Genet and Ramet Survivorship under Different Mortality Regimes—A Cellular Automata Model

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A computer simulation experiment is presented which attempts to relate survival of genets (clones) and ramets in laterally spreading clonal organisms, for example a herbaceous perennial, to density-independent mortality caused by spatially localized disturbances of different frequency and size. The model used is based on a two-dimensional cellular automaton approach (Wolfram, 1984, *Physica* **10D,** 1). The results of the simulations emphasize the crucial importance of the size of the patches of disturbances for the survival of both genets and ramets.

1. Introduction

Plants are sessile organisms, in which the situation in the near environment, especially the spatial relation to neighbouring plants, is of great importance for the fitness of an individual plant (Mithen *et al.*, 1984; Hutchings, 1986). Plants are also modular organisms. Many plants, especially herbaceous perennials, exhibit clonal growth, i.e. produce laterally spreading shoots that became physiologically and (eventually) physically independent units (ramets), suffering mortality more or less independent of each other (Cook, 1979). These traits—sessility, modularity and clonality—make two-dimensional cellular automata (Wolfram, 1984; cf. also other papers in the same issue) a promising tool for building models of population dynamics and species coexistence of herbaceous perennials. A two-dimensional cellular automaton consists of an array of discrete sites, with each site carrying a discrete value. The value of each position is updated in discrete time steps depending of the values in a neighbourhood of sites around it, according to uniform rules. These rules are typically deterministic, but they may even be stochastic. There is a growing interest in such models in plant ecology (Barkham & Hance, 1982; Crawley & May, 1987). Similar models have been used for some time in population genetics, such as the two-dimensional extensions of the stepping-stone approach for modelling gene flow (Rohlf & Schnell, 1971; Comins, 1982; Turner *et al.*, 1982).

In an earlier paper about two rosette herbs (Inghe & Tamm, 1985), a simple model was used to predict the survival of genets from calculated depletion curves and bifurcation frequencies of rosettes. However, that model assumed completely statistically independent deaths of the ramets, which is unrealistic if the daughter ramets are placed closely together (which they were) and if mortality is caused by coarse-grained patchy disturbances (which it partly was). Here, I present a simple stochastic cellular automaton simulation model which intends to explore the relationship between clonal growth and genet survival under different regimes of density-

independent mortality caused by spatially localized disturbances, where both the size of the disturbances and the total area affected is varied.

2. The model

For the sake of clarity, I present the technical features of the model in numbered points, with explanations and justifications added in brackets after each point.

(i) Simulations is carried out in a universe of 3600 sites (cells), arranged in a square of 60 rows and 60 columns. Each site can either be empty, or occupied by exactly one ramet. (The size of the universe was partly chosen out from considerations of the limited memory and speed of the used microcomputer. If, to make a realistic example, a mature ramet is considered to occupy a site of 2×2 cm^2, the universe will correspond in size to a "permanent plot" of $1 \cdot 2 \times 1 \cdot 2$ m^2.)

(ii) Sites are assumed to be placed in a square lattice. (Some models, e.g. Crawley & May, 1977, use a hexagonal lattice, which is the densest way to pack circular units of equal size on a plane. That may be somewhat more realistic, but a greater neighbourhood of sites is then needed to represent the same number of distances from the cell to be updated, and I have not thought that to be good economy of computer time for the present aims.)

(iii) To avoid edge effects, the universe has wrap-around margins, so that the upper row and the bottom row are neighbours to each other, and the rightmost column and the leftmost column are neighbours to each other. (Real populations, of course, have edges of diverse kinds. However, it is convenient to begin with a homogeneous, universe-like space, and introduce various complications in a step-wise manner later on.)

(iv) Each site have a neighbourhood of 12 sites (Fig. 1), representing three distances from the site. For each site in the neighbourhood, there is a certain probability P_I for a ramet growing there, and providing it is the only ramet in the neighbourhood, to colonize the central site from time t to $t+1$ (e.g. one generation of the model), if it is unoccupied. The actual probabilities used in the simulation experiment are shown in Fig. 1(a). If more than one ramet compete for colonizing an empty site, the actual probability for a ramet in position I to colonize the empty place, P_I', is given by

$$P_I' = \frac{P_I}{\displaystyle\sum_{i=1}^{12} P_i} \left(1 - \prod_{i=1}^{12} (1 - P_i) \right)$$

where P_i ($i = 1, 2, 3, \ldots, 12$) is a value from one of the 12 positions in Fig. 1(a) if the position is occupied and otherwise zero. The expression within the parentheses is the probability that any ramet in the neighbourhood colonizes the empty site. The expression in front of it is the proportion of that probability assigned to the ramet in position I. (Applying Lovett Doust's (1981) phalanx-guerilla dichotomy, the expansion probabilities chosen may be considered to represent a clonal herb
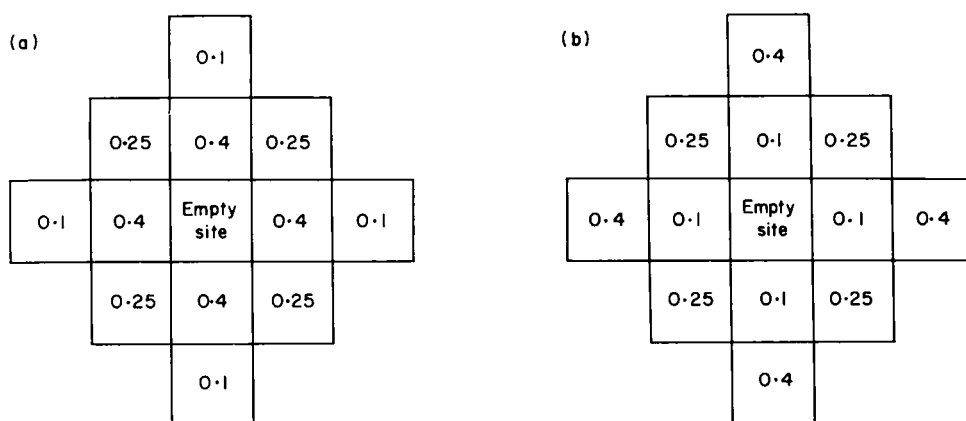
(a)

	0·1	
0·25	0·4	0·25
0·1	0·4	Empty site	0·4	0·1
0·25	0·4	0·25
	0·1	

(b)

	0·4	
0·25	0·1	0·25
0·4	0·1	Empty site	0·1	0·4
0·25	0·1	0·25
	0·4	

FIG. 1. The probability (P_i) of an empty site to be colonized within one generation by a sole ramet growing in different positions of the neighbourhood. (a) Colonizing probabilities chosen to represent a clonal herb growing in the phalanx mode. (b) Colonizing probabilities chosen to represent a clonal herb growing in the guerilla mode.

growing in the phalanx mode, i.e. with most of the daughter ramets placed very near the original ramet. Reiterated undisturbed growth gives a roughly circular clone with a nearly closed advancing front. If Fig. 1(a) is viewed as an empty zone of expansion around a single ramet—which is completely valid as long as one ramet is considered in isolation, although not the way the actual computations are carried out—it is easy to see that an average of three daughter ramets will be produced in one generation, which seems to be within the realm of biological realism, if one generation of the model is viewed as one year in nature.)

(v) Death of ramets is caused by randomly choosing squares in a grid of non-overlapping squares covering the universe and killing all ramets present within them. Edge effects are averted by letting the position of the square grid vary randomly in both spatial dimensions between generations. The size of the squares (measured as side length in cell units, A) and total number of cells affected per generation (L) are the two parameters varied between simulation runs. Note that the non-overlapping method of sampling squares within a closed grid keeps L exactly constant between generations within runs, but it constrains the A-values chosen to be factors of 60—the length of the universe. (Obviously, in nature far from all disturbances cause 100% mortality among affected ramets of all plant species. Nor do many disturbance agencies make square-formed, non-overlapping disturbances of exactly uniform sizes. But there are disturbers who approach 100% killing effectiveness, for example wild boars, who often remove the whole turf when foraging. Besides, even if some of these four simplifications ought to be removed to achieve a closer fit to observed natural conditions, they can all easily be fairly strictly followed in long-term field experiments. There is no death of single ramets due to competition or senility. This is certainly wrong in many cases. On the other hand, frequently

competition appears to be ineffective in removing grown-up ramets (Grubb, 1977), and senility may be virtually absent in some ramet morphologies (Inghe & Tamm, 1985).)

(vi) A simulation starts by "sowing" 50 genets, each consisting of one ramet, at random over the universe, which is then exposed to death events according to (v). This is called generation zero. The following generations each consists of an episode of clonal growth (iv) followed by an episode of death (v). Output—number of ramets and their genet identity—is at the end of each generation; an example is displayed in Fig. 2. (Seed regeneration does not occur outside the initial "sowing" event. Recruitment by seedlings is indeed believed to be as a rule a rare event in clonal herbs (Cook, 1985), although reviewing of made species studies yields a more complicated picture, Eriksson, in press.)
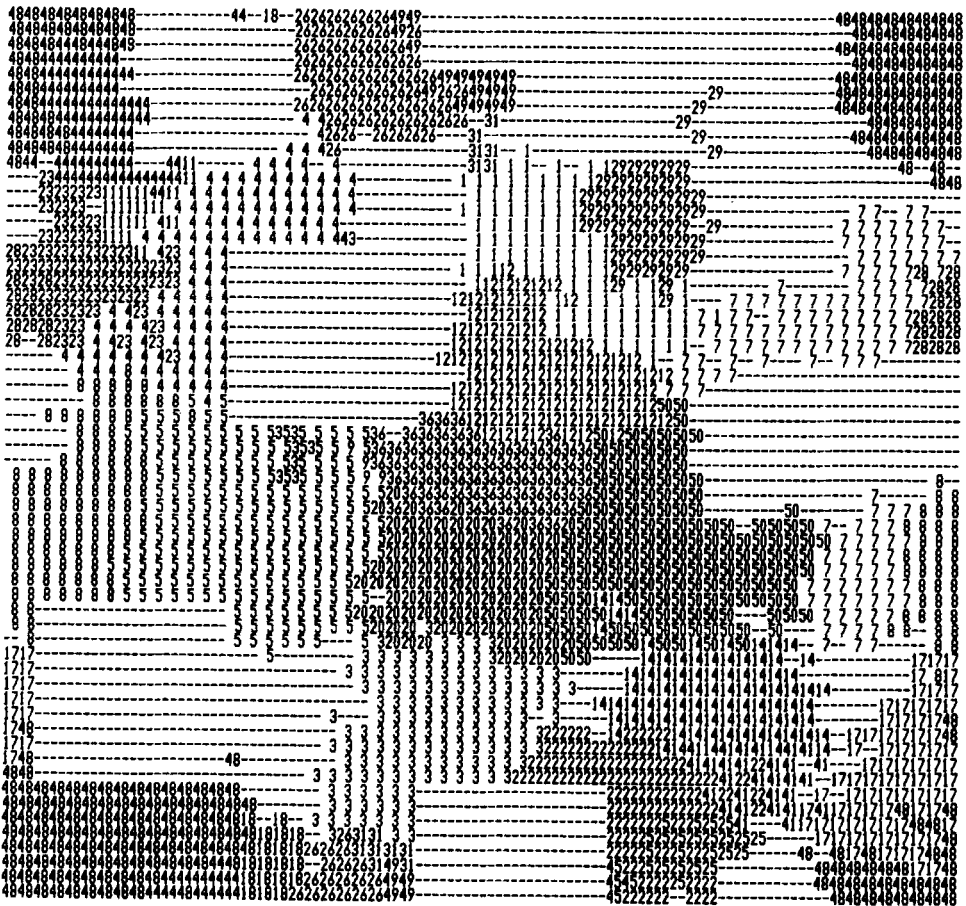

FIG. 2. A computer outprint mapping the position of ramets after 16 generations in a run where $A = 12$ and $L = 432$. The position of the three "fresh" mortality squares are clearly visible.

(vii) The explored parameter values are shown in Fig. 3. Three runs of 250 generations was made for each combination of parameter values. (Keeping to the 2×2 cm^2 cell example above, mortality squares vary in size between 2×2 and 60×60 cm^2. This is plausible for many types of animal- and man-made disturbances, although some biotic and many abiotic disturbances are much bigger. The total area affected per generation/year (L) may reach unrealistic values in some of the small-squared combinations, but those are included to cover the whole field of parameter values up to the limit where the ramet populations rapidly go to extinction. The number of replicates have been kept low, to cover more parameter combinations instead. Most differences in ramet and genet number between replicates appeared in the first few generations, due to good or bad luck for the population of one-or few-unit-genets present then, but these differences became damped out or eclipsed by fluctuations later on.)
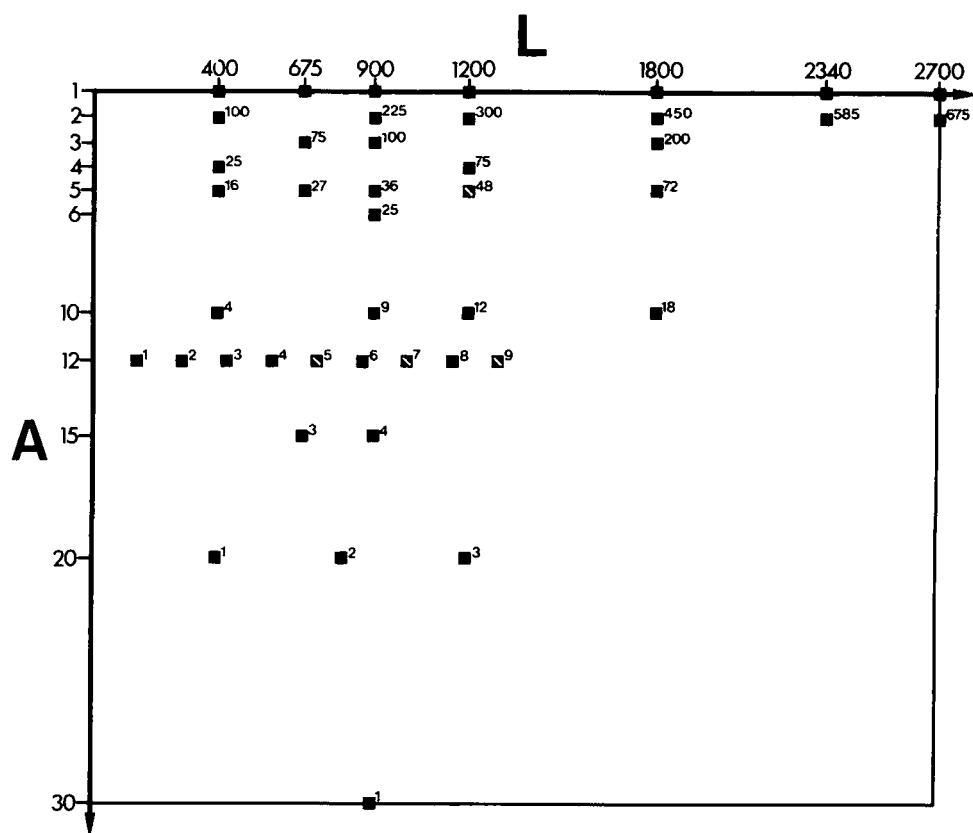

FIG. 3. Combinations of parameter values used in the main simulation experiment (■) and in the "competition" simulation experiment (◼). The number besides each square is the number of mortality squares per generation, i.e. L/A^2. The A-axis is turned around to enhance visual compatibility with the bottom planes of Figs 4(a–b).

(viii) Besides this, four unreplicated runs of 120 generations were done where 25 of the clones introduced at the start were of the type already described [Fig. 1(a)], while 25 were of the more guerilla-like (Lovett Doust, 1981) type in Fig. 1(b). This "competition simulation" had the additional rule that ramets of the phalanx-type could colonize ("overgrow") sites occupied by ramets of the guerilla-type with the same ease as if the sites were unoccupied. (The expansion probabilities of the guerilla type also produce a clone that expands in a roughly circular fashion, but with a more irregular front than in the phalanx type, with a deep of around 4–5 cell units before all space is occupied. The assumptions of total competition superiority for the phalanx type can perhaps be justified as a postulated trade off for investment in strong, competitive daughter ramets vs. investment in long stolons or rhizomes, although it may be exaggerated, and therefore give unduly conservative results for possibilities of coexistence. Crawley & May (1987) use the same rule for a perennial vs. an annual (where it may be more valid), and, leaving the question of genetic identity aside, our guerilla-type can indeed alternatively be viewed as an annual which, contrary to in their model, have localized seed dispersal.)

3. Results

The mean number of ramets and of genets respectively remaining in the simulations after 250 generations are shown by Figs 4(a–b).

With unit-sized mortality squares $(A = 1)$ the number of ramets lies closely to $3600 - L$ for L-values up to around 1200 [cf. dotted line on the back-wall of Fig. 4(a)], indicating that most emptied sites are recolonized within one generation. For higher values of L, ramet number drops more significantly below $3600 - L$, and reach zero for $L = 2700$. Even in a model assuming unlimited spatial dispersal a zero point must eventually be reached when L increases. However, with the spatially restricted dispersal of this model such a point must be reached even sooner because the random dispersal of many one-unit mortality squares must necessarily create some greater gaps somewhere sometimes; gaps which takes several generations to fill from the border inwards. The greater fluctuations in ramet number between generations for $L = 2340$ as compared to $L = 900$ [Figs 5(a–b)] are certainly caused by the bigger stochastic component in the number, size and shape of these compound gaps.

While preserving the generally convex† shape of the slopes, higher A-values cause successively steeper drops towards zero as L increases. For example, $A = 12$ makes ramet survival impossible for L-values half as big as for $A = 1$. The interpolated boundary for ramet survival is outlined as a curved dashed line on the bottom plane of Fig. 4(a). In two cases near this boundary [marked by arrows in Fig. 4(a)], situated in the region of high A-values, one of the three runs reached zero values within 250 generations. Ramet number fluctuates violently between generations in this region, and sometimes a run of generations with bad fortune (i.e. where the few big mortality squares happen to be placed over the most densely populated areas) may be fatal. Even Fig. 5(c) shows cases where the ramet population dropped

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†"Convex" and "concave" are used here in their visually descriptive, non-mathematical sense.
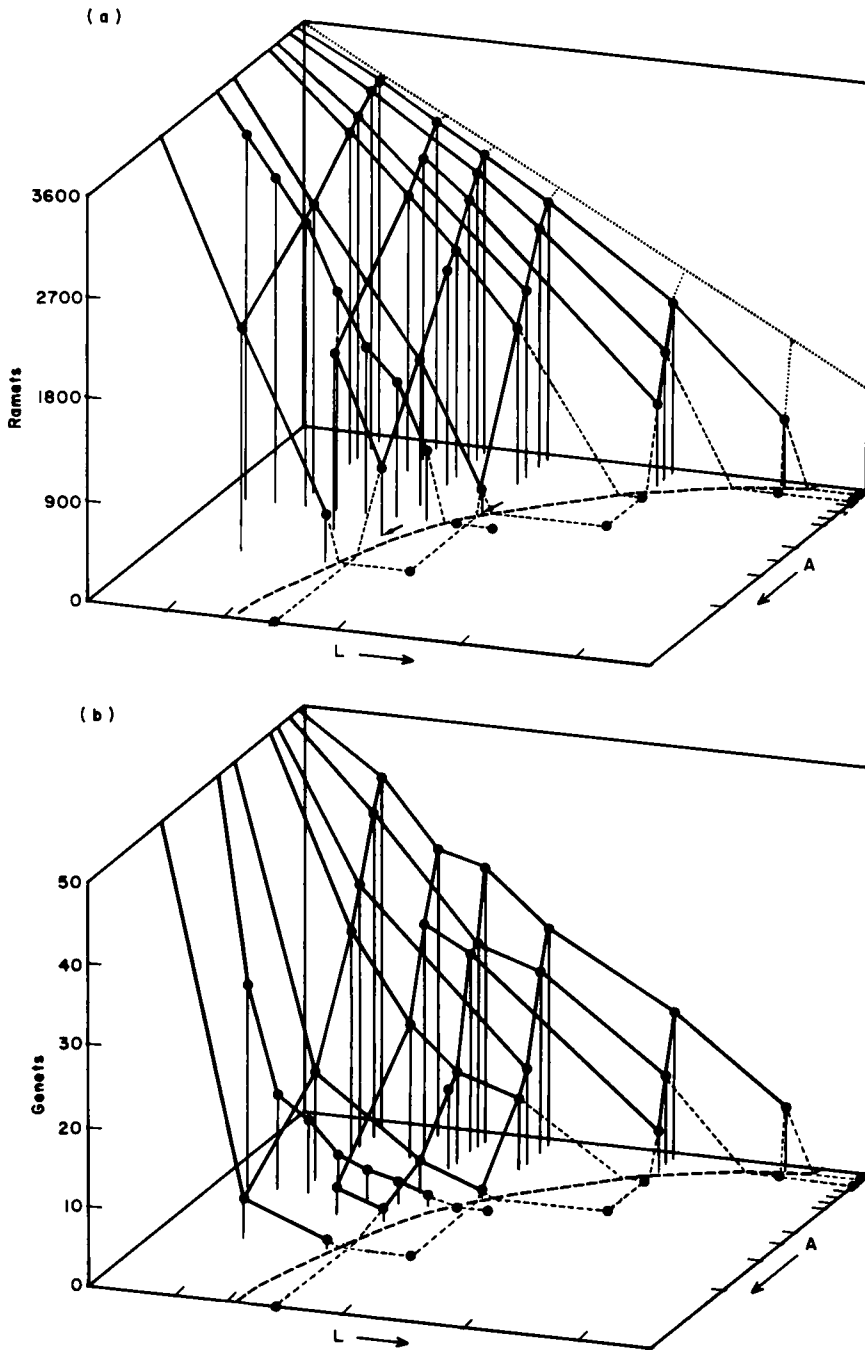
FIG. 4. Three-dimensional diagrams showing the number of ramets (a) and genets (b) (mean of three runs) after 250 generations for the tested parameter combinations in the main simulation experiment. See text for further explanations.
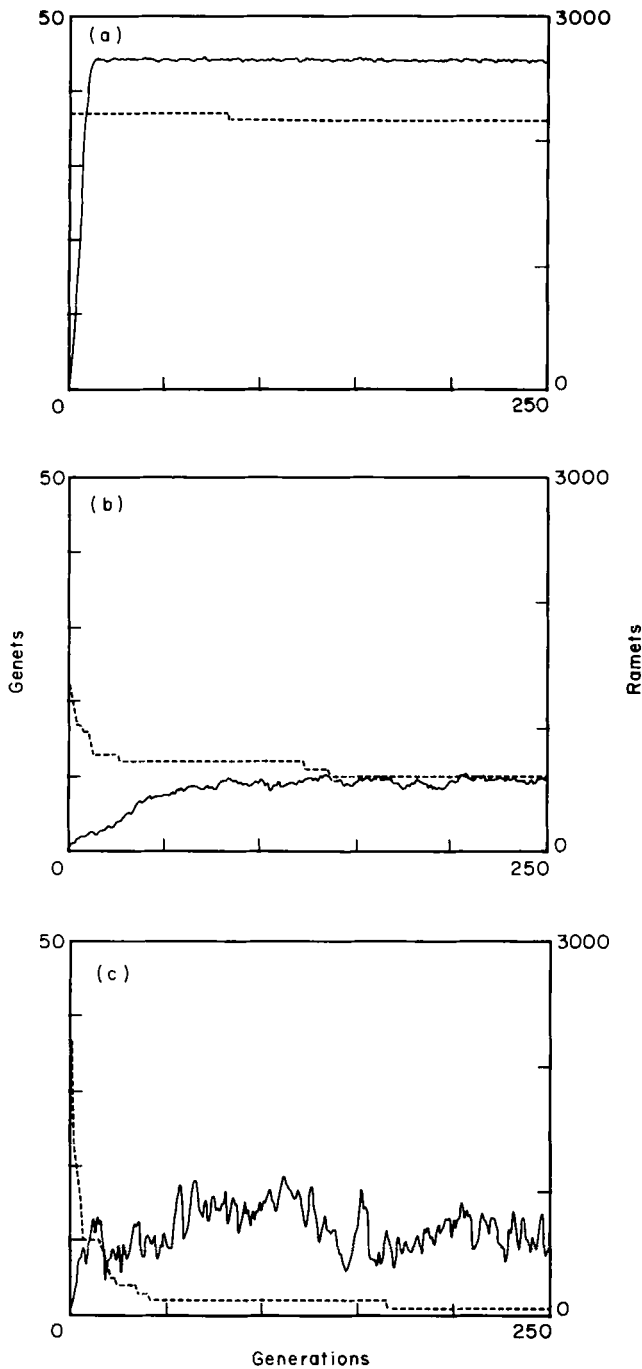
FIG. 5. Changes in the number of ramets (———) and genets (- - -) throughout three simulation runs in the main simulation experiment. (a) $A = 1$, $L = 900$. (b) $A = 1$, $L = 2340$. (c) $A = 15$, $L = 900$.

to dangerously low values, for a point somewhat more removed from the ramet survival boundary line.

The growth of the ramet population through time can be followed in the leftmost column of Fig. 6. Ramet number grows rapidly in the beginning, except in the regions where extinction occurs soon, reaching a pseudo-carrying capacity after about 20 generations. After this, the most notable change is a displacement of the zero line to the left; most pronounced for higher A-values and certainly due to the above-mentioned stochastic fluctuations.

The genet (or clone) number after 250 generations combine to a plane of a flat to concave shape [Fig. 4(b)], markedly different from the convex shape of the ramet numbers of Fig. 4(a). The depletion of genet number through time (Fig. 6, middle column) does not reach a standstill within 20 generations, as for ramet number, but continues, although with diminishing rate, throughout the span of the simulations, carving out a successively deeper glacier niche-like concavity and creating a widening zone with very few remaining ramets. It can be argued that for all $L > 0$, genet number eventually will reach 1 (that is, if the ramet population escapes extinction)— although this will take an increasingly long time for lower values of L or A—because in each case a patch is opened for recolonization there is, when more than one clone is left, a certain probability that it will be placed in the border region between two clones. Now, the border of a small clone tends to be more convexly curved than that of the bigger clone, which means that an empty unit placed close to the border will have a greater probability to have a position in its neighbourhood of potential colonizers to be occupied with a ramet of the bigger clone, than with one from the smaller clone. This argument presupposes the existence of clear borders between the clones, and there mostly are for the phalanx-like colonization prob- abilities used in the present simulation (cf. Fig. 2). If, on the other hand, ramets of different clones would come to grow randomly intermixed, the eventual "victory" of a single clone will likewise be probable, in analogy to the mechanisms operating on alleles in genetic drift.

The evolving differences in shapes for the planes extrapolated for ramet and genet numbers, respectively, imply that the corresponding genet size pattern also evolves (Fig. 6, rightmost column). From around 20 generations, i.e. when ramet number begins to level off, a conspicious elongated dome of big genet sizes develops in the region of high A-values, with the crest for L-values near below the extinction line. (Although, for only three replicates, the exact position and shape of the crest vary with the big stochastical fluctuations mentioned above.)

Figures 7(a–c) show genet number for the three "competition" simulations with an A-value of 12. The phalanx clones clearly win out for the lowest L-value. One guerilla clone is the sole survivor for the highest L-value, with a ramet population (not shown in the figure) fluctuating between 150 and 742 during the last 70 generations. (This outcome is hardly accidental, as no phalanx clones survived until 120 generations in the thrice replicated run for the same parameter values in the main simulation experiment.) At the intermediate L-value members of both clone types survive. The number of ramets for the single guerilla clone vary between 212 and 596, and the total number of ramets for the two phalanx clones vary between
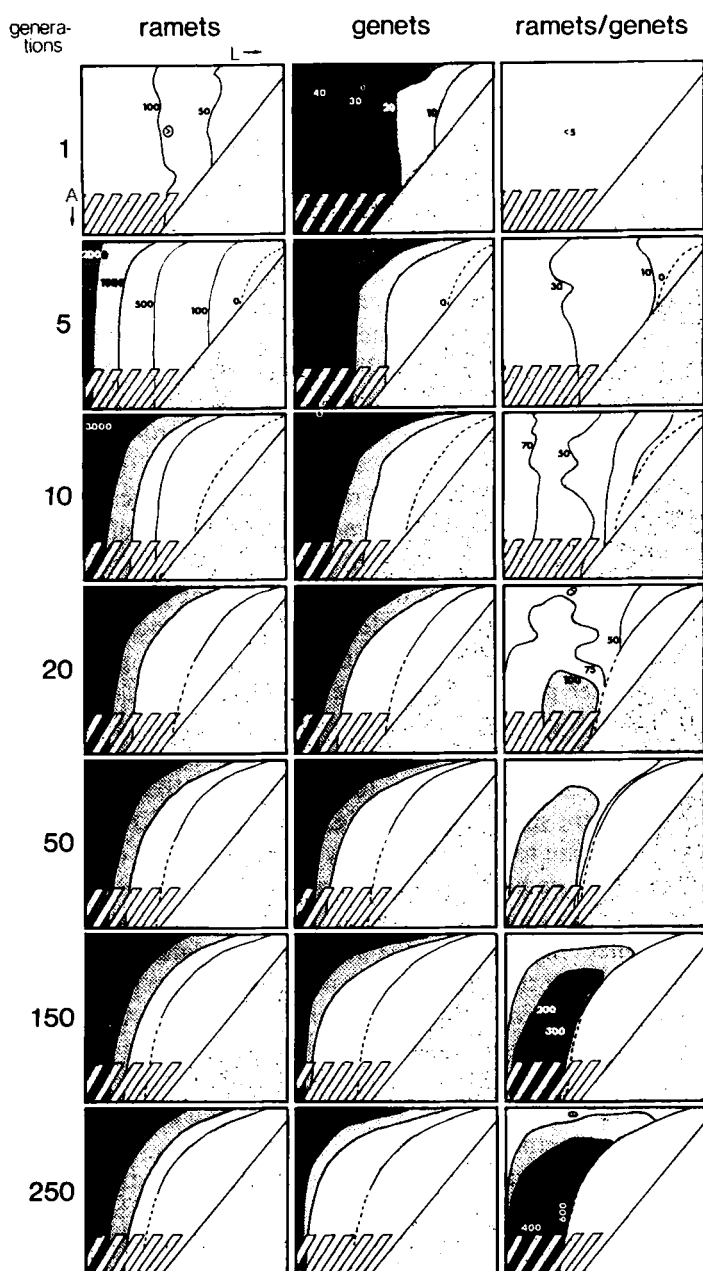
FIG. 6. Contour diagrams showing the number of ramets (leftmost column), number of genets (middle column), and mean genet size (rightmost column) for some generations in the main simulation experiment. Scales and axis directions for the diagrams are the same as in Fig. 3. Contours are hand-interpolated from the means of the three runs for each of the tested-parameter combinations. The irregularity dotted area in the diagrams covers the regions where no (or, down to the left, very few) parameter combinations were tested.
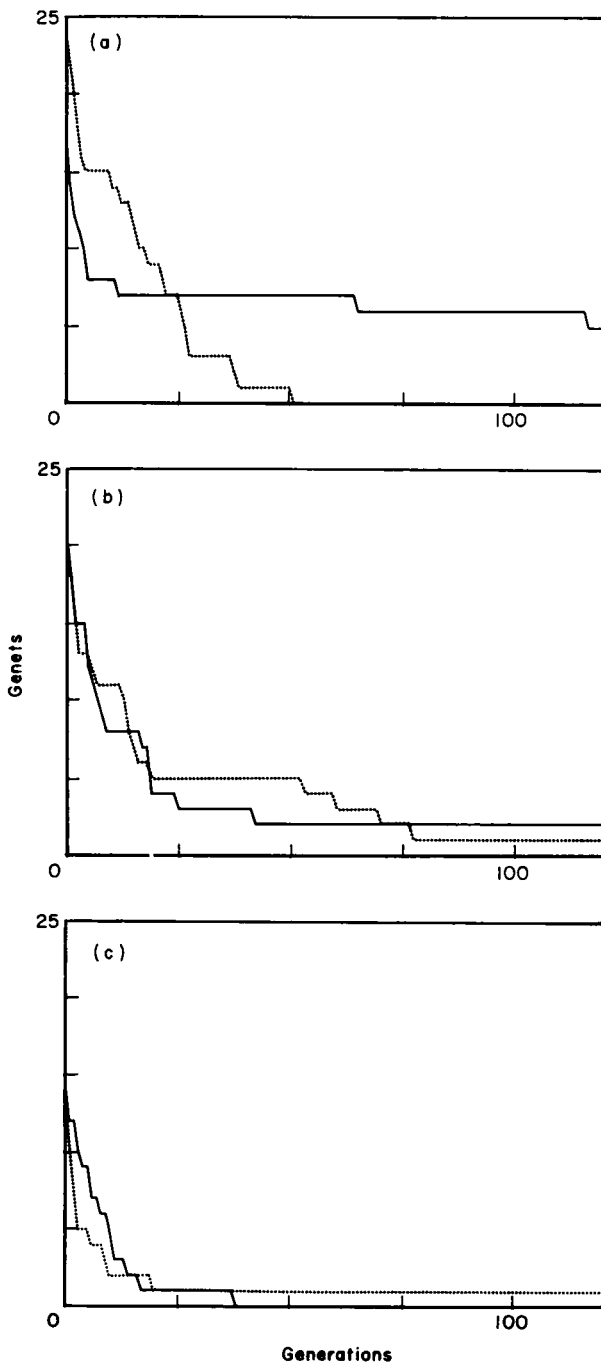
FIG. 7. Changes in number of genets in three of the "competition" simulation runs. (——) competitive phalanx clone type; ($\cdots$) non-competitive guerilla clone type. (a) $A = 12, L = 720$. (b) $A = 12, L = 1008$. (c) $A = 12, L = 1296$.

244 and 744, during the last 50 generations. The result for the fourth run (with $A = 5$, $L = 1200$) resembles that of Fig. 7(a). A preliminary conclusion may therefore be that the guerilla type can survive in a narrow zone outside the survival limit for the phalanx clones (i.e. with higher A- or L-values), and that coexistence is possible in a narrow zone just inside that limit.

4. Discussion

The simulations clearly shows the paramount role of the size structure of the effect of mortality agents for the growth and survival of the population of ramets, and for their clone structure.

The one-unit cases ($A = 1$) approximate non-spatial models (e.g. Inghe and Tamm, 1985), where only overall mortality is varied. However, this now appears as a special, limiting case, where disturbances (or other mortality agents) are of the same size as a single specimen. Disturbances of a somewhat bigger relative size (or, more precisely, width) can have a much bigger effect, especially on clone number, and size. The size of, for example, cow-pats, the pits of badgers and wild boars, the runways of voles, the trampling of big animals, including men and his vehicles, certainly belongs to this size category, from an ordinary herb ramet's "point of view". A greater capacity of lateral expansion (i.e. a larger neighbourhood) than used in the simulations presented here would push the frequency isolines for ramets and genets upwards (as for the faster-expanding guerilla clones in the "competition" simulation), but hardly alter the pattern qualitatively.

However, the model assumed 100% ramet mortality within the mortality squares, and it seems obvious that even a rather low survival probability within them would profoundly facilitate recolonization of the emptied area, especially for the real big A-values, by reducing the mean distance to the nearest potential recolonizer. In nature, selection pressure may be high for such a capacity for persistence in spite of severe disturbances.

The results concerning the clonal structure (number and mean size of genets) illuminates the capacity of the big-sized disturbances to rapidly weed out genets, leaving only one or a few to expand to a size where they may be comparatively "secure". (Even if, as argued above, the survival of a single (or no) clone may be the eventual outcome even for small A-values, that end-point is hardly attained within time-spans of ecological relevance in those cases.) Such a depletion of the local genetic variation implies a decreased capacity for adaptations to spatial microenvironmental heterogeneity (due to both loss of genes from the population and increased inbreeding reducing genetic recombination), and may also increase susceptibility to attacks of pathogens.

Coffin & Lauenroth (1988) explicitly address the effects of disturbance size upon turnover rate for clones and for total cover of the perennial steppe grass *Bouteloua gracilis* in a computer simulation using empirically derived frequency and size distribution data for grass clones and (in order of decreasing frequency and increasing size) cattle faecal pats, ant mounds and animal burrows. Ant mounds and animal burrows was found to contribute differentially more to clone turnover rate than to

plant cover turnover rate, a result qualitatively in line with that predicted from our model. However, although covering time-spans of up to more than half a million years, there is no growth of the clones or clonal fragments in their model, which in other respects is rather similar to ours. Inclusion of empirically derived data for lateral growth of *Bouteloua* may improve its accuracy considerably.

The realism of this model, of course, is limited to scenarios where seedling establishment occurs only very rarely, usually after a widespread disturbance such as a fire, or a severe flooding. Inclusion of more or less continuous seed dispersal and seedling establishment in the model may generate more complex, but perhaps more widely applicable, clonal patterns.

The runs with the two different types of genets represent another possible extension of the model towards greater realism and complexity by including competition effects and other neighbourhood interactions. If interpreted as a perennial-annual competition, the outcome is broadly in line with the equilibrium model of Crawley & May (1987) in the general conditions found necessary for coexistence, although the models are not directly comparable. More developed models along the same line could shed light over mechanisms of coexistence of genotypes and species; exploring the continuum spanning the apparent (scale-dependent) dichotomy between equilibrium and non-equilibrium processes in this respect.

In a greenhouse competition experiment, Schmid and Harper (1985) found *Bellis perennis* (phalanx type) to be competitively superior at high planting densities and *Prunella vulgaris* (guerilla type) to be competitively superior at low planting densities. The different outcomes were maintained even when a complete vegetation cover was established in all plots, so the role of competitive overgrowth was not similar to that of our simulations. Neither was there a regime of perpetual disturbances. Nevertheless, provided that competitive overgrowth occurs to some degree, the predicted outcome of a field or greenhouse experiment involving these two species, where disturbances of different sizes and frequencies are applied as different treatments, should be qualitatively similar to that of the made simulations.

Finally it should be mentioned that it is possible to integrate models of the above-mentioned type with population genetic models of the same brand, including factors as breeding systems, pollen dispersal and somatic selection, thereby enabling analysis of the interaction between ecological interactions and microevolution.

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