinations tested. For example, a uniform gradient in stress (the inverse of resource availability) could alone control the final relative abundance of three types from initially equal mixtures (Fig. 12, gradient). A classical replacement
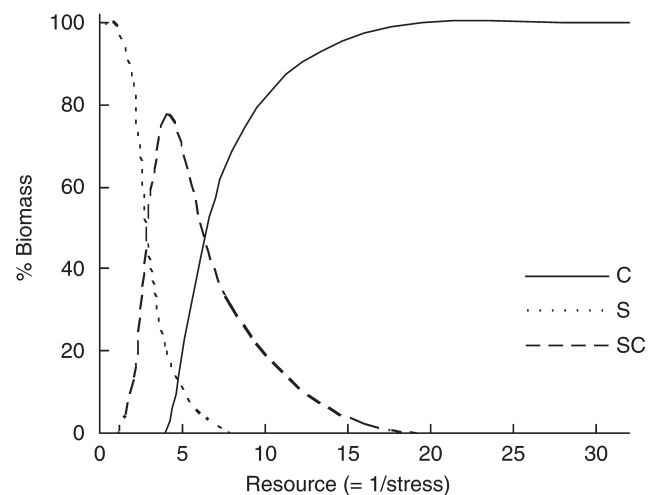

Fig. 12. Showing the percentage of total final biomass achieved by three coexisting functional types C, S and SC (see Table 2). Each simulation began with grid width, above-ground height and below-ground depth all set at 120 cells. Into this were planted populations of 20 individuals of each of the three plant types, randomly distributed. The simulation ran for 150 iterations. The smooth curves join the mean data from 20 replicate runs. The level of initial nutrient resource was increased in geometric steps, 0·5, 1, 2, . . . 32 (from Colasanti *et al.*, 2001).
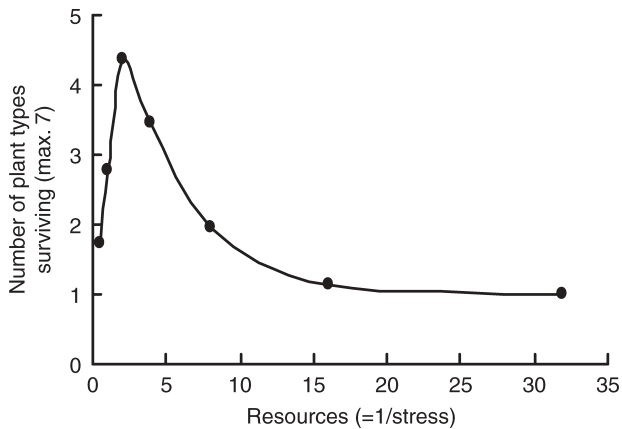
FIG. 13. A simulation as in Fig. 12, but initially involving all seven functional types. This diagram reproduces a stress-driven version of Grime's humpbacked model (from Colasanti *et al.*, 2001).

series was obtained (Whittaker *et al.*, 1973) in which the niche of type S corresponded to low resource availability, that of type C to high availability, and that of type SC to intermediate availability.

When all seven types are introduced in equal mixture, the number of surviving types gives a measure of biodiversity. A stress gradient (Fig. 13) and a disturbance gradient (Fig. 14) both produced a biodiversity curve with a maximum part-way through its range, though the disturbance regimes were more deleterious to the survival of types over-all. Both curves are entirely in agreement with field observations. The 'humpbacked' shape was first noted by Grime (1973) and elements were reprised by Connell (1978) as part of his 'intermediate disturbance hypothesis'. Further discussions of this shape

were offered by Rosenzweig and Abramsky (1993) and Colasanti *et al.* (2001).

Community simulations under combined gradients

A more exhaustive competition experiment involved an initially equal mixture of all seven types grown under all possible factorial combinations of seven levels each of environmental stress and disturbance. The driver of biodiversity in this case was total biomass (productivity), a result of the joint effect of each stress and disturbance combination. The expectation was that the final abundance of types would follow the comprehensive humpbacked model described by Grime (1979), i.e. where biomass is low on account of either high environmental stress or high environmental disturbance, non-competitive, specialist types make up all, or almost all, of the few species present. Where both stress and disturbance are low, most or all of the few species present were of competitive type. In between, in a zone of moderate biomass, there were many more types present, mostly intermediates between the extremes mentioned. An abundance of field data and reviews (references in Colasanti *et al.*, 2001) support this biomass-driven humpbacked relationship. Our results (Fig. 15) appear to be entirely in accordance with this model; the data in our scatter diagram support the humpbacked quadratic polynomial trendline at $P < 0 \cdot 001$.

The stability of biodiversity

The humpbacked model, particularly in its biomass-driven form, is of innate relevance to the now considerable diversity-productivity debate (Grime, 1973, 1998; Marañón and Garcia, 1997; Grace, 1999; Stevens and Carson, 1999; Weiher, 1999; Kaiser, 2000; Spehn *et al.*, 2000). In our model, however, when tests are run well beyond the normal stopping point of 150 iterations, the curve in Fig. 15 gradually declines in height (Fig. 16), though its
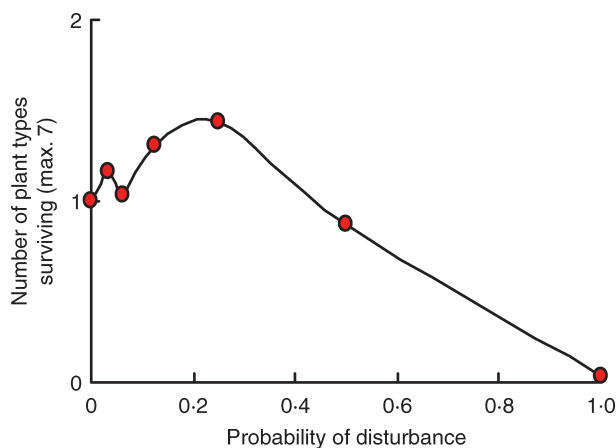

FIG. 14. A simulation as in Fig. 12, but initially involving all seven functional types. This diagram reproduces a disturbance-driven version of Grime's humpbacked model. A randomly selected cell in the ground-surface row was defined the central point of a trampling event of width ten cells. When trampled, all material in columns within the trample width was destroyed both above- and below-ground and the liberated nutrient resources entered the below-ground environment. Trampling probability per cell per iteration was flexed from 0, 1/32, 1/16, . . . 1 (from Colasanti *et al.*, 2001).
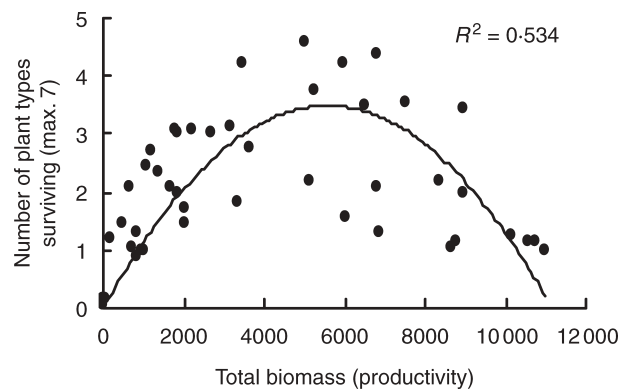

FIG. 15. A simulation, initially involving all seven functional types, reproducing a productivity-driven version of Grime's humpbacked model. Each point represents a unique combination of seven probabilities of disturbance (see Fig. 14) and seven levels of nutrient resource (see Fig. 13). Means at 150 iterations of the model are plotted for 20 replicate runs. The fitted curve is a quadratic polynomial through the origin, $y = 0 \cdot 00125x - 0 \cdot 000000112x^2$ (from Colasanti *et al.*, 2001).
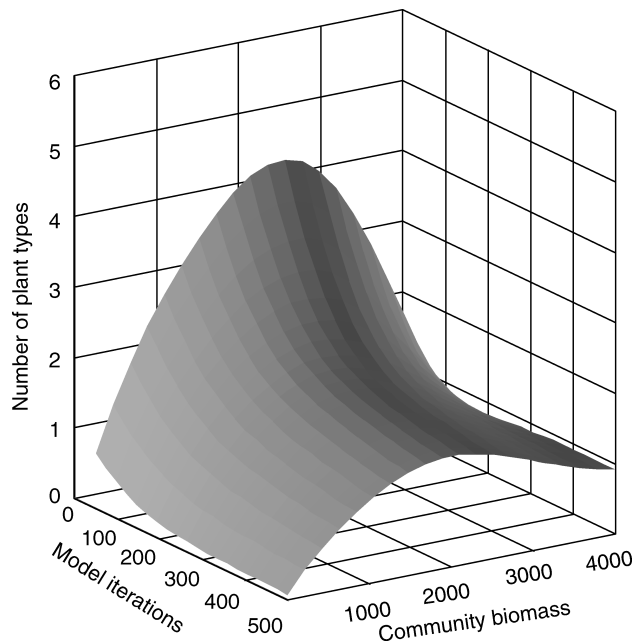
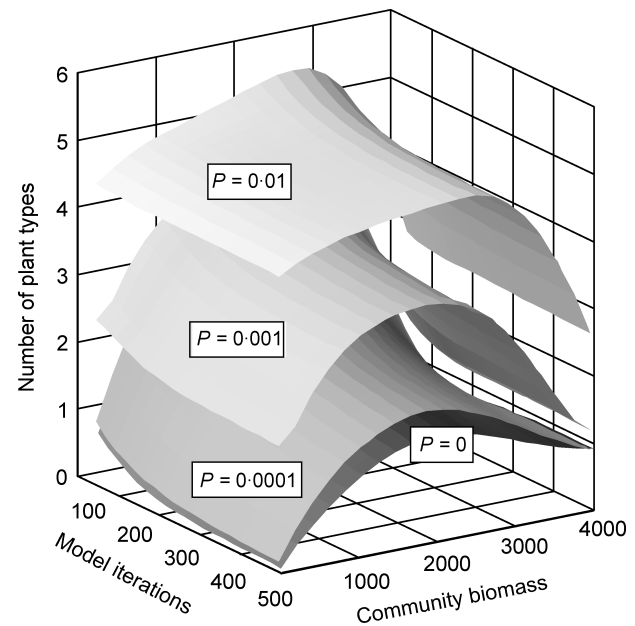FIG. 16. The marked decay with time in the humped shape shown in Fig. 15.

FIG. 17. A possible mechanism for the elimination of the decay with time shown in Fig. 16 (the lowest surface depicted here). The upper surfaces show the results of flexing the probability that, within a single model iteration, a virtual 'propagule' establishes in an unoccupied, resourced, CA cell. The propagule is selected randomly from an equal mixture of all seven types of plant in a virtual 'seed rain' of single-celled individuals introduced from outside the model.

humpbacked shape remains. We consider that, in accordance with current theory (Hutchings *et al.*, 2000), environmental heterogeneity at, or immediately above, the scale of the whole plant is an agent which, on both temporal and spatial bases, could prevent this decay. Also, the loss of biodiversity might be alleviated if model communities were open to the incursion of propagules from external sources. A preliminary test of the latter mechanism (Fig. 17) shows this to be a distinct possibility. Further work on this effect is in progress.

DISCUSSION

Our aim in this work was to see whether, starting from the simplest possible ruleset, a module-based simulation was capable of reproducing some of the most fundamental properties of plant topology and behaviour across a wide range of ecologically relevant spatial scales. We made, in effect, a formal test of the powers of plant metamerism, 'serial repetition ... of unit structures ... which are either identical or homologous in structure' (White, 1984).

Because of the similarity between the high-level dynamics of our model and those of real plants, we conclude that such metamerism may indeed form the basis of many of the recognized features of the growth of real plants. That these are easily reproducible by the simple mechanistic methods that we have embraced in this work supports the belief that several fundamental aspects of plant form and function, including morphology and interactions with the environment and with other plants, can be described simply and adequately in terms of modular self-assembly and resource capture and utilization.

Although such CA modelling can potentially bring a number of benefits to the study of vegetation dynamics,

the correct interpretation of CA requires an understanding of its limitations. CA models should, of course, be viewed as an adjunct to, rather than a replacement for, more conventional methods of scientific investigation, i.e. hypothesis-testing by means of real-world experiments and the capture of whole systems into formal mathematical structures (Colasanti, 2000). It is undoubtedly true that CA models can facilitate the investigation of complex systems more easily and transparently than can reductive methods (Drake and Weishampel, 2001; BenDor *et al.*, 2006). This is particularly true of the non-linear spatial relationships between identifiable individuals that are found in plant communities (Arii and Parrott, 2006). In particular, CA models readily permit the investigation of meta-level or emergent processes that can be attributed to the collective behaviour of the system but which arise from, and are only described at, the level of the individual. In the context of plant ecology, examples of such phenomena are resistance, resilience, invasibility and biodiversity (Wu and David, 2002; Wang *et al.*, 2003). However, CA achieve their high-level outcomes by means of algorithmically incompressible simulations: the results cannot be predicted analytically (Lett *et al.*, 1999). In this, of course, they mirror the real systems to which they correspond in that they deliver purely practical outcomes rather than solutions of over-arching mathematical or statistical formulations. In the case of CA representations of animal ecosystems, distinct methodological problems can arise from, for example, the issue of synchronous versus asynchronous updates of states (Ruxton and Saravia, 1998) or that involving the precise configuration of the underlying

matrix (Berjak and Hearne, 2002). However, the seasonal and stationary nature of plant–environment systems makes them much less affected by such problems (Ermentrout and Edelstein-Keshet, 1993; Balzter *et al.*, 1998).

Clearly, the many high-level plant properties demonstrated here (self-shading, external resource depletion, active foraging, plasticity in allocation and morphology, self-thinning, competitive replacement series, intermediate stress/disturbance phenomena, humpbacked control of biodiversity by productivity) are emergent features arising without high-level controls from anywhere within the system. These properties conform exactly to current ideas on emergent phenomena (e.g. Bunge, 2003), namely 'those that arise from interactions between the components of a system over time in unexpected, nontrivial ways'. The components of our model, and their interactions, are both relatively simple in nature, but the resulting system may be described as complex, not merely complicated, because the emergent features arise specifically from unpredictable patterns of interaction between the components. Our modelling therefore suggests that the emergence of complexity in plant form and function has come solely from the actions of a 'selfish module', a component whose one 'endeavour' is to procreate itself whenever and however it can within the limits set by its own internal rulebase.

We conclude that within our modelling, whole-plant behaviour, and ultimately population dynamics, can be explained as an emergent property of lower-level activity by plant modules. We have also seen that flexing the properties of plant modules in ways that are grounded in real observations can create a range of ecologically distinct plant types which are capable of mimicking high-level community processes remarkably well. There is thus a clear suggestion that emergence from lower-level activity could also be the true explanation of the natural processes that the model addresses. However, we still face the more difficult question as to whether this method is the one actually used by nature, or whether nature achieves the same result by a more complex route.

Until this larger question can be resolved, CA modelling will remain important more generally. This is because it can proceed far more quickly than real-life experiments, thus helping to explore many 'what if' questions much sooner. Within the research formalism described by Harper (1982) in terms of precision–realism–generality, we believe that the present generation of CA models now offers a very interesting new combination for modelling plant resource-capturing properties and community dynamics, namely precision = moderate, realism = moderate, generality = high. Many high-level plant community processes now await exploration from this unique perspective and, as resource dynamics is a concept that extends beyond the plant–environment interface, CA work involving further trophic levels is also in prospect.

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