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A coupled map lattice model of the growth of plant monocultures

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Abstract

A coupled map lattice (CML) model is used to analyse the role of neighbourhood effects and competition on spatial patterns and size hierarchies in annual plant monocultures. The results are compared with those from a traditional model of circular zones, and show that the CML results are highly robust over a range of densities. Asymmetric competition is observed to give rise to increased size variability compared to symmetric competition. Spatial effects are concluded to be secondary to the degree of competitive asymmetry.

Keywords: Competition, intraspecific; Population dynamics; Size variability; Spatial interactions

1. Introduction

In this paper we examine two of the major processes that are commonly thought to govern spatial and morphological patterns in plant monocultures. These are (1) neighbourhood/spatial effects and (2) the form of competition between individuals (Mead, 1966; Mack and Harper, 1977; Weiner, 1990). We are particularly concerned with the effect that these processes have on individual plant growth and the generation of size hierarchies in monocultures, because size directly affects both survival and fecundity.

Most plant populations show great variability in plant size, and there has been much interest in the determinants of size variation (Benjamin and Hardwick, 1986; Weiner, 1986). With a few notable exceptions (Turner and Rabinowitz, 1983; Ellison, 1987), populations of plants grown at higher densities show greater size inequality than populations grown at lower densities (Weiner and Thomas, 1986; Schmitt et al., 1987; Knox et al., 1989). Two alternative views of how competition contributes to the generation of size hierarchies have been advanced. One view holds that competition among plants is usually asymmetric, i.e. larger plants are able to obtain a disproportional share of contested resources, suppressing the growth of smaller plants; this asymmetry exaggerates size differences (Weiner, 1990). An opposing view emphasizes the role of spatial effects. Because plants do not grow in a perfectly uniform pattern, individuals vary in the degree of crowding they experience. Hence variation in growth rates, caused by differences in local neighbourhood conditions, leads to size differences (Bonan, 1988,1991).

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A full mechanistic understanding of plant competition is far beyond our present understanding. We know that competition depends upon which resources are being contested (Fowler, 1984) and on plant morphology (Geber, 1989). Larger plants shade smaller ones, so competition for light appears to be asymmetric (Weiner, 1990), but competition below ground may be more symmetric (Weiner, 1986; Wilson, 1988). The presence of density-dependent mortality (self-thinning) has complicated these questions, because it is the smallest plants that die, reducing the size variation. Since plant competition is local, spatial structure of the population is believed to be very important, but this has proved difficult to demonstrate.

We present the results from two different models aimed at (i) examining the effects of space and competition on individual plant growth and (ii) generating testable results on the relationships between size variability, density dependence, self-thinning and growth rates for further field studies. Both models use an individual plant approach, as this is thought to be the appropriate level on which to measure plant growth (Silander and Pacala, 1985; Czárán and Bartha, 1992; Ford and Sorrensen, 1992; McGlade, 1993; Judson, 1994). In particular we test:

- the assertion by Bonan (1988,1991) that a positive relationship between density and size inequality is evidence for neighbourhood effects and does *not* indicate the presence of competitive asymmetry.
- the claim by Miller and Weiner (1989) that neighbourhood effects without asymmetry can only give rise to a positive relationship between density and size inequality over a range of very low densities. In their models increasing inequality at higher densities occurred only when competition was asymmetric.

Our main model is a coupled map lattice (Hassell et al., 1991; Bignone, 1993) based on a square grid. The second model comes explicitly from Bonan (1988,1991) and uses circular zones of influence about each plant; the only difference is that we treat the boundaries as continuous or wrap-around. These schemes are both appropriate for modelling sessile organisms. In each case the overlaps between neighbouring plants are calculated and the growth modelled for four types of competition (absolute asymmetry, relative asymmetry, absolute symmetry, relative symmetry). Stochasticity is limited to the random distribution of seedlings in the stand, so that neighbourhood effects are isolated. Whilst previous models have considered uniform patterns of plants, these are not realistic for natural populations and so we did not use them here. Finally, because density-dependent mortality has been said to mask the effects of asymmetric competition, we have suppressed death by restricting growth to be non-negative.

2. The coupled map lattice model (CML)

2.1. Coupled map lattice models

A coupled map lattice (CML) is usually based on a square grid of cells. Each cell has a continuous variable which is updated every time step as a function of its own value and those of the cells in a specified neighbourhood. In contrast with cellular automata (Wolfram, 1986; Ermentraut and Edelstein-Keshet, 1993), the values are not restricted to integers and are generated deterministically. A toroidal coupled map lattice is one in which the boundaries are periodic (Haefner et al., 1991). The neighbourhood of any cell on a boundary includes cells on the opposite boundary; the left and right boundaries are considered to be joined, likewise the top and bottom edges.

2.2. The mathematical model

Our model uses a toroidal CML where the value of each cell represents the mass of the plant present. The mass is given as a proportion of the maximum possible plant size attainable by an uninhibited plant, multiplied by a factor of 1.1. This factor allows for possible over-shooting caused by the discrete nature of the mathematical model. Each cell has a fixed area equal to one fifth of the maximum area attainable by a plant grown under the conditions set by the model. This is justified as follows. The ('von Neumann')

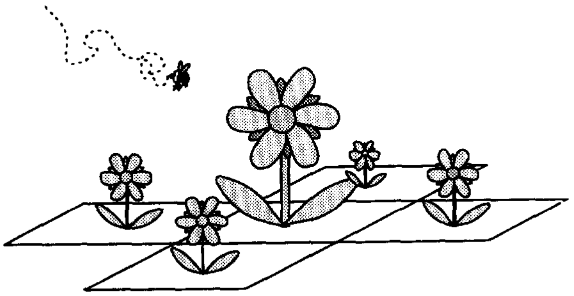

Fig. 1. Configuration of the lattice cell neighbourhood.

neighbourhood of a cell consists of its four nearest neighbours and itself – a total of five cells (Fig. 1). As this is a model of competition between plants, we have restricted plant growth so that it is never larger than its neighbourhood (or zone of influence). If this rule were violated, the plant would grow into regions where the model could not treat the interactions. Hence a suitable cell size is one fifth of the maximum area occupied by a single plant. The following mathematical model controls the growth of the plants through time. It is an extension of the model of Aikman and Watkinson (1980) and includes explicit spatial effects.

The change in mass (Δm_i) of plant i from one time step to the next is given by Eq. 1. a_i is the area covered by plant i and is given by the '3/2 self-thinning rule' of Eq. 2 (Westoby, 1984). l_i is the growing area lost via competition, g is the intrinsic growth rate of the plant, b and c are constant parameters and Δt is the time step.

$$\Delta m_i = \left(g(a_i - l_i) - bm_i^2\right)\Delta t \tag{1}$$

$$a_i = cm_i^{2/3} \tag{2}$$

We need to establish the lost growing area for a plant in the lattice as a result of the competitive regime under consideration. This involves finding the areas by which neighbouring plants overlap each other. Firstly, the maximum size for a plant that is not experiencing competition $m_i^{\max}$ is obtained from Eq. 1 by taking $l_i = 0$ and $\Delta m_i = 0$:

$$ga_i = bm_i^2 \Rightarrow m_i^{\max} = \left(\frac{gc}{b}\right)^{3/4}$$

Hence, by Eq. 2, the area of each lattice cell, α, as the maximum mass is divided over five sites, is:

$$\alpha = \frac{c}{5}\sqrt{\frac{gc}{b}}$$

Assuming that a plant overflowing its own cell expands equally into the areas occupied by its four neighbours, the overlap into a neighbouring cell of plant i is:

$$\max\left(\frac{a_i - \alpha}{4}, 0\right)$$

and hence the total overlap between two neighbours i and j is:

$$\Omega_{i,j} = \max\left(\frac{a_i - \alpha}{4}, 0\right) + \max\left(\frac{a_j - \alpha}{4}, 0\right)$$

The overlap is nonlinear because of the presence of the 'max' function, but it is continuous in terms of both of the plant masses. A discontinuity arises in the derivative (which is a Heaviside step function), but this reflects the underlying biological assumption that plants do not interact until they reach a certain size. The circular neighbourhood model also implicitly contains this same nonlinearity. This pairwise overlap function leads to Eq. 3, which gives the total overlap of the area of the plant, Ω_i. *nhd* denotes the four-cell neighbourhood described above. (This is not a perfect model of the overlap of areas, but is a good approximation of the infinitely recursive series of overlaps that would have to be considered for an exact representation.)

$$\Omega_i = \sum_{j \in nhd} \max\left(\frac{a_i - \alpha}{4}, 0\right) + \max\left(\frac{a_j - \alpha}{4}, 0\right) \tag{3}$$

The area lost to competition, l_i, depends on the four types used in the model:

- For *absolute asymmetry*, the larger plant of two plants takes resources from the entire overlap area; equal-sized plants will share the area equally.
- For *absolute symmetry*, plants divide the area equally.

- For relative situations, the overlap is weighted by the relative masses: linearly for *relative symmetry*, quadratically for *relative asymmetry*.

Hence Eq. 4 can be derived to give the total area lost to competitors under the different regimes, respectively:

$$l_i = \begin{cases} \sum\limits_{j \in nhd} \frac{1}{2}\Omega_{i,j} \\ \sum\limits_{j \in nhd} \dfrac{m_j}{m_i + m_j}\Omega_{i,j} \\ \sum\limits_{j \in nhd} \dfrac{m_j^2}{m_i^2 + m_j^2}\Omega_{i,j} \\ \sum\limits_{j \in nhd} \phi_{i,j}\Omega_{i,j} \end{cases} \tag{4}$$

where:

$$\phi_{i,j} = \begin{cases} 0 & m_i > m_j \\ 1 & m_i < m_j \\ \frac{1}{2} & m_i = m_j \end{cases}$$

As self-thinning may mask the effects of local neighbourhood interactions and variations in competitive regime, density-dependent mortality is suppressed in this model. When $\Delta m_i < 0$, plant growth is prevented by setting this increment to zero.

2.3. Analysis of the basic model

The model of Eqs. 1 and 2 is appropriate for annual plants. This section considers the density-dependent behaviour of the model when applied to a symmetric mean field or non-spatial scenario. If a certain number of plants is grown in a fixed area, then, under symmetric competition, each plant has a fixed maximum growing area, denoted by A. If the plants are able to reach the maximum mass, $m^{\max} = (gc/b)^{3/4}$, before they suffer competition, then clearly the plants grow to this terminal size. If they fill the available area, no further growing space exists and their growth is restricted. This modifies the maximum size by changing the growing area a_i to A, so that $m^{\max} = \sqrt{gA/b}$. There is thus a threshold density, above which the maximum plant mass is constrained. This threshold can be determined by setting the area in Eq. 2 to A. Hence the density-dependence of the terminal mass is given by:

$$m^{\max} = \begin{cases} \sqrt{\dfrac{gA}{b}} & A < \sqrt{\dfrac{gc^3}{b}} \\ \left(\dfrac{gc}{b}\right)^{3/4} & A \geq \sqrt{\dfrac{gc^3}{b}} \end{cases}$$

Hence the maximum yield per unit area, Y, can be obtained in terms of the density, $\rho \equiv 1/A$:

$$Y = \begin{cases} \rho\left(\dfrac{gc}{b}\right)^{3/4} & \rho < \sqrt{\dfrac{b}{gc^3}} \\ \sqrt{\dfrac{g\rho}{b}} & \rho \geq \sqrt{\dfrac{b}{gc^3}} \end{cases}$$

However, the maximum yield does not become infinite as growing space declines to zero, because the growing time is restricted for annual plants. A suitable range of densities for the model must therefore be estimated.

3. The circular neighbourhood model

An alternative spatial model of plant monoculture development involves the construction of circular neighbourhoods (or 'zones of influence') (Ford and Diggle, 1981; Firbank and Watkinson, 1985). The simulations allow plants to grow on a square plot. The plot edges are treated toroidally, as with the coupled map lattice. Seedlings are randomly distributed over the plot and growth is simulated using the same model as before (Eqs. 1 and 2). The technique for allocation of seedlings ensures that the zones of influence do not initially overlap so that competition cannot occur immediately. The area of a plant (Eq. 2) is translated into a circle of appropriate radius centred on the plant.

The spatial scheme is illustrated in Fig. 2, which represents a plot occupied by eight plants, labelled A to H. Plants A and B overlap the plot edge. In order that the plot may be treated as a torus, A* and B* are created as imaginary or

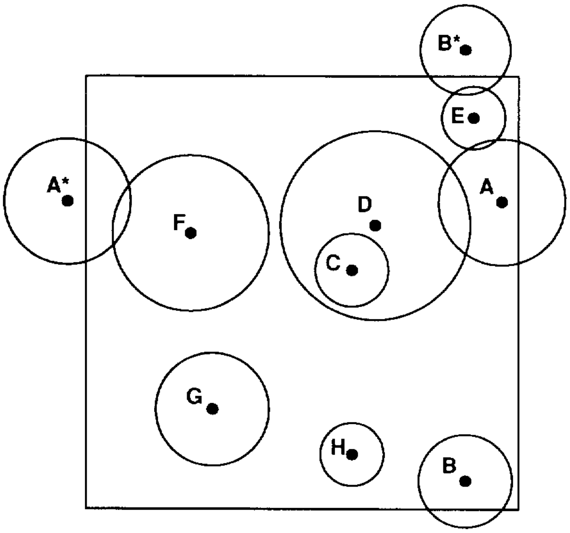

Fig. 2. Schematic representation of eight plants, A–H. A* and B* are 'virtual' plants, generated to satisfy the toroidal (periodic) boundary conditions.

'virtual' plants. These have 'real' effects on neighbours E and F (respectively). Thus G and H have no close neighbours; B, C and F have one neighbour; D and E have two neighbours; A has three neighbours (D, E and F). Plant C is entirely within the zone of influence of plant D and under absolutely asymmetric competition would not be able to grow.

To calculate the growing area lost to competition, l_i, the overlaps between neighbouring plants are needed. The overlap between two interfering neighbours, i and j, with zones of radius p and q respectively, which are a distance d apart, is:

$$\Omega_{i,j} = p^2 \cos^{-1}\left(\frac{p^2 + d^2 - q^2}{2pd}\right) + q^2 \cos^{-1}\left(\frac{q^2 + d^2 - p^2}{2qd}\right) - qd \sin\left(\cos^{-1}\left(\frac{q^2 + d^2 - p^2}{2qd}\right)\right)$$

where:

$$p = \sqrt{\frac{cm_i^{2/3}}{\pi}} \text{ and } q = \sqrt{\frac{cm_j^{2/3}}{\pi}}.$$

If one plant is entirely contained within the zone of influence of another, then the overlap is equal to the area of the smaller circle ($cm_i^{2/3}$). The lost growing area is then calculated according to the type of competition, as in Eq. 4. In this model the neighbourhood *nhd* of plant i consists of all plants whose zones of influence overlap plant i. Again, mortality is avoided by constraining the mass increment to obey $\Delta m_i \geq 0$.

4. Population statistics and simulation parameters

4.1. Statistical measures

The following statistics were used to examine the plant population statistics of the two models. The mean mass μ (Eq. 5) is averaged over the lattice/plot, denoted by L. The coefficient of variation (Eq. 6) is the standard deviation adjusted for the mean mass. This provides a good measure of the variability within a population. Another indicator of variability is the Gini coefficient, which is related to the Lorenz curve of cumulative frequencies. Eq. 7 gives a relatively unbiased estimator of the Gini coefficient for $\|L\| > 100$ (Weiner and Solbrig, 1984; Dixon et al., 1987; Bendel et al., 1989).

$$\mu = \frac{1}{\|L\|} \sum_{i \in L} m_i \tag{5}$$

$$\text{coefficient of variation} = \frac{1}{\mu} \sum_{i \in L} \frac{(m_i - \mu)^2}{\|L\| - 1} \tag{6}$$

$$\text{Gini coefficient} = \frac{\sum_{i \in L} \sum_{j \in L} |m_i - m_j|}{2\|L\|(\|L\| - 1)} \tag{7}$$

Table 1
Parameter values for the growth equations 1 and 2

g	25	$\mathrm{g\ m^{-2}\ day^{-1}}$
b	0.00147	$\mathrm{g\ day^{-1}}$
c	0.00434	$\mathrm{m^{-2}\ g^{-2/3}}$

4.2. Computational details

Table 1 gives the parameters for Eqs. 1 and 2, which are taken from Bonan (1991). A time step of $\Delta t = 1$ day was used, after comparative simulations showed negligible need for smaller steps. Seedlings are sown with size $0.1g$, which is small enough (by several orders of magnitude) to ensure that there is no competition in the first few times steps. Previous studies of spatial plant growth involve the variation of the initial mass and parameters g, c or b. These variations are usually taken to be Gaussian. Such distributions are often used to represent a variety of biological phenomena, e.g. genetic variation, micro-environmental heterogeneity and variation in seedling emergence times. The parameters are taken to be constant here so that spatial/neighbourhood effects and the influence of the competitive regime may be studied. Runs with a uniform distribution of initial seedling mass between 0 and $0.1g$ produced very similar results to those with a constant seedling size of $0.1g$.

The CML model was run on grids of 20 by 20, 50 by 50 and 100 by 100 cells. Densities are expressed here as the proportion of cells occupied by plants, ranging from 0.1 to 1.0. The circular neighbourhood model was run on a square plot with dimensions of $0.1m$. Densities are given in terms of the number of plants randomly distributed on this plot; specifically the ten values are 7, 19, 37, 61, 91, 127, 181, 233, 291 and 355 plants, as used by Bonan (1991). This range extends to higher values than the CML; the latter is restricted by the ratio of neighbourhood size to cell size. Repeated simulations were run to produce smoother averaged results. The statistical variables considered are mean, coefficient of variation and Gini coefficient. The distribution of sizes was also considered.

5. Results

5.1. Coupled map lattice model

The growth of plants through time, for five different densities in the range 0.2 to 1.0, is illustrated by Fig. 3. The absolute symmetric regime is illustrated here, but the form of growth is similar for all of the types of competition. The mass is seen to increase sigmoidally with time and to decrease as density rises. Equilibrium has been (approximately) attained within the 200 time steps. These results shown are those obtained from a 20 by 20 grid. The model was also run for larger grid sizes, but as the growth did not differ in any way, we have used a smaller grid size for computational speed.

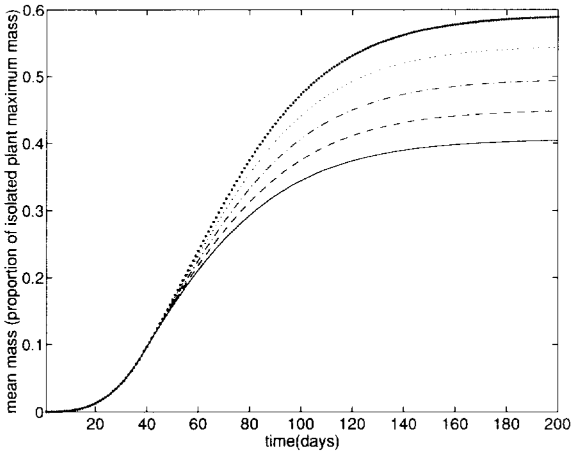

Fig. 3. Mean mass (proportion of maximum isolated plant size) of plants grown under a coupled map lattice model as a function of time. The five curves show different densities, from 0.2 (···) to 1.0 (—) rising in steps of 0.2. Competition is absolutely symmetric.

The model was then run for 200 time steps (= 200 days) on a 50 by 50 lattice, for ten different densities in the range 0.1 to 1.0. The results were averaged over 50 simulations. Figs. 4a–c give the dependence on density of mean mass, coefficient of variation and Gini coefficient.

The distribution of plant sizes after 500 time steps is shown in Figs. 5a–d for density 0.5. These graphs were produced by a single run on a 50 by 50 lattice. The large time used ensured that the equilibrium was reached in all cases. At this density of 0.5, the distributions contain fewer peaks as the degree of asymmetry increases, but they become narrower. When the density was set at 1.0, we obtained a single very sharp peak for all competitive types.

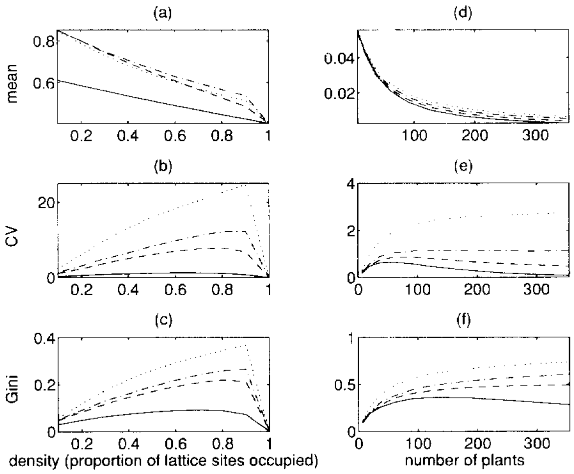

Fig. 4. (a)–(c) Results for the CML model at time 200 days. (a) Mean mass (proportion of maximum isolated plant size) as a function of density. (b) Coefficient of variation of mass as a function of density. (c) Gini coefficient of mass as a function of density. (d)–(f) Results for the circular neighbourhood model at time 100 days. (a) Mean mass (gm) as a function of number of plants (equivalent to density). (e) Coefficient of variation of mass as a function of number of plants. (f) Gini coefficient of mass as a function of number of plants. In all cases the competitive types are absolute symmetry (—), relative symmetry (---), relative asymmetry (-·-·-) and absolute asymmetry (···).

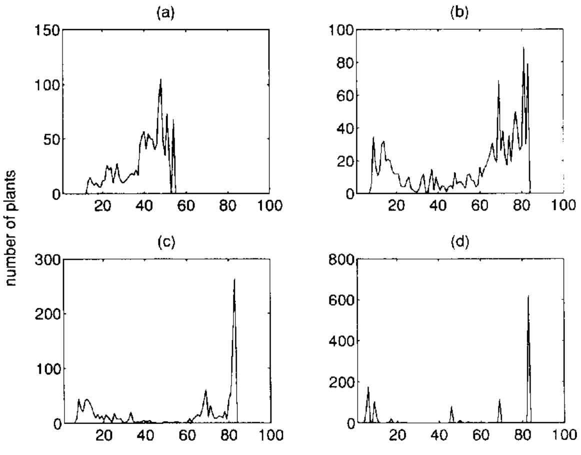

Fig. 5. Distribution of plant sizes at time 500 and density 0.5 for the CML model, as a percentage of the maximum size of an isolated plant. (a) Absolute symmetry. (b) Relative symmetry. (c) Relative asymmetry. (d) Absolute asymmetry.

5.2. Circular neighbourhood model

The model was run for 100 time steps at ten different densities (7 to 355 plants in the plot) and the results averaged over 100 simulations. Figs. 4d–f give the dependence on density of the three statistics of mass: mean, coefficient of variation and Gini coefficient. The model was run for the higher densities of 400, 450, 500 and 550, but the results showed no different behaviour. It should be noted that these new results using Bonan's model are different from those reported in Bonan (1991), in particular the results here are smooth due to the number of replicated runs.

5.3. Self-thinning

Whilst the condition $\Delta m_i \geq 0$ prevents density-dependent mortality, it is of interest to find the extent to which this constraint is implemented. The two models were run for 100 time steps and the number of plants where the mass

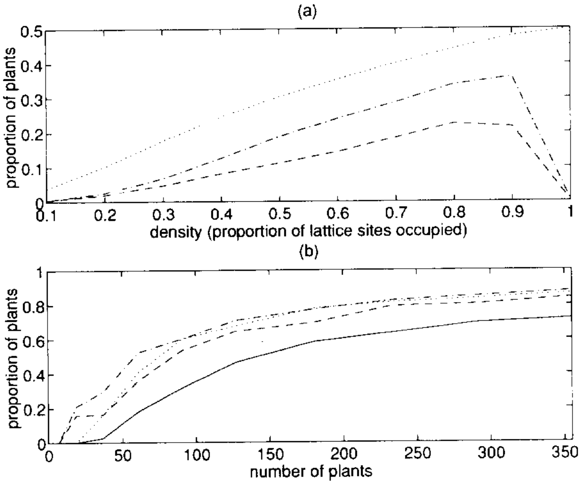

Fig. 6. The proportion of plants which stop growing by time 100 days. (a) CML model, shown as a function of density. (b) Circular neighbourhood model, shown as a function of initial number of plants. In both cases the competitive types are absolute symmetry (—), relative symmetry (---), relative asymmetry (-·-·-) and absolute asymmetry (···). (The values are so low in the CML model for absolute symmetry (a) that the curve (—) is not easily distinguished from the horizontal axis).

increment was reset to zero was found as a function of density. The circular neighbourhood model was run once because of the highly intensive computation, whereas the CML was averaged over 50 simulations. Figs. 6a and b illustrate the results. The degree of self-thinning that would occur, if permitted, increases with the level of asymmetry, particularly for the CML.

6. Discussion

Our results show that the mean mass decreases as density increases (Figs. 4a and d). Because mass in the CML is given as a proportion of maximum isolated plant size, it is clear that size has been constrained by competition. We would thus consider competition to be a boundary constraint on plant size as previously described by Goldberg (1987).

Growth of the plants is sigmoidal, so the early phase is exponential. Turner and Rabinowitz (1983) claim that variation in the early exponential phase of growth leads to the generation of size hierarchies. However, we have found that interference does not occur immediately, as mass is the same for all densities for the first 50 or so time steps (Fig. 3). As the initial plant masses are constant and no competition occurs during the early part of growth, there can be no size hierarchy formation at this stage. Variation in growth rates can thus only occur when competition sets in *after* the exponential stage of growth.

The mean mass of plants is similar for all the competitive schemes, except for the absolute symmetry in the CML (Fig. 4a). This may be attributed to the equal sharing of resources, i.e. two neighbours of a similar size in adjacent cells prevent each other growing. If there is any asymmetry present, at least one of the plants is able to grow. Because of this, the even spacing of plants caused by the regularity of the lattice and interference by neighbours the total population yield is suppressed.

The coefficient of variation and Gini coefficient demonstrate the existence of variation in the population allowing us to see that size hierarchies are formed (Figs. 4b, c, e and f). The variation increases as the density rises, because higher densities lead to earlier and stronger interactions between plants. The variation is considerably greater with absolute asymmetric competition. There is a clear difference between the coefficient of variation for relative symmetry and absolute asymmetry, which are the most commonly considered modes of competition (Figs. 4b and e). The difference is less marked with the Gini coefficient (Figs. 4c and f). Bendel et al. (1989) have noted that the coefficient of variation is more sensitive to hierarchy differences than the Gini coefficient. It is therefore reasonable to state that the formation of hierarchies can distinguish between symmetric and asymmetric competition, as claimed by Miller and Weiner (1989) and Weiner (1985,1986,1990) but disputed by Bonan (1988,1991). There is, however, some variation even in the symmetric case. This confirms that spatial/neighbourhood effects do play a role in the generation of size variability (Bonan, 1988,1991), but they are secondary to the competitive regime. The use of the four different symmetries illustrates the progressive nature of competition mechanisms. It is relevant to express the conclusion as follows: *higher variability at higher densities implies greater asymmetry in neighbourhood interactions.*

There is a sudden decrease in all the mass statistics at the highest density of the CML (Figs. 4a–c) which is caused by the regularity of the lattice. This is because for low and intermediate densities, the plants are scattered through the grid, whereas when the lattice is full (density 1.0), the plants are necessarily regularly spaced, so the randomness of the spatial distribution is lost. The rate of increase in the coefficient of variation and Gini coefficient for both models falls off as density rises. This reflects a decrease in the effective randomness of the distribution as the initial density of plants is increased. There is less variation at higher densities in the overlapping of zones of influence and so the growth rates and hence the plant sizes are more similar.

The hierarchy is still able to remain strong in the asymmetric case and there is a large variation in plant sizes (Figs. 5c and d). Here the asymmetry dominates the plant growth and the distribution is of secondary importance in determining the final population structure. The size distribution plots (Figs. 5a–d) give an insight into the effects of the degree of asymmetry on the population structure. Symmetric competition results in a wide distribution, which is skewed to the right because of the suppression of mortality. Absolute asymmetry restricts the plants to a discrete set of sizes.

The levels of self-thinning (Figs. 6a and b) exhibit an appreciable difference between the two models. The coupled map lattice shows that greater asymmetry leads to more density-dependent mortality, as suggested by Bonan (1988). The self-thinning is less dependent on symmetry in the circular neighbourhood model. Greater asymmetry means that large plants cause the death of smaller plants, whereas with symmetry, similar neighbours will reduce each others' growth rather than bring about death. These discrepancies between the models demonstrate that the type of spatial distribution used is important.

The comparison of the two types of model (CML and circular neighbourhood model) highlights the issue of the aims of ecological modelling (Wissel, 1992). The excessive computation of the latter type of model limits the extent of investigation of the system. The CML allows critical mechanisms to be quickly and thoroughly studied and general results extracted; it is ideal for use at low and intermediate densities. The current implementation of the CML does have the shortcoming of limiting the upper end of the density range. However, the model is suitable for extension to higher densities by developing the use of larger neighbourhoods (such as the 9-cell 'Moore' neighbourhood).

In summary, the results of both models support the view that size hierarchies can be used as evidence to distinguish between asymmetric and symmetric competition (Weiner and Thomas, 1986) over the alternative view that size hierarchies are evidence for neighbourhood effects (Bonan, 1988,1991). Theory suggests that asymmetric competition can be a key factor in determining size variation in plant populations and communities.

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References

Aikman, D.P. and Watkinson, A.R., 1980. A model for growth and self-thinning in even-aged monocultures of plants. Ann. Bot., 45: 419–427.

Bendel, R.B., Higgins, S.S., Teberg, J.E. and Pyke, D.A., 1989. Comparison of skewness coefficient, coefficient of variation and Gini coefficient as inequality measures with populations. Oecologia, 78: 394–400.

Benjamin, L.R. and Hardwick, R.C., 1986. Sources of variation and measurement of variability in even-aged stands of plants. Ann. Bot., 58: 757–778.

Bignone, F.A., 1993. Cells–gene interactions simulated on a coupled map lattice. J. Theor. Biol., 161: 231–249.

Bonan, G.B., 1988. The size structure of theoretical plant populations: spatial patterns and neighbourhood effects. Ecology, 69: 1721–1730.

Bonan, G.B., 1991. Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. Ann. Bot., 68: 341–347.

Czárán, T. and Bartha, S., 1992. Spatiotemporal dynamic models of plant populations and communities. TREE, 7(2): 38–42.

Dixon, P.M., Weiner, J., Mitchell-Olds, T. and Woodley, R., 1987. Bootstrapping the Gini coefficient of inequality. Ecology, 68: 1548–1551.

Ellison, A.M., 1987. Density-dependent dynamics of *Salicornia europa* monocultures. Ecology, 68: 737–741.

Ermentraut, G.B. and Edelstein-Keshet, L., 1993. Cellular automata approaches to biological modelling. J. Theor. Biol., 160: 97–133.

Firbank, L.G. and Watkinson, A.R., 1985. A model of interference within plant monoculture modelled as a spatial stochastic process. J. Theor. Biol., 116: 291–311.

Ford, E.D. and Diggle, P.J., 1981. Competition for light in a plant monoculture modelled as a spatial stochastic process. Ann. Bot., 48: 481–500.

Ford, E.D. and Sorrensen, K.A., 1992. Theory and models of inter-plant competition as a spatial process. In: D.L. DeAngelis and L.J. Gross (Editors), Individual-Based Models and Approaches in Ecology: Populations, Communities and Ecosystems. Chapman and Hall, New York, pp. 363–407.

Fowler, N.L., 1984. The role of germination date, spatial arrangement and neighbourhood effects in competitive interactions in *Linum*. J. Ecol., 72: 307–318.

Geber, M.A., 1989. Interplay of morphology and development on size inequality: a *Polygonum* greenhouse study. Ecol. Monogr., 59: 267–288.

Goldberg, D.E., 1987. Neighbourhood competition in an old-field plant community. Ecology, 68: 1211–1223.

Haefner, J.W., Poole, G.C., Dunn, P.V. and Decker, R.T., 1991. Edge effects in computer models of spatial competition. Ecol. Model., 56: 221–244.

Hassell, M.P., Comins, H.N. and May, R.M., 1991. Spatial structure and chaos in insect population dynamics. Nature, 353: 255–258.

Judson, O.P., 1994. The rise of the individual-based model in ecology. TREE, 9: 9–14.

Knox, R.G., Peet, R.K. and Christensen, N.L., 1989. Population dynamics in loblolly pine stands: changes in skewness and size inequality. Ecology, 70: 1153–1166.

Mack, R.N. and Harper, J.L., 1977. Interference in dune annuals: spatial pattern and neighbourhood effects. J. Ecol., 65: 345–363.

McGlade, J.M., 1993. Alternative ecologies. New Sci., 137: 14–16.

Mead, R., 1966. A relationship between individual plant-spacing and yield. Ann. Bot., 30: 301–309.

Miller, T.E. and Weiner, J., 1989. Local density variation may mimic effects of asymmetric competition on plant size variabilty. Ecology, 70: 1188–1191.

Schmitt, J., Eccleston, J. and Ehrhardt, D.W., 1987. Dominance and suppression size-dependent growth and self-thinning in a natural *Impatiens capiensis* population. J. Ecol., 75: 651–665.

Silander, J.A. and Pacala, S.W., 1985. Neighbourhood predictors of plant performance. Oecologia, 66: 256–263.

Turner, M.D. and Rabinowitz, D., 1983. Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa*. Ecology, 64: 469–475.

Weiner, J., 1985. Size hierarchies in experimental populations of annual plants. Ecology, 66: 743–752.

Weiner, J., 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor*. Ecology, 67: 1425–1427.

Weiner, J., 1990. Asymmetric competition in plant populations. TREE, 5(11): 360–364.

Weiner, J. and Solbrig, O.T., 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia, 61: 334–336.

Weiner, J. and Thomas, S.C., 1986. Size variability and competition in plant monocultures. Oikos, 47: 211–222.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res., 14: 167–225.

Wilson, J.B., 1988. The effect of initial advantage on the course of plant competition. Oikos, 51: 19–24.

Wissel, C., 1992. Aims and limits of ecological modelling exemplified by island theory. Ecol. Model., 63: 1–12.

Wolfram, S., 1986. Theory and Applications of Cellular Automata. Advanced Series on Complex Systems, Vol. 1. World Scientific, Singapore.