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The emergence of primary strategies in evolving virtual-plant populations

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ABSTRACT

A common practice by those searching for generalities in ecological systems has been to form species groups according to similarities in their suites of traits (termed a 'strategy'). Field and theoretical studies have strongly suggested that resource availability and disturbance frequency have played primary selective roles in the evolution of species traits that has resulted in the existence of a predictable pattern of strategy variation within a resource–disturbance parameter space. We investigated whether this recognizable pattern (of strategy variation) would emerge if model plant populations evolved in environments contrasting in nitrogen availability and disturbance frequency alone. To address this, a mutable single plant model was developed that incorporated 29 mutable parameters controlling plant life history, physiological and morphological traits. Populations of these were 'grown' in a spatially explicit model environment that allowed mechanistic competition for light and nitrogen and long-term, multi-generational simulations. The strategies that evolved showed a pattern of variation that strongly conformed to plant strategy theory. Our model provides strong supporting evidence that resource availability and disturbance frequency can act as primary selective forces in plant evolution, resulting in the existence of predictable, environmentally correlated suites of traits. However, several plant traits did not evolve as predicted by field evidence and the reasons for this are discussed.

Keywords: evolutionary computation, individual based model, mutable single plant model, plant strategies, primary strategies.

INTRODUCTION

The occurrence of suites of traits common to species inhabiting similar environments (termed a 'strategy') is well known in ecology (Begon *et al.*, 1996; Crawley, 1997; Grime, 2001). The evolutionary explanation, that similar environmental selection pressures have resulted in the evolution of similar suites of traits, is also well established (Begon *et al.*, 1996; Stearns and Hoekstra, 2000). Strategy theorists have predicted the existence of

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repeated patterns of evolutionary specialization in all species due to the primacy of such environmental factors as evolutionary selection pressures (MacArthur and Wilson, 1967; Grime, 1979, 2001; Pianka, 1980; Greenslade, 1983; Southwood, 1988; Stearns, 1989; Bolker and Pacala, 1999). This theory has been the topic of much discussion and debate in ecology over recent decades (reviewed in Grime, 2001).

Strategy theory is particularly well developed for plants (e.g. Grime, 1979, 2001; Sibly and Grime, 1986; Tilman, 1988; Grubb, 1998; Westoby, 1998; Bolker and Pacala, 1999; Wilson and Lee, 2000). The availability of resources for plants to assimilate into biomass, and the impact of disturbance events (which remove biomass), have been seen as primary selective factors for the suites of traits that allow plant survival in an area (Grime, 1979, 2001; Tilman, 1988). However, field and theoretical evidence has suggested that different suites of traits are selected under different combinations of these environmental variables (Grime, 1979, 2001; Tilman, 1988; Grime *et al.*, 1997; Bolker and Pacala, 1999). This environment–strategy association is thought to occur because biophysical constraints on plant traits and their evolution result in different optimal trait combinations in different environments, with resources and disturbance being the primary selective factors (Grime, 1979, 2001; Southwood, 1988; Westoby, 1998). Therefore, plant strategy theory predicts that species strategies will vary on a continuum between the ‘extreme strategies’, associated with the environment that they are adapted to (Grime 1979, 2001; Tilman, 1988). This has led to the identification of ‘primary strategies’. These are strategies that are associated with the extreme combinations of resource availability and disturbance frequency (Grime, 1979, 2001; Tilman, 1988).

Grime (1979, 2001) in particular has argued for the existence of three primary strategies for plants: competitors that are adapted for rapid resource utilization and long-term site occupation; ruderals that are adapted to highly disturbed sites by growing and reproducing quickly; and stress tolerators that persist in low resource environments. There is some field and theoretical evidence to support this theory (Grime, 1979, 2001; Taylor *et al.*, 1990; Chapin *et al.*, 1993; Grime *et al.*, 1997; Bolker and Pacala, 1999). However, it still remains unclear whether the environmental factors that correlate most strongly with the main axes of strategy variation (resources and disturbance) do indeed cause predictable evolutionary outcomes and whether or not they are the primary drivers of plant strategy variation (Grime, 2001). Here our intention was to study the evolution of model plant populations in environments contrasting in nitrogen availability and disturbance frequency alone, to determine whether recognizable primary plant strategies would evolve, and if they would contrast in a pattern consistent with field and theoretical evidence. However, to do this required a model that incorporated traits affecting plant life history and function, their evolution as well as their effects on plant–plant and plant–environment interactions. Therefore, it was also partly our intention to develop a tool by which the evolution of plant traits could be studied, including their interrelationships, constraints and evolutionary trade-offs.

METHODS

Model

The model had two main components: a virtual environment (spatial array) and a mutable model of single plant growth (MSPM). Plant evolution was simulated by allowing many MSPMs to grow, reproduce and compete for resources in the virtual environment for a large number of generations. The model was iterative, with a time step (assumed relevant to the physiology of resource capture) of 1 h. During an iteration, the rates of plant processes and plant state variables were assumed to be constant.

Even by today's standards the model presented below is complex and parameter-rich. This was necessary to incorporate the relevant traits that affect a plant's ability to grow, reproduce and interact with its environment. However, to prevent the model from becoming overwhelmingly complex and to limit ourselves to a manageable set of results, we made some critical modelling assumptions. We confined the model plants to competing for space, nitrogen and light in the absence of any other potentially limiting variables such as herbivory, biomechanical constraints or water. This is despite the large body of evidence that these are also important factors in the evolution of plant form and function (e.g. Chapin *et al.*, 1993; Crawley, 1997; Niklas, 1997; Aerts and Chapin, 2000). As a result, the plants that evolved could only fundamentally differ in their life histories and abilities for resource capture. Furthermore, we made simplifying assumptions regarding the evolutionary process. Seeds were asexually produced with the same mutable parameters as their parent (but with a probability of mutation). No genetic linkage between traits was assumed – that is, each trait could mutate independently. However, with no direct linkage between the parameters, the strategies that evolved were in no way pre-determined, but instead evolved as a result of the evolutionary selection process in our model.

Environment

The environment was modelled as a 10×10 square cell toroidal array to eliminate edge effects, in which a maximum of one plant could occupy a cell. Above-canopy light was constant and uniform and, after initialization, total nitrogen in the array was also constant. Each cell had homogeneously distributed (within cell) pools of organic and inorganic nitrogen. The organic pool was increased by dead plant biomass and decomposed (releasing nitrogen into the inorganic pool) according to the model: $M_{t+1} = M_t e^{-k}$, where M is the mass of the organic nitrogen pool, t is time (number of iterations) and the decay coefficient, k, is a linear function of the cell organic nitrogen concentration (Aerts, 1997). Only the organic nitrogen pool was available for plant uptake. Diffusion of inorganic nitrogen between cells was calculated using the nitrogen diffusion coefficients in Jungk (1991). Diffusion only occurred in the X–Y plane and a Z plane (soil depth) of 0.1 m was assumed to allow calculation of cell nitrogen concentrations.

The mutable single plant model (MSPM)

The MSPM simulated the entire plant life cycle from germination to mortality. Key plant traits and responses to be included in the MSPM were identified from literature on plant strategies (McDonald, 1989; Ingestad and Ågren, 1992; Lambers and Poorter, 1992; Chapin *et al.*, 1993; Anten *et al.*, 1995; Robinson, 1996; Aerts, 1997; Eissenstat and Yanai, 1997; Grime *et al.*, 1997; Schmitt, 1997; Lambers *et al.*, 1998; Peuke and Jeschke, 1998; Reich *et al.*, 1999; Schieving and Poorter, 1999; Aerts and Chapin, 2000; Grime, 2001; Standing, 2001). Crucially, the MSPM had 29 mutable parameters that affected plant growth and development (Table 1), ultimately affecting lifetime seed production. Each mutable parameter inherited by the seed from its parent had the same probability of mutating. The mutation probability was set so that, on average, one parameter out of the 29 would mutate

Table 1. Description of the 29 mutable parameters in the MSPM

Parameter/plastic response	No. mutable parameters
Carbon storage	3 (Fig. 1)
Nitrogen storage	3 (Fig. 2)
Maximum carbon storage capacity	1
Maximum nitrogen storage capacity	1
Carbon remobilization rate from storage	1
Nitrogen mobilization rate from storage	1
Specific leaf area of leaf carbon allocation	4 (Fig. 1)
Leaf carbon allocation	4 (Fig. 1)
Above-ground carbon allocation	4 (Fig. 1)
Nitrogen uptake	2 (Fig. 2)
Maximum lifespan	1
Maximum carbon fixation per unit nitrogen	1
Proportion of nitrogen allocated to seeds	1
Interval between seed production events	1
Root foraging propensity (see text)	1

Note: Each plastic response had two or more mutable parameters (see Figs 1 and 2 for a detailed description of these).

for each seed produced. Upon mutation, parameters were changed by a randomly chosen magnitude (between 1% and 20%) and vector (positive or negative). By creating small differences to MSPMs through random mutation, different trait combinations were tested for fitness in the virtual environment. If, on average, a new strategy resulted in improved reproductive performance, it would have a greater chance of increasing its abundance in the MSPM population. Similar to recent studies (Warren and Topping, 2001; Strand *et al.*, 2002; Yedid and Bell, 2002), this approach avoided the assumption of a fitness criterion. Instead, the model simulated natural selection for the mutable parameter combinations (plant strategies) that resulted in improved reproductive performance in the simulated environment.

Structurally, each model plant consisted of a stem, leaves and nine roots. Leaves were evenly distributed within a cylinder (height defined by stem height) with the horizontal projection of leaf area on the ground (A_z) determined by the scaling relationship: $A_z = YW^b$, where W is plant weight and Y and b are constants. Plant canopy development and leaf overlap were restricted to occur within the plant locus and the eight neighbouring cells (first-order neighbourhood). The nine roots occupied different soil cells, with one root in the plant locus cell and the others in each of one of the eight neighbouring cells. Individual plants fixed carbon (photosynthesis) as a function of incident light, total leaf area and leaf nitrogen content with total light interception being an exponential decay function of the overlapping leaf area of neighbouring plants. After deducting respiratory carbon costs (constant per unit plant weight), fixed carbon was distributed among the different organs according to a series of mutable plastic allocation rules (Table 1, Fig. 1). Therefore, despite our model plants being restricted to a highly simplified morphology (such as only having nine roots), they could evolve their own allocation rules and responses to increase their fitness in a given environment (such as their strategy for allocation among the nine root pieces).

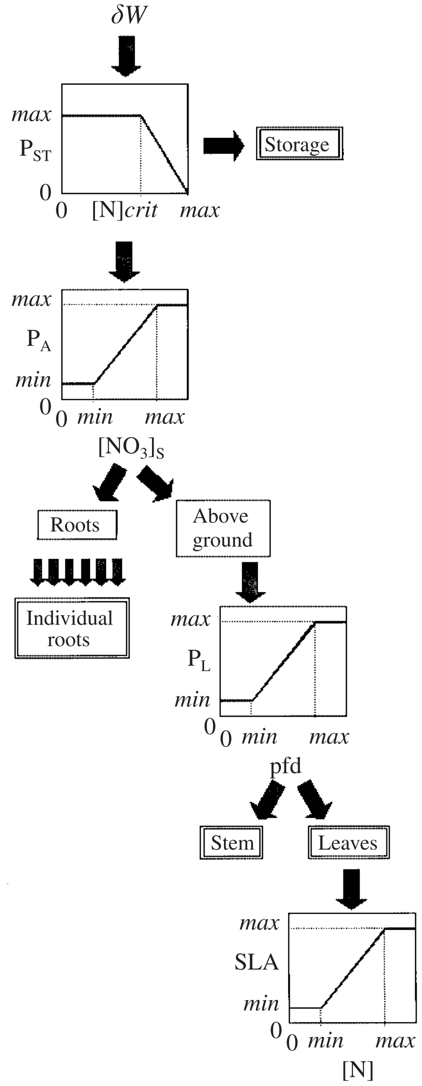


Fig. 1. The allocation of newly incremented carbon (δW) among MSPM components. Graphs illustrate plastic responses for carbon allocation in the MSPM where *min*, *max* and *crit* are mutable parameters. By varying the *min*, *max* and *crit* parameters, different plastic responses – or degrees of phenotypic plasticity – could be created. Definitions: P_{ST} = proportion of carbon allocated to storage, [N] = plant nitrogen concentration, P_A = proportion of carbon allocated to above-ground components, $[NO_3]_S$ = shoot nitrate concentration, P_L = proportion of carbon allocated to leaves, pfd = above-plant photon flux density, SLA = specific leaf area.

Individual root nitrogen uptake was a function of the cell nitrogen concentration, the root biomass and a nitrogen uptake scalar (Table 1, Fig. 2). The nitrogen uptake scalar and the nitrogen storage response were both modelled as mutable plastic responses (Table 1, Fig. 2). Leaf and root mortality rates were linear functions of plant nitrogen concentration,

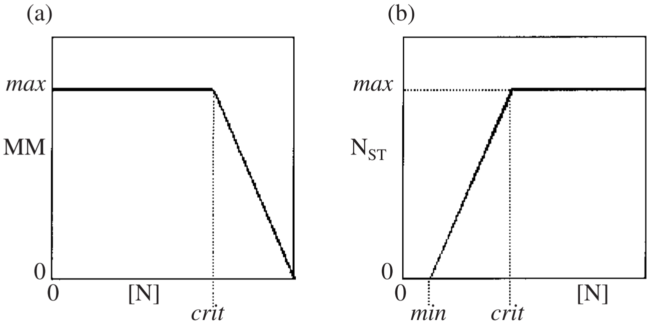


Fig. 2. Plastic responses controlling nitrogen uptake (a) and nitrogen storage (b) in the MSPM. *min*, *max* and *crit* are mutable parameters. By varying the *min*, *max* and *crit* parameters, different plastic responses – or degrees of phenotypic plasticity – could be created. Definitions: MM = nitrogen uptake scalar, [N] = plant nitrogen concentration, N_{ST} = proportion of nitrogen allocated to storage.

with 50% nitrogen resorption by the plant occurring during leaf mortality. Dead matter was returned to the organic matter pool in the soil cell at the plant locus. A plant could ‘die’ for four different reasons: (i) if it reached its maximum life span (see Table 1); (ii) if its nitrogen concentration went unrealistically low; (iii) if its respiratory costs exceeded its carbon gains through photosynthesis; or (iv) if it experienced a random disturbance event. Dead plants were added to the organic matter pool of the soil cell at the plant locus.

Seeds were produced at plant mortality (except in the case of disturbance) or at a particular frequency within a plant’s lifetime (Table 1). Seed number was a function of the above-ground plant nitrogen content and an allocation coefficient (Table 1). Grime (2001) argues that the regenerative phase (seed production and germination) of a plant is subject to quite separate selective pressures from those affecting the established (growing plant) phase. Although allowing seed size to vary may have altered the outcome of our results, for simplicity, and the fact that we solely wanted to look at the growing plant phase, we kept seed size constant throughout. After seed production, each seed was allocated to a random cell. Seeds immediately germinated in empty cells, with the germinating seed being randomly chosen from the seeds present in that cell.

Experimental protocol

Three different levels of organic nitrogen supply were chosen based on values given for global patterns of soil nitrogen storage (Post *et al.*, 1985). These were designated high nitrogen, medium nitrogen and low nitrogen, with nitrogen contents of 2, 1.05 and 0.1 $kg \cdot m^{-3}$, respectively. The soil carbon to nitrogen mass ratio always started at 15 : 1, representative of the data of Post *et al.* (1985). Initial test runs indicated that simulation results varied over a large range of disturbance probabilities. Therefore, to maximize the contrast between disturbance regimes, disturbance was varied on a log (base 10) scale. The probabilities of a disturbance event occurring in any iteration were 0.01, 0.001 and 0.0001 for high, medium and low disturbance, respectively. A disturbance event was simulated by generating a square of random size, between one cell and 10 × 10 cells, that was cleared of all plant matter, and all nitrogen was returned to the organic matter pool. This killed the plants in the cells (before they could produce seeds) and provided clear cells ('gaps') for the establishment of new plants. For low-nitrogen/high-disturbance simulations, the plants in the array always went extinct before 2 million iterations. Decreasing the disturbance probability to 0.005 allowed the runs to persist for 2 million iterations and these results are presented for the low-nitrogen/high-disturbance scenario. All nine combinations of the three levels of nitrogen and disturbance were simulated for 2 million iterations. This time period was chosen because it gave contrasting evolutionary pathways in a manageable period of time (on average 12 h on a 400 MHz Pentium III processor). It should be noted that no checks were made to determine whether the evolutionary dynamics had reached equilibrium. All simulations started with a uniform distribution of organic nitrogen among soil cells and 50 randomly selected cells were allocated a single plant seed. Random values, within defined limits, were chosen for every mutable parameter in each seed. Twenty replicate simulations, determined using a power analysis ($P(\text{type II error}) < 0.05$, based on five initial simulations for each environmental scenario), were performed for each of the nine environmental scenarios.

Evidence of the evolution of multiple strategies within a simulation (e.g. stable strategy combinations) was not detected in any of our simulations (determined by variance analysis of the mutable parameters in each simulation). Therefore, to compare the plants that evolved in the simulations, we took the average of the 29 mutable parameters (see Table 1 for details) and 10 plant state variables (biomass, nitrogen content, nitrogen concentration, stem height, stored carbon, stored nitrogen, above- to below-ground biomass ratio, leaf area, leaf area to leaf weight ratio, leaf to stem biomass ratio), for each simulation, first at 5000 iterations and again at 2 million iterations. Averages from the 180 simulations were then ranked for each variable to standardize the data values. These averages were then input into 'MINITAB$^{\text{TM}}$ Statistical Software V13.20' and compared by using the multivariate analysis techniques of principal components analysis (PCA) and similarity (cluster) analysis. Analysis of variance (ANOVA) was used to test for any significant effects of the environmental variables and time on the average traits or PCA axis scores.

SIMULATION RESULTS

Comparing the plant strategies at 5000 iterations to those at 2 million iterations (Fig. 3A) revealed a distinct separation along a primary axis of variation strongly correlated with the time difference (ANOVA: $F = 296.683$, $P < 0.001$). At 5000 iterations, the separation along Axis 1 was not significantly correlated with either environmental variable and separation along Axis 2 was significantly correlated with nutrient availability only (ANOVA: $F = 35.56$, $P < 0.001$). In contrast, the 2 million iteration results from the same environments showed close aggregation and significant correlations of both axis scores with nutrient availability and disturbance frequency (Fig. 3A; ANOVA: nutrient availability with Axis 1, $F = 11.59$, $P < 0.001$; nutrient availability with Axis 2, $F = 137.6$, $P < 0.001$; disturbance probability with Axis 1, $F = 127.22$, $P < 0.001$; disturbance probability with Axis 2, $F = 20.46$, $P < 0.001$). This indicates the occurrence of contrasting evolutionary pathways in the different environments and a change from similar, sub-optimal, plant strategies at 5000 iterations to more optimal, specialized and environmentally associated strategies at 2 million iterations. Three groups are apparent at 2 million iterations (Fig. 3B): plants that evolved in the high disturbance environments occupy the far left of the ordination, those from

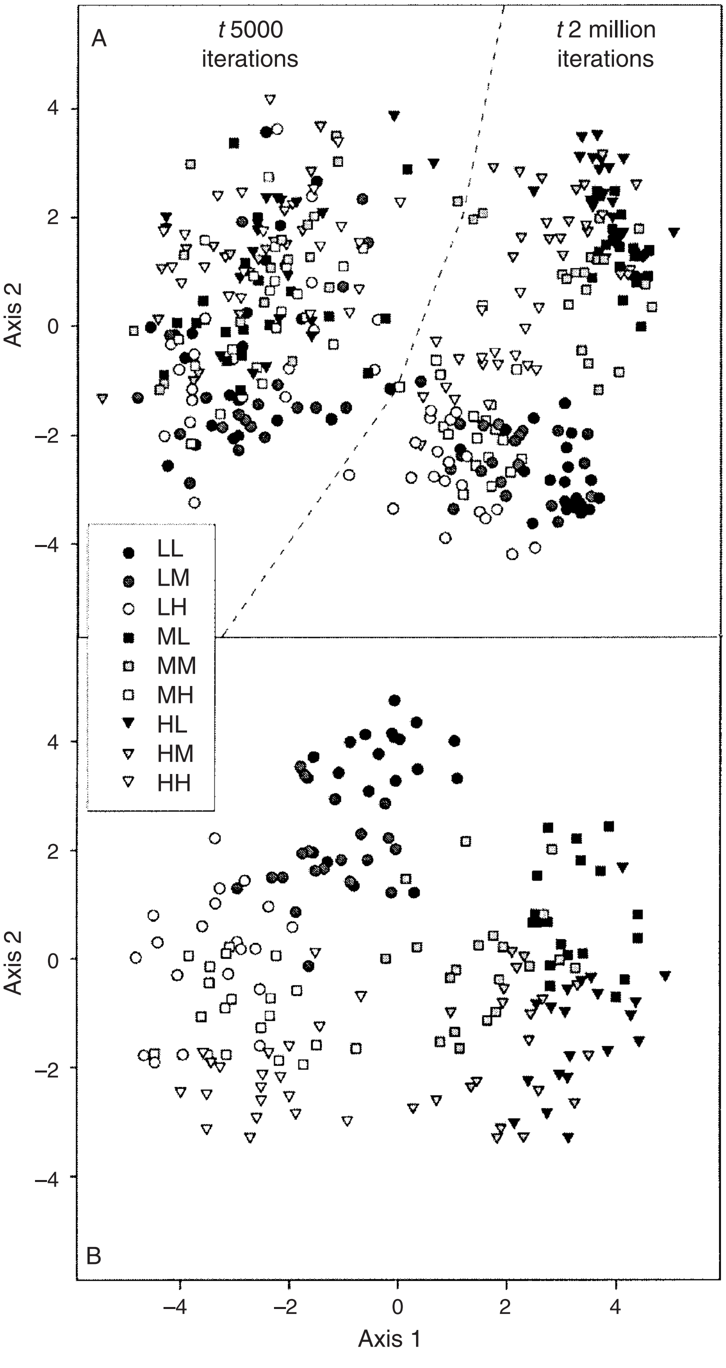
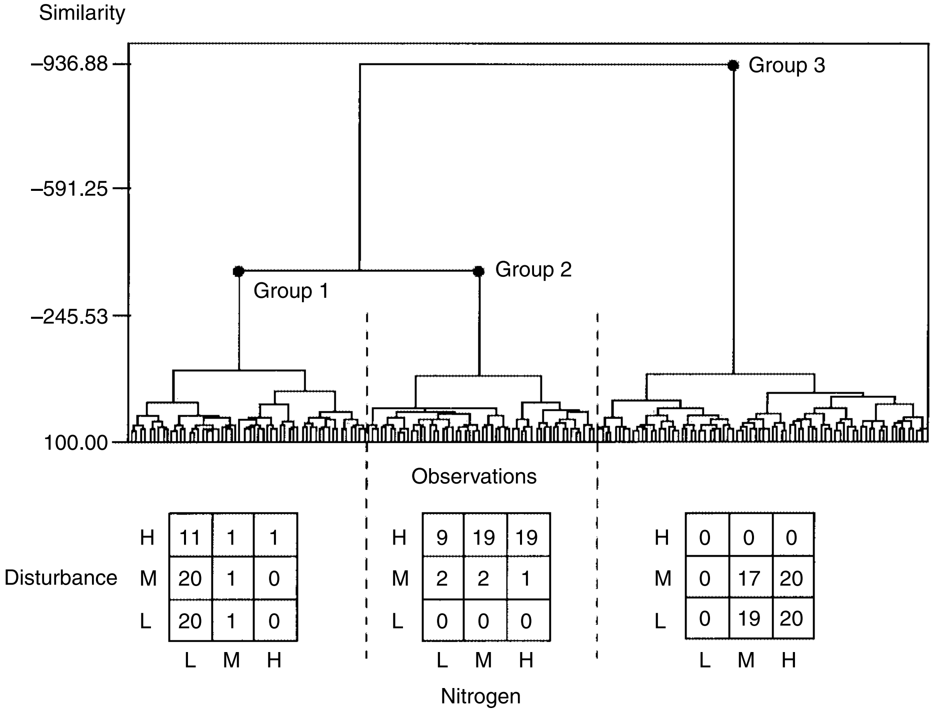


Fig. 3. Principal components analysis (PCA) of the mean plant strategies in all 180 simulations: (A) 5000 iterations and 2 million iterations simulation results combined; (B) 2 million iteration simulation results only. Both graphs share the same Axis 1. Key codes correspond to the simulation nitrogen level (first letter) and disturbance frequency (second letter) with L, M and H being low, medium and high, respectively.

lower-disturbance/high-nitrogen environments occupy the far right, and those from the low-nitrogen/low-disturbance environments occupy the top. Analysis of variance revealed that disturbance probability, but not nitrogen availability, had a significant effect on the Axis 1 scores in Fig. 3B ($F = 204.123$, $P < 0.001$), but that both environmental variables had a significant effect on the Axis 2 scores (nitrogen: $F = 7.535$, $P < 0.001$; disturbance: $F = 23.925$, $P < 0.001$). Similarity analysis split the simulations into three groups corresponding to the three obvious groups in Fig. 3B (Fig. 4). These results reveal a primary axis of dissimilarity separating plants that evolved in low-nitrogen and/or high-disturbance environments (groups 1 and 2) from the rest (group 3). Plants in groups 1 and 2 then clearly separate, at a higher level of similarity, into plants evolving in high-disturbance environments and those evolving in lower-disturbance/low-nitrogen environments (with low-nitrogen/high-disturbance strategies occupying both groups). Below, we have termed groups 1, 2 and 3 'stress tolerators', 'ruderals' and 'competitors', respectively, after Grime (1979).

Analysis of the plant traits in these groups reveals similarities to plants found in analogous environments in nature in both their growth characteristics and their mutable parameters, as well as several notable contradictions (Table 2). Morphologically, the competitors had a greater biomass, height and leaf area than the other two groups, with the stress tolerators being the smallest in these characteristics. Ruderals had the highest



Disturbance	L	M	H
H	11	1	1
M	20	1	0
L	20	1	0

Disturbance	L	M	H
H	9	19	19
M	2	2	1
L	0	0	0

Disturbance	L	M	H
H	0	0	0
M	0	17	20
L	0	19	20

Fig. 4. Similarity analysis of the mean plant strategies in the 180 evolved populations. Simulation membership to each of the three most distinct groups is quantified underneath each group. Clustering was formed using the 'Ward' linkage method and 'Manhattan' distance measure (see Kent and Coker, 1992, for a review of this method).

Table 2. Significant differences in the plant strategies of the three primary groups identified in a similarity analysis of the mean strategies at 2 million iterations

Group in Fig. 2	1	2	3
Morphology			
Biomass	Low	Medium	High
Nitrogen	Low	Medium	High
Height	Low	Medium	High
Nitrogen concentration	Low	High	Low
Leaf area	Low	Medium	High
Specific leaf area	Medium	High	Low
Above : below ground biomass ratio	Medium	High	Low
Proportion of biomass leaves	High	Low	Low
Stored nitrogen	Low	High	Low
Stored carbon	Medium	Low	High
Life history			
Lifespan	Medium	Low	High
Proportion nitrogen allocated to seeds	High	High	Low
Interval between seed production events	High	Low	Medium
Phenotypic responses			
Above : below ground allocation ratio plasticity	Medium	Low	High
Leaf area : leaf weight plasticity	Low	High	Medium
Differential root allocation plasticity	High	High	Low
Nitrogen uptake rate per unit root	High	Low	High
Nitrogen storage propensity	High	Low	High
Carbon storage propensity	High	Low	High
Nitrogen remobilization rate	Medium	Low	High

Note: Significant differences were assessed using analysis of variance on the ranked data. Group numbers correspond to the group numbers in Fig. 4.

nitrogen concentrations, shoot to root biomass ratios, leaf area to leaf weight ratios and stored the most nitrogen. Stress tolerators evolved to have some surprising traits such as intermediate above- to below-ground biomass ratios, and the allocation of the highest proportion of their biomass to leaf production (analogous to rosette plants in nature). In terms of life history, the competitors evolved to live for a long time while allocating a low proportion of resources to seed production and reproducing relatively infrequently. In contrast, ruderals had the opposite characteristics. Stress tolerators lived for an intermediate length of time, reproducing very infrequently but making a large reproductive effort when doing so. In terms of their growth strategies, the competitors evolved high nitrogen uptake capacities, below- to above-ground biomass allocation plasticities and a high capacity for nitrogen and carbon storage. The stress tolerators evolved similar characteristics but evolved a greater root foraging response. In contrast, the ruderals had low capacities for resource storage, had a high root foraging ability but a low ability to differentially allocate carbon between above- and below-ground biomass.

DISCUSSION

Our model has generated a tantalizing mix of results, some that conform to plant strategy theory and others that contradict field evidence. The emergence of a triangle in the ordination parameter space separating competitors, stress tolerators and ruderals, is in clear support of plant strategy theory (Bolker and Pacala, 1999; Grime, 2001). What the model has shown is that differences in nitrogen availability and disturbance frequency alone can result in the evolution of three primary strategies associated with three extreme combinations of these conditions, and the intermediate environmental conditions evolving strategies that lie on a continuum between the three extremes. The fourth extreme environmental state, namely low nitrogen/high disturbance, was found to be incompatible with the long-term persistence and, hence, evolution of the plant populations. This is a significant finding because it is the first time that the 'untenable triangle' hypothesized by Grime (1979) has received theoretical support (Westoby, 1998; Wilson and Lee, 2000), albeit within the major assumptions of our model. The presence of the untenable triangle, and the non-linear ways in which the strategies vary with individual environmental factors (confirmed by the fully nested ANOVA on the PCA in Fig. 3B), indicates an interaction effect between disturbance frequency and nitrogen availability in the evolution of plant strategies. In other words, the strategy that evolves in our model environments is dependent on the state of both environmental factors.

Our model also evolves plants with an intriguing mix of traits, some of which conform to plant strategy theory and field evidence, while others contradict it. However, because of the simplifying assumptions in the model (see p. 1069), both in terms of the model environment and the simplified morphology and physiology in the model, this was not unexpected. For example, the ruderals and stress tolerators evolved to maintain a high proportion of above-ground nitrogen, partly by reducing above- to below-ground allocation plasticities. This mechanism evolved because there was selection to maximize seed production in those environments. Obviously in real life many more physiological variables affect seed production. Plants have been shown to vary their reproductive frequency, effort and seed characteristics in response to environmental change (see, for example, Silvertown, 1988). Our simplifying assumptions prevented this from happening. However, for simplicity, it was not our intention to examine the reasons why every individual trait did or did not evolve as predicted. Our intention was to determine whether the characteristic pattern of plant strategies in the field would evolve in model plant populations experiencing different nitrogen and disturbance regimes. Even those traits that did evolve as predicted by field evidence may have done so 'for the wrong reasons'.

We propose that a much more physiologically realistic model than that presented here is required to investigate the constraints and trade-offs shaping plant functional evolution. For example, the maximum carbon fixation per unit nitrogen (termed 'photosynthetic nitrogen use efficiency') and the leaf area per unit leaf weight (termed 'specific leaf area') are both almost always higher in species adapted to high nitrogen environments than those adapted to low nitrogen environments (Lambers and Poorter, 1992; Poorter and Evans, 1998; Aerts and Chapin, 2002), completely the opposite from what was predicted by our model. However, an explanation for this occurrence in nature is that plants of lower nitrogen environments allocate a higher proportion of their nitrogen allocated to their leaves to non-photosynthetic compounds, mainly in the form of leaf defences (Dijkstra, 1989; Lambers and Poorter, 1992; Evans, 1998; Poorter and Evans, 1998; Aerts and Chapin, 2002). Hence, we predict that if herbivory was incorporated into our model, as well as the ability for the MSPMs to allocate nitrogen between different functional parts (such as leaf defences), the resultant strategies would conform closer to field evidence.

The highly simplified environment and plant structure resulted in the evolution of other, counterintuitive plant growth responses. The dynamics of biomass allocation between above- and below-ground parts and the dynamics of nutrient uptake were especially interesting. Theory and field evidence indicate that plants in extremely low-nutrient environments have high root biomass to shoot biomass ratios, have slow nutrient uptake kinetics, and are less responsive to environmental change, in terms of growth responses, than their high-nutrient environment counterparts (for reviews, see Lambers and Poorter, 1992; Aerts and Chapin, 2000; Grime, 2001). Our plants did not contrast in this way. In the low-nutrient/medium- and low-disturbance environments, the population was always less than the maximum of 100 (usually about 60 individuals), in contrast to the medium- and high-nutrient environments. This suggests that nutrient availability was keeping the carrying capacity of the environment below 100 individuals – that is, the seed production of the population was never sufficient to ensure that every cell was immediately re-colonized when it became empty. By restricting seed size to a set number, and restricting seed production to a function of above-ground biomass, we imposed a possibly false selection pressure on the low-nutrient environment plants to maintain a high proportion of biomass above ground to ensure that at least one seed was produced. This is probably the cause of the relatively high above- to below-ground biomass ratio and the intermediate biomass allocation plasticity in the plants of the low-nutrient environments. These findings highlight an important point to consider when explaining the effects of environmental conditions on the evolution of phenotypic plasticity; namely, that the traits affected by the plastic response may differ in different environments.

Whether or not the plastic response of differential carbon allocation between above- and below-ground biomass is affected by the nutrient availability of the environment remains a controversy in plant ecophysiology (Reynolds and D'Antonio, 1996, and references therein). Our model suggests that the evolution of this plastic response may be affected by various other traits, and that its evolution may be a complicated (possibly non-linear) function of resource availability (and possibly other factors).

The low-nutrient environment plants also evolved rapid resource uptake responses and high abilities to allocate carbon among root pieces. This indicates that there was greater selection pressure in the low-nutrient environments to respond to spatial and temporal variation in nutrient availability than in the high-nutrient environments. This may indeed reflect the fact that there was greater spatial and temporal variation in nutrient availability in those environments (a variable we never measured). In the more highly populated environments of higher nutrient availability, cells would have been more likely to have a large number of competing roots in them; hence any heterogeneity would have been rapidly shared out among competing individuals. In contrast, in the low-nutrient environments there were more empty cells. As a result, there would have been more chance that a plant may have experienced a low competition nutrient patch. Gersani *et al.* (2001) used game theory to show that plants should first exploit unoccupied soil patches, then those occupied by competitors and, lastly, those occupied by their own roots. Our results support this finding and the finding by Robinson and Van Vuuren (1998) that plants in low-nutrient environments tend to have higher nutrient uptake rates per unit root.

Finally, it was not possible to ascertain whether or not the trends in the resource storage responses (carbon and nitrogen storage plastic responses and remobilization rates; Table 2) conformed to real-life patterns due to the lack of data available for comparison. There is some evidence that plants in low-resource environments evolve the 'luxury consumption' response in which they take up and store nutrients when they become available (Clarkson, 1967; Grime, 2001). However, the exact reason for this occurrence is controversial (Grime, 2001). What our results do suggest is that the evolution of resource storage responses may be affected by the environmental conditions in which the plants evolve, and suggest the directions in which this may occur.

What is clear from this study is that this modelling tool (evolutionary models) is a useful way of investigating species functional evolution, including the evolution of phenotypic plasticity. Although it is highly complex and parameter-rich, it has produced a set of results that can be compared with those for plants in real environments and can be used to investigate further the environmental factors, constraints and trade-offs that are responsible for the suites that we observe in real plants. The reasons why multiple strategies did not evolve within a simulation require further investigation. The fact that the populations were small and fully mixed (random seed dispersal) intuitively suggests that there was little opportunity for divergent evolution because more fit strategies could have dominated the seed bank and, hence, the population. However, we propose that this modelling approach offers a promising way to investigate the factors that promote the evolution of biodiversity.

REFERENCES

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**: 439–449.

Aerts, R. and Chapin, F.S., III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.*, **30**: 1–67.

Anten, N.P.R., Schieving, F. and Werger, M.J.A. 1995. Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species. *Oecologia*, **101**: 504–513.

Begon, M., Harper, J. and Townsend, C. 1996. *Ecology: Individuals, Populations and Communities*, 3rd edn. Oxford: Blackwell Science.

Bolker, B.M. and Pacala, S.W. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, **153**: 575–602.

Chapin, F.S., III, Autumn, K. and Pugnaire, F. 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.*, **142**: S76–S92.

Clarkson, D.T. 1967. Phosphorus supply and growth rate in species of *Agrostis* L. *J. Ecol.*, **55**: 111–118.

Crawley, M.J. 1997. Life history and environment. In *Plant Ecology* (M.J. Crawley, ed.), pp. 73–131. Oxford: Blackwell Science.

Dijkstra, P. 1989. Cause and effect of differences in specific leaf area. In *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants* (H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons, eds), pp. 125–140. The Hague: SPB Academic.

Eissenstat, D.M. and Yanai, R.D. 1997. The ecology of root lifespan. *Adv. Ecol. Res.*, **27**: 1–60.

Evans, J.R. 1998. Photosynthetic characteristics of fast- and slow-growing species. In *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences* (H. Lambers, H. Poorter and M.M.I. Van Vuuren, eds), pp. 101–119. Leiden: Backhuys.

Gersani, M., Brown, J.S., O'Brien, E.E., Maina, G.M. and Abramsky, Z. 2001. Tragedy of the commons as a result of root competition. *J. Ecol.*, **89**: 660–669.

Greenslade, P.J.M. 1983. Adversity selection and the habitat template. *Am. Nat.*, **122**: 352–365.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Chichester: Wiley.

Grime, J.P. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. Chichester: Wiley.

Grime, J.P., Thompson, K., Hunt, R. *et al.* 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**: 259–281.

Grubb, P.J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives Plant Ecol. Evol. Syst.*, **1**: 3–31.

Ingestad, T. and Ågren, G. 1992. Theories and methods on plant nutrition and growth. *Physiol. Plantarum*, **84**: 177–184.

Jungk, A. 1991. Dynamics of water movement at the soil–root interface. In *Plant Roots, the Hidden Half* (J. Waisel, A. Eshel and U. Kafkafi, eds), pp. 455–481. New York: Marcel Dekker.

Kent, M. and Coker, P. 1992. *Vegetation Description and Analysis: A Practical Approach*. Chichester: Wiley.

Lambers, H. and Poorter, H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.*, **23**: 187–261.

Lambers, H., Poorter, H. and Van Vuuren, M.M.I., eds. 1998. *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences*. Leiden: Backhuys.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McDonald, A.J.S. 1989. Phenotypic variation in growth rate as affected by N-supply: its effects on net assimilation rate (NAR), leaf weight ratio (LWR) and specific leaf area (SLA). In *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants* (H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons, eds), pp. 35–44. The Hague: SPB Academic.

Niklas, K.J. 1997. *The Evolutionary Biology of Plants*. Chicago, IL: University of Chicago Press.

Peuke, A.D. and Jeschke, W.D. 1998. The effects of light on induction, time courses, and kinetic patterns of net nitrate uptake in barley. *Plant Cell Environ.*, **21**: 765–774.

Pianka, E.R. 1980. On *r*- and *K*-selection. *Am. Nat.*, **104**: 592–597.

Poorter, H. and Evans, J.R. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, **116**: 26–37.

Post, W.M., Pastor, J., Zinke, P.J. and Stangenberger, A.G. 1985. Global patterns of soil nitrogen storage. *Nature*, **317**: 613–616.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, V., Violin, J.C. and Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**: 1955–1969.

Reynolds, H.L. and D'Antonio, C. 1996. The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant and Soil*, **185**: 75–97.

Robinson, D. 1996. Resource capture by localized root proliferation: why do plants bother? *Ann. Bot.*, **77**: 179–185.

Robinson, D. and Van Vuuren, M.M.I. 1998. Responses of wild plants to nutrient patches in relation to growth rate and life form. In *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences* (H. Lambers, H. Poorter and M.M.I. Van Vuuren, eds), pp. 237–257. Leiden: Backhuys.

Schieving, F. and Poorter, H. 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytol.*, **143**: 201–211.

Schmitt, J. 1997. Is photomorphogenic shade avoidance adaptive? Perspectives form population biology. *Plant Cell Environ.*, **20**: 826–830.

Sibly, R.M. and Grime, P.J. 1986. Strategies of resource capture by plants – evidence for adversity selection. *J. Theor. Biol.*, **118**: 247–250.

Silvertown, J. 1988. The paradox of seed size and adaptation. *Trends Ecol. Evol.*, **4**: 24–26.

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*, **52**: 3–18.

Standing, D.B. 2001. Growth and survival of plants in patchy environments. PhD thesis, University of Aberdeen.

Stearns, S.C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.*, **3**: 259–268.

Stearns, S.C. and Hoekstra, R. 2000. *Evolution: An Introduction*. Oxford: Oxford University Press.

Strand, E., Huse, G. and Giske, J. 2002. Artificial evolution of life history and behaviour. *Am. Nat.*, **159**: 624–644.

Taylor, D.R., Aarssen, L.W. and Loehle, C. 1990. On the relationship between *r*/*K* selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, **58**: 239–250.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton, NJ: Princeton University Press.

Warren, J. and Topping, C. 2001. Trait evolution in an individual-based model of herbaceous vegetation. *Evol. Ecol.*, **15**: 15–23.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**: 213–227.

Wilson, J.B. and Lee, W.G. 2000. C-S-R triangle theory: community-level predictions, tests, evaluation of criticisms, and relation to other theories. *Oikos*, **91**: 77–96.

Yedid, G. and Bell, G. 2002. Macroevolution simulated with autonomously replicating computer programs. *Nature*, **420**: 810–812.