

THE EFFECT OF CLONAL INTEGRATION ON PLANT COMPETITION FOR MOSAIC HABITAT SPACE

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Abstract. Physiological integration between ramets has been observed in several clonal plant species. But consequences of integration on the competitive ability and spatial development of genets have received little attention so far. This study is an attempt to examine the population- and community-level implications of integration in a spatially explicit model.

We have simulated different resource patterns in a cellular automata, varying the proportion (p) and size (s) of resource-rich patches and the average resource level in the area (h). We compared the efficiency of integrator to splitter genets in exploring and utilizing the resource patches. In the integrator, ramets that belonged to the same genet were physiologically connected and shared the resource taken up by any part of the genet. In the splitter, all ramets were autonomous, i.e., survival and reproduction of each ramet only depended on the local resource conditions. Thus, the integrator sensed and responded to environmental heterogeneity on a larger spatial scale than the splitter. Integration can be interpreted as sharing the risk of genet mortality among interconnected ramets, while splitting represents risk spreading among autonomous ramets. In each simulated habitat type, we followed the course of competition between splitter and integrator genets for 500 generations.

First, we examined the effect of environmental heterogeneity on the result of competition. We fixed the average resource level in the area and changed the spatial distribution of the resource by varying p and s . We found that the smaller the proportion of favorable sites, the better it is to integrate. But already a small deviation from random to clumped resource distribution (i.e., relatively small s) made the integrator competitively inferior to the splitter. In the next step, we varied the overall resource richness in the area. High productivity of the habitat promoted the dominance of integrators. The simulations demonstrated that there were habitat types in which one of the strategies (the integrator or the splitter) rapidly excluded its competitor. But at the medium range of environmental parameters, long-term coexistence of the strategies became possible. As integration proceeded simultaneously with horizontal growth and exploration of new patches, integrators remarkably differed from splitters in their pattern of space occupation. A spatial statistical analysis revealed that splitters maintained strong spatial association with the resource: splitting promoted habitat selection. Integration, on the other hand, led to gap-filling, fugitive spatial behavior. For a range of realistic habitat patterns, we need not expect the exclusion of any of the pure strategies—splitters and integrators can coexist.

Key words: *cellular automata; clonal plants; community structure; competition for gaps; environmental heterogeneity; physiological integration; population dynamics; resource uptake; risk spreading; spatial interactions.*

INTRODUCTION

Clonality is widespread among herbaceous plants. According to estimations in various habitats in the temperate zone, clonal growth occurs in up to 70–80% of the species in several plant communities (van Groenendael and de Kroon 1990, Klimes et al. 1997). A characteristic feature of clonal organization is that each genetic individual (genet) consists of semiautonomous constructional units (ramets). Newly emerging ramets import nutrients, water, hormones, etc., from the parent

until they become established, but once established, the progeny does not strictly depend on parental support. Each ramet is, at least potentially, capable of developing all the organs that are necessary for the survival and reproduction of a whole plant (Harper and Bell 1979, Jackson et al. 1985).

In spite of the potential autonomy of established ramets, the actual degree of their physiological interdependence varies greatly among the species (for review, see Pitelka and Ashmun 1985, Marshall 1990, Kelly 1995, Alpert 1996a, van Groenendael et al. 1996). Two extreme strategies can be distinguished: genet splitters vs. integrators. In a typical genet splitter, the established ramets do become physiologically independent (see Eriksson and Jerling 1990). The interconnections

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(stolons, rhizomes, etc.) gradually cease transporting material, even may senesce and decay as the new ramets root and become self-supporting (Pitelka and Ashmun 1985, Schmid and Bazzaz 1987). In some species, developmentally programmed fragmentation has also been observed (Eriksson and Jerling 1990, Kelly 1995, Wilhalm 1996).

In contrast to splitters, a typical integrator maintains the between-ramet connections throughout the lifespan of ramets, and extensive movement of water, mineral nutrients, and assimilates can be observed within the clone. Experimental studies have demonstrated that in some species, such as *Lycopodium annotinum*, *Carex bigelowii*, *Distichlis spicata*, and *Fragaria chiloensis*, significant translocation can occur to distances of a meter of magnitude (Headley et al. 1988, Carlsson et al. 1990, Alpert 1990, 1996b, respectively), and a resource can be transported over that distance in 1 min (Callaghan 1980). Integrated domains have been found to encompass >10 ramet generations (Jónsdóttir and Callaghan 1988, Carlsson et al. 1990). Thus, ramet autonomy remains only a potential, used when the interconnection breaks down due to herbivory or other physical damage (see Pitelka and Ashmun 1985, Schmid and Bazzaz 1987, Marshall 1990). In normal conditions, a whole connected system of ramets can behave as a single integrated physiological unit (sensu Watson 1986).

Even in a highly integrated clone, the actual degree of resource translocation depends on the resource status of ramets (see Pitelka and Ashmun 1985, Marshall 1990). It can be expected that the more heterogeneous the environment the more significant is the effect of integration on the performance of ramets (as proposed, for example, by Hutchings and Slade 1988, Stuefer et al. 1994, Wijesinghe and Handel 1994, Alpert 1996a, Wijesinghe and Hutchings 1997). However, it is difficult to generalize from the existing empirical data, for two reasons. First, the effects of different aspects of the spatial pattern (like its grain, contrast, etc.) are often not distinguished, and spatial heterogeneity is not quantitatively characterized (cf. Oborny 1994, Stuefer 1996). Secondly, most of the experiments have been conducted in simple two-ramet systems (one "donor" and one "recipient" ramet) or on short linear clonal fragments (see Pitelka and Ashmun 1985, Marshall 1990, Kelly 1995, Stuefer 1996 for reviews). Similarly, mathematical models of clonal integration have been constructed only for pairs of ramets (Eriksson and Jerling 1990, Caraco and Kelly 1991), or for one donor and multiple recipients, where the environment is homogeneous for all the recipients (Gardner and Mangel 1999). Very little is known about the costs and benefits of integration in more realistic situations, when a whole branching system of ramets lives in a mosaic of resource patches. To our knowledge, the simulation model that we present here is the first attempt to study physiological integration in a spatially explicit way.

Cellular automata provide a convenient tool for modelling spatial competition in structured habitats. Space is represented as a regular array of "cells" (in the forthcoming model, discrete sites in a square lattice). Each cell can have one of a finite number of states (empty vs. occupied by a particular genet). The change of the state of each cell (extinction from or colonization into the cell) is a function of its own state and of the state of the neighboring cells. Cellular automata can be efficiently used for modelling how fine-scale, local interactions produce characteristic spatial structures on the mesoscale and how these structures control the global dynamics of populations (e.g., Hogeweg 1988, Czárán and Bartha 1989, Durrett and Levin 1994, Oborny 1994, Oborny and Cain 1997; see Czárán 1998 for review). For clonal organisms, cellular automata models have been used to explore coexistence criteria of horizontally spreading genets under different assumptions concerning the birth, death, and competition of ramets (Karlson and Jackson 1981, Karlson and Buss 1984, Crawley and May 1987, Inghé 1989, Herben 1992, 1996, Silvertown et al. 1992, Oborny 1994, Winkler and Schmid 1996). None of the models have considered the possibility of exchange of resources or information between ramets.

A novel feature of the model that we present in this paper is that the states of ramets that belong to the same genet are not necessarily independent. In the case of the integrator strategy, the ramets are enabled to redistribute the resource among themselves. Since not only neighborhood interactions but also ancestry-based interactions occur, the model can be regarded as an extension of a typical cellular automata.

In the Monte Carlo simulation that we present here, integrator clones compete with splitters in mosaic environments which consist of resource-rich and resource-poor patches. The only trait in which the modelled clones differ is the presence vs. absence of integration. We do not assume any plastic morphological response for the concentration of the resource in either of the strategies. We study the process of competition in seven habitat types, changing the total amount of resource over the area, and the number and size of relatively favorable patches. We follow the changes of good and bad areas covered by splitters vs. integrators over time. We compare which strategy is more efficient in selectively placing ramets into good sites and how competitive exclusion occurs. We use an information statistical model to study how collective spatial structures are formed during the competition for the mosaic of resource patches.

We expect that the splitter differs from the integrator in its pattern of space occupation. Therefore, not only the total amount, but also the spatial distribution of the resource should strongly influence the result of competition. Our objective is to predict how habitat conditions influence competitive dominance of the inte-

grator in an ecological time scale and selection for integration in an evolutionary time scale.

METHODS

We study the spontaneous spatial development of two species, a splitter and an integrator. Equal numbers of propagules of the species are placed in a simulated mosaic habitat and then allowed to grow clonally and compete for space. Probabilities of survival and vegetative reproduction of the ramets at a site depend on the amount of the resource available. The species are modelled in a way that enables the comparison of an extreme, “pure” splitter to a “pure” integrator strategy. In the splitter, there is no clonal integration at all. Each ramet reacts to the local amount of the resource individually. In the integrator strategy, on the other hand, all ramets share the resource that is encountered by the genet, thus, the amount of the resource is averaged over the area covered by the clone. The habitats are modelled as random mosaics of resource-rich and resource-poor sites.

We study the effect of three habitat characteristics: (1) the proportion of resource-rich patches over the area, (2) the size of the patches, and (3) the total amount of resource distributed among the patches, i.e., habitat richness. Our goal is to examine what environmental conditions facilitate competitive exclusion or, alternatively, coexistence of the strategies. We group the simulation results accordingly. First, we tune the parameter values to produce long-term coexistence. Then we examine how each habitat condition (from 1 to 3) shifts this balance towards the winning of the splitter or the integrator. The process of spatial competition may go along with characteristic changes in the distribution and microhabitat preference of the strategies. We examine these by an information theoretical method of pattern analysis.

The simulation model

In the cellular automata, space is represented by a square lattice. It consists of 100×100 cells and has toroidal topology (wrapped-around boundaries). We apply this borderline condition to preclude edge effects. Competition for space (both between and within the strategies) is directly implemented in the model at the unit spatial scale. The automata has two layers. Layer 1 stores the information about the actual distribution of the resource. Layer 2 represents the field on which the two strategies compete.

Layer 1: the resource.—The resource is distributed in a mosaic pattern. (The resource layer is shown in Figs. 4 and 5.) Each cell has two potential states: favorable (resource-rich) vs. unfavorable (resource-poor). Spatial distribution of the resource can be characterized by two parameters: the size of the mosaic patches (s) and the proportion of favorable sites (p). The distribution is static throughout the simulation and is determined as follows: the grid is subdivided into

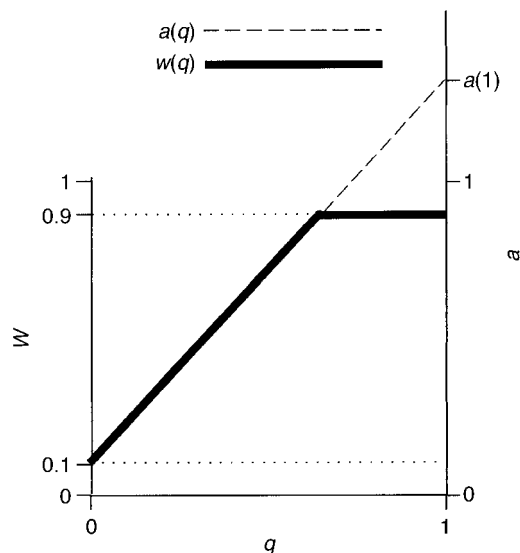


FIG. 1. The relationship among patch quality (q), resource status of the patch (a), and the survivorship/reproduction response (w) of the ramets that live in the patch. The dashed line shows the amount of resource as a function of patch quality, $a(q)$. The left-side vertical axis is scaled from 0 to 1 and represents probability of survival and reproduction in a particular patch. Accordingly, the solid bold line shows $w(q)$. See *Methods* for detailed explanation.

an orthogonal mosaic of square patches sized $s \times s$. Exactly a fraction p of the mosaic patches is randomly chosen and qualified as favorable (p being 0.25, 0.5, and 0.75, respectively). The rest of the patches are unfavorable. We use $s = 1, 2$, and 5 in the simulations. Thus, the habitat is spatially random on the scale of patch size (s). This scale can be equal to or bigger than ramet size.

Quality of each cell is characterized by the variable q . Favorable sites have $q = 1$; unfavorable sites have $q = 0$. q can be intermediate in the case of integrator clones, which average the site quality in their occupied area ($0 < q < 1$; see the rule for integration in *Layer 2: the competing populations*). The amount of resource in each cell, a , is a function of q (Fig. 1). $a(q)$ is measured relatively, according to its effect on the survival and reproduction of ramets. The minimum amount of resource, $a(0) = 0.1$, enables a ramet to survive and reproduce with the probability $w(0) = 0.1$. (The exact rules for survival and reproduction are discussed in *Layer 2: the competing populations*.) At the maximum resource level, $a(1)$, the probability of survival and reproduction is $w(1) = 0.9$. We chose these parameter values in order to give some chance (0.1) for survival and reproduction even in the worst condition and the same small chance for failure in the best condition. In other words, there is always some random disturbance in the system with probability 0.1. The plateau in $w(q)$ is a result of the assumption that performance of a ramet cannot be improved beyond the threshold 0.9. The sur-

plus resource is either lost (splitter) or exported to other members of the clone (integrator).

Considering a pair of ramets, one in a good site and one in a bad site, the plateau in $w(q)$ gives advantage to integration, because

$$\frac{w(0) + w(1)}{2} < w\left(\frac{1}{2}\right). \quad (1)$$

That is, averaging patch quality is worthwhile for the genet. This simple reasoning agrees with general results of Eriksson and Jerling (1990), who elegantly demonstrate that integration between ramet-pairs is favorable if the resource utilization curve (in our case, $w(q)$) is concave (see also Caraco and Kelly 1991). Taking the rule for a two-ramet system as a starting point, we examine the effect of integration in a branching system of ramets, which can occupy and abandon good and bad sites during its spatial development. This is the main reason for applying a spatially explicit model.

For the sake of simplicity, $a(q)$ is linear. The slope of $a(q)$ expresses the contrast (c) between good and bad patches:

$$c = a(1) - a(0). \quad (2)$$

In those sets of simulations where we vary the proportion of good patches (p) and the size of the patches (s), we fix the total amount of resource over the area and change only its spatial distribution. In a final series of simulations, we investigate the effect of total resource supply. We change the average amount of resource per cell, i.e., mean habitat richness (h):

$$h = a(0) \times (1 - p) + a(1) \times p. \quad (3)$$

For example, if $h = 0.9$, then each cell should support a ramet in the best conditions, at $w(q) = 0.9$, provided that the resource was evenly distributed. The deviations from this ideal situation come from the fact that the resource is patchily distributed. Exactly a proportion $1 - p$ of the cells contains less resource ($a(0) = 0.1$), and p proportion receives the extra ($a(1) > 0.9$). At each value of h and p , $a(1)$ and c can be calculated

from Eqs. 2 and 3. Table 1 shows all the parameter combinations that were used in the simulations.

Layer 2: the competing populations.—This layer shows the spatial distribution of the clones (A and B in Figs. 4 and 5). Each simulation is initiated by sowing 50 propagules in the grid at random, 25 for each strategy. The genets propagate by each ramet trying to put daughter ramets into the empty sites within its Neumann neighborhood (four nearest cells). The chance of success depends on the amount of resource available to the mother ramet. Splitters and integrators differ in the way in which the resource supply for the ramets is calculated.

The splitter consists of independent ramets. Therefore, the amount of resource $a(q)$ available to each ramet is exactly the local resource content in the underlying resource layer: $a(0) = 0.1$ or $a(1) = 0.9$. In contrast, the integrator genets distribute the available resource evenly among the ramets belonging to them. In a genet consisting of N ramets, out of which n_f are positioned in favorable sites, each ramet receives $a(q)$ amount of resource, where $q = n_f/N$. Thus, patch quality q is averaged in the clone: $0 \leq q \leq 1$. The presence or absence of averaging is the only difference between our integrators and splitters; all parameter values are the same for the two strategies in each competition process.

Each time step of the simulation program consists of a reproduction step and a survival step. In the reproduction step, empty cells can be colonized from neighboring cells that contain reproducing ramets. The chance of reproduction for each neighboring ramet is $w(q)$. If there is only one candidate to colonize an empty cell, it can do it unconditionally, but if more mother ramets try to delegate offspring into the same cell, one of the new ramets succeeds, the others die. If two or more mothers attempt to occupy the same empty cell, one of the candidates is chosen as the winner. The chance for each competing mother to win is proportional to its own $w(q)$. Propagation update of the cellular automata is succeeded by a survival update. A ramet survives in a cell for the next time step with

TABLE 1. Parameter combinations in the simulated habitats.

Simulation	p	s	h	$c = (h - 0.1)/p$
Reference	0.5	2	0.9	1.6
A1) Decreasing the proportion of good patches	0.25	2	0.9	3.2
A2) Decreasing patch size	0.5	1	0.9	1.6
A3) Decreasing habitat richness	0.5	2	0.8	1.4
C1) Increasing the proportion of good patches	0.75	2	0.9	1.0667
C2) Increasing patch size	0.5	5	0.9	1.6
C3) Increasing habitat richness	0.5	2	1	1.8

Notes: Variables are defined as follows: p is the proportion of favorable sites; s is the size of resource-rich patches; h characterizes the total amount of resource distributed over the area (Eq. 3); c is the contrast between rich and poor patches (Eq. 2). The amount of resource in poor patches is constant, $a(0) = 0.1$. Thus, c can be calculated from p and h . (See *Methods: The simulation model: Layer 1* for further details.)

probability $w(q)$. Thus, $w(q)$ is a general measure of the performance of a ramet in a cell of quality q .

Each simulation ran for 500 time steps. We saved the actual pattern in layers 1 and 2 in every 50th time step. For each combination of the environmental parameters (p , s , and h), 20 repetitions were made.

*Information statistical analysis
of the simulated patterns*

Our goal is to examine how the splitter–integrator community is being spatially organized according to the pattern of the resource. To what extent do the spatial positions of resource patches determine the distribution of splitter and integrator ramets, and what is the degree of spatial interdependence between the two strategies? We choose a way of pattern analysis in which the distribution of individual strategies can be directly related to their spatial interactions with each other and with the resource. Thus, we apply an information statistical method proposed by Juhász-Nagy (1984). The method was originally developed for the study of vegetation patterns (for example, see Juhász-Nagy and Podani 1983, Bartha et al. 1995). In the forthcoming analysis, we handle the pattern of the resource as if the resource was a third “species,” since the binary data on its occurrence (rich = 1; poor = 0) are collected similarly to the data of the splitter and integrator (present = 1; absent = 0). Thus, three components (the resource, the splitter, and the integrator) will be considered.

We subdivide the lattice in both layers into a mosaic which consists of 2×2 unit cells. This rescaling is necessary for studying co-occurrences, because on the unit scale ($s = 1$) the strategies completely exclude each other. We construct a two-way contingency table for each species pair: the splitter–integrator, the splitter–resource, and the integrator–resource. A contingency table for any species x and y contains the number of co-occurrences and separate occurrences of x and y in the grid. Considering all repetitions, contingency values in 20 tables are averaged and divided by the main sum (2500, the number of 2×2 units in the grid), to express the average relative frequencies of the species combinations.

We analyze the information content of the tables applying the model proposed by Juhász-Nagy (1984). First we regard single-species patterns. For species x , let $m_{0(x)}$ and $m_{1(x)}$ respectively denote the relative frequencies of absence and presence of x in the grid ($m_{0(x)} + m_{1(x)} = 1$). The joint Shannon entropy of $m_{0(x)}$ and $m_{1(x)}$,

$$H_x = -m_{0(x)} \times \log m_{0(x)} - m_{1(x)} \times \log m_{1(x)} \quad (4)$$

characterizes *heterogeneity* of the species. Log is log to the base 2, and H_x is measured in Bits. The spatial heterogeneity is minimal ($H_x = 0$) when x is present everywhere or is missing from the whole area. H_x reaches its maximum ($H_x = 1$) when x covers exactly half of the area. Importance of the entropies on the

margins of the contingency table, H_x and H_y , can be explained by the fact that they impose an upper limit upon the degree of spatial interaction between x and y .

Regarding the contingency tables, we can characterize how strongly the presence and absence of one component determines the presence and absence of the other, thus measuring *association* between the two patterns. Spatial association between x and y is defined as follows:

$$A_{xy} = H_x + H_y + \sum_{k=1}^4 z_k \times \log z_k \quad (5)$$

where z_k stands for the value in the k th cell of the contingency table. If the positions of x are random with regard to the positions of y , and vice versa, i.e., the patterns are independent, then $A_{xy} = 0$. On the other hand, if the positions of x are fully determined by the positions of y (for example, the splitter occurs everywhere where the integrator is absent and never grows together with it), then the association is $A_{xy} = \min[H_x, H_y]$. Association is maximal when two maximally heterogeneous patterns completely determine each other ($H_x = H_y = 1$, and $A_{xy} = 1 + 1 - 1 = 1$). These relations can be visualized by a Venn diagram (see D in Figs. 4 and 5). Each area is proportional to the value of a function. We use triangles to represent the values of heterogeneities, H_x for each x . Overlaps between the triangles represent the values of pair-wise associations, A_{xy} for each x and y . Upper and lower limits of mutual associations can be read directly from the upper and lower limits of the corresponding areas.

We follow the temporal development of pattern in two typical cases: when the splitter wins (Fig. 4) and when the integrator wins (Fig. 5). We show the state of the automata and the corresponding information statistical functions four times from the beginning to the end of the competitive exclusion.

Limitations of the model

1) We assume that the splitter and the integrator are identical in every respect but integration. There is no difference in the architecture of genets, etc. In natural conditions, there are many factors that determine competitive behavior. We make this simplifying assumption for the actual purpose: to focus only on the effect of integration.

2) We do not assume any plastic adjustment of runner length or branching frequency to resource conditions, i.e., the architecture of the clones is rigid. Our actual goal is to study the effect of integration separately from the effect of architectural plasticity.

3) Juvenile, nonestablished ramets are subsidized by their parents both in the splitter and in the integrator. Degree of parental support is included into the probability of birth (see $w(q)$ in *Layer 2: the competing populations*). Only later, when potential independence has been attained does splitting vs. integration become

an option. This assumption is probably not far from reality. Several studies suggest that export of resources to juveniles is general in clonal plants, even in those which later split (Pitelka and Ashmun 1985, Marshall 1990, Schmid 1990, Schmid and Bazzaz 1991, Alpert 1996a).

4) Averaging of the resource levels is possible, because the resource moves from higher to lower concentrations. The opposite, withdrawal of a resource from poor ramets, also occurs in nature (Pitelka and Ashmun 1985), but in the present case it would be disadvantageous, because the resource utilization function, $w(q)$, is concave (see Eriksson and Jerling 1990). It may be an interesting future task to test the effect of the shape of $w(q)$ on the direction and magnitude of transport in the different habitat types.

5) There is no cost of integration involved. The only cost is indirect: integration can occasionally diminish the competitive ability of the whole clone. Donor ramets pay the price of supporting the recipients, but in total, no resource is lost from the system. In reality, maintenance of the connecting tissues can have metabolic costs (Pitelka and Ashmun 1985, Kelly 1995). This may be counterbalanced by the fact that stolons and rhizomes can be utilized for storage.

6) The resource pattern is temporally constant (static). The only temporal change in resource availability is due to the propagation of competitor clones. In fact, integration can be a way of "buffering" not only spatial, but also temporal variation (see Eriksson and Jerling 1990, Caraco and Kelly 1991). We can tentatively predict that changing the resource pattern in time should give extra advantage to integration. But, as our preliminary results show, this advantage depends on the spatial parameters (p , s , and h) as well. So, effects of temporal variability need detailed studies in the future, including both externally imposed and internally generated (e.g., depletion–reallocation) resource dynamics.

7) Recruitment from seeds is negligible after the initial time step. The only way of dispersal is clonal propagation. Dispersal limitation often proves to be an important factor in spatial competition, because it may protect the competitively inferior species from exclusion (Czárán 1998). Relaxing this limitation may change the result of competition. Again, this is an important matter for future studies.

8) Ramets of the same clone are identical. In reality, pathways and magnitude of resource transport can largely depend on the state of ramets. Size, age, and physiological state (for example, flowering vs. vegetative ramet) may all influence the actual export–import relationship (Pitelka and Ashmun 1985, Jónsdóttir and Watson 1997). This is especially important for the transport of photoassimilates, which is governed by source–sink relations (see Marshall 1990). In the present simple model, we assume that the transport is not directional, and it is quick enough to distribute the

resource evenly before a developmental step (birth of a new ramet) happens. Representation of the internal architecture of each clone and of the state of each ramet would make an important conceptual advance in the model.

9) We consider a single limiting resource (or more resources that co-occur). Stuefer and his colleagues (1994, 1996) draw attention to the fact that if there are spatially negatively correlated resources, integrated clonal species can take advantage from spatial division of labor. Each ramet can morphologically specialize for the uptake of the locally abundant resource, and the connected ramets can exchange resources. This phenomenon has been demonstrated in *Glechoma hederacea*, *Potentilla anserina*, *Potentilla reptans*, and *Trifolium repens* (Stuefer et al. 1994, 1996, Alpert and Stuefer 1997). Thus, within-ramet specialization can give an additional advantage to integration.

Czárán (1998) suggests distinguishing between tactical and strategic models, according to the goal of modelling. Our model is strategic (or a toy model, sensu Dyson 1985), because we wish to demonstrate general trends in the resource use and competitive behavior of splitters vs. integrators. The model is not suitable for making direct, quantitative predictions about particular species in the field because of the strict assumptions that are listed above.

RESULTS

We found that competition between the splitter and integrator could result in competitive exclusion as well as long-term coexistence. When exclusion occurred, either of the two strategies could win, depending on the amount and spatial pattern of the resource.

Fig. 2 shows examples for the time course of competition under different habitat conditions. The integrator always started to spread faster than the splitter. In those habitats in which the integrator was destined to win, it quickly outcompeted the splitter (Fig. 2: A1, A2, and C3), whereas the splitter was relatively slow in excluding the integrator (Fig. 2: C1, E2, and A3). In the reference case (Fig. 2: B), propagation of the splitter against the integrator was so moderate that 500 generations were not enough to let the splitter attain dominance, even though the final outcome should be the disappearance of the integrator. In such habitats, long-term coexistence of the strategies can be predicted.

The balance between the splitter and the integrator that was experienced in the reference case could be readily shifted toward the extinction of one of the strategies by manipulating the environmental parameters: the proportion of good patches (p), the size of patches (s), or the overall resource richness of the habitat (h).

1. *The effect of the proportion of good patches.*—In the reference case (Fig. 2: B), half of the patches were good and the other half were bad ($p = 0.5$). When we decreased the proportion of good patches, we distrib-

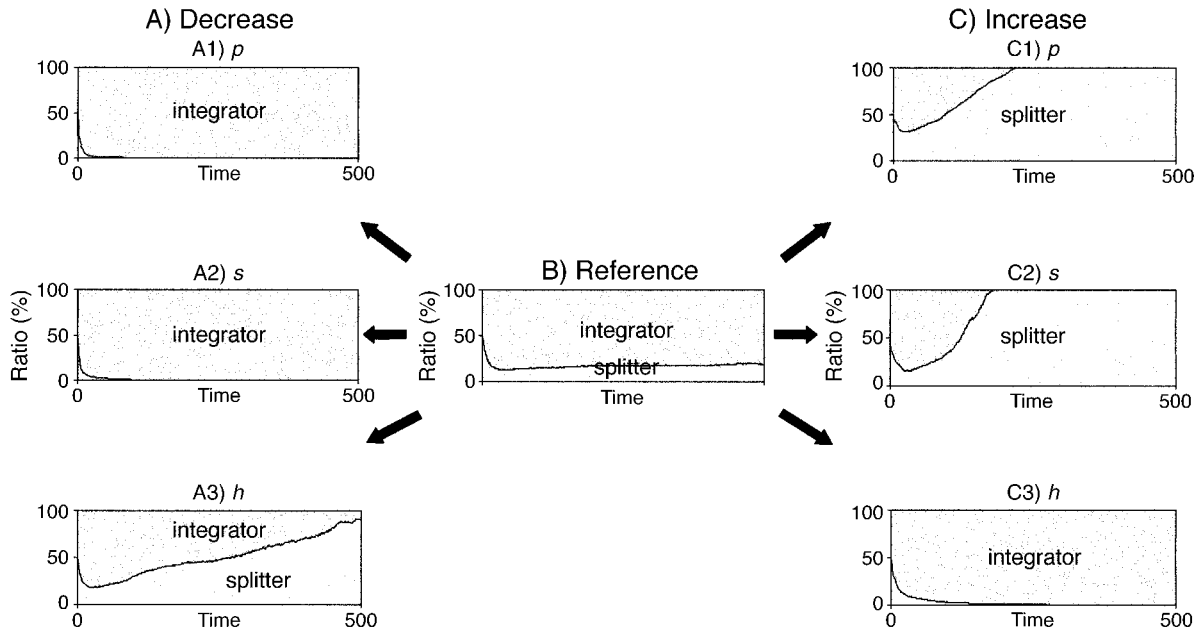


FIG. 2. Changes in the ratio of integrator to splitter ramets in the population over time. Each diagram represents a habitat type (as denoted in Table 1). The reference case (B) is in the middle. The left side shows the effect of decreasing p , s , and h , respectively; the right side presents effects when these parameter values were increased. In each diagram, horizontal axes range from time 0 to 500. Vertical axes show the ratio of splitter to integrator ramets in the population (dark to light grey areas); y-axis scales indicate percentages. Total height (100%) represents the whole ramet population. The curves start from 50%, because the initial number of propagules is equal for the two strategies that survive by the 500th time step are written on the diagrams. Each diagram was gained by a single, typical run of the simulation program.

uted the same amount of resource over the area, but concentrated it in a smaller number of good patches ($p = 0.25$). This led to the dominance of the integrator (Fig. 2: A1). In contrast, when we spread the resource more evenly among a larger number of good cells ($p = 0.75$), the splitter dominated (Fig. 2: C1).

2. *The effect of patch size.*—In the reference case (Fig. 2: B), the resource pattern was rather fine-grained. Size of the mosaic patches was only double the length of a clonal growth step ($s = 2$). Decreasing the patch size to $s = 1$ was beneficial to the integrator (Fig. 2: A2). It is interesting to observe the dramatic change in the opposite direction. Even a small increase in patch size (to five units) led to the overdominance of the splitter (Fig. 2: C2). Note that $s = 5$ still signifies a rather fine-grained habitat, considering that one unit represents an estimated distance between two connected ramets.

3. *The effect of habitat richness.*—The reference (Fig. 2: B) was a habitat in which the total amount of resource should exactly carry the maximum population size, if the resource was evenly distributed ($h = 0.9$; see a more detailed explanation in *Methods: The simulation model: Layer 1: . . .*). A small decrease in habitat richness gave advantage to the splitter (Fig. 2: A3). We cannot present the case when the splitter completely excludes the integrator within 500 time steps, because if the habitat is poorer than $h = 0.8$ the plateau in $w(q)$ disappears. We preferred changing the width of the

plateau, but not the shape of the utility function. However, even in the present case we can predict that the integrator would later disappear. When we increased the habitat richness to $h = 1$, the integrator excluded the splitter (Fig. 2: C3). So, a relatively small change in the total amount of resource caused an observable change in the dominance relations.

While Fig. 2 shows examples from single runs of the simulation program, Fig. 3 summarizes the results that were gained from 20 repetitions in each habitat type. The outcome of competition is consistent with the results in single runs. In addition, Fig. 3 offers an opportunity for comparing the microsite choice of splitters vs. integrators. In every case in which the splitter stayed alive by the end of the simulation (Fig. 3: C1, C2, A3, and B), it strongly preferred the good sites, putting almost no (<5%) ramets into the resource-poor area. In contrast, the integrator occupied both patch types (see Fig. 3: A1, A2, A3, C3, and B). The higher the ratio of bad sites in the habitat, the higher the number of integrator ramets utilizing bad patches (compare Fig. 3: A1 and B). In case of long-term coexistence between the strategies (Fig. 3: B), the integrator occupied a larger area in the same habitat than did the splitter. When one of the strategies won, the integrator always attained larger cover, compared to the splitter (see Fig. 3: A1 and C1 vs. A2 and C2).

Microhabitat preference and dominance in the patches can be better explained if we examine the development

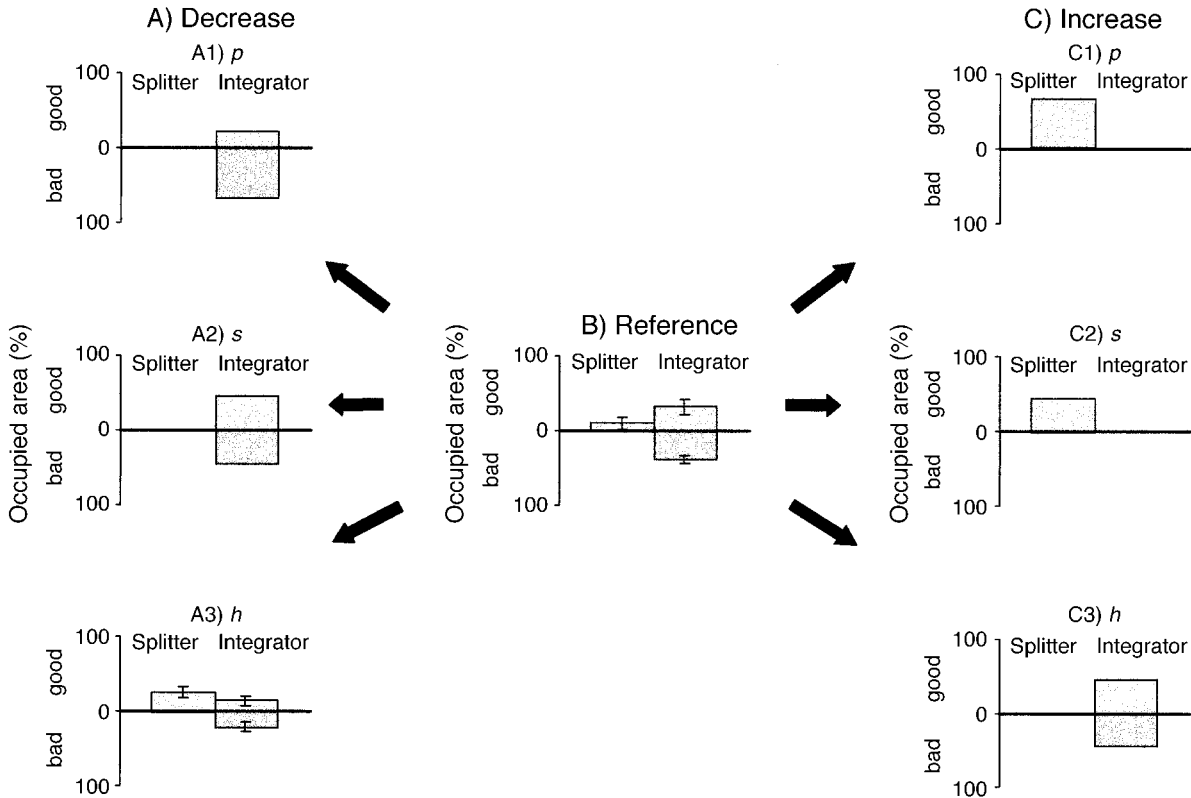


FIG. 3. The percentage of good and bad sites occupied by the competing strategies after 500 time steps (mean \pm 1 SD). The diagrams represent habitat types in the same arrangement as in Fig. 2. In each habitat type, the data were gained from 20 repetitions of the simulation. Bars show the mean number of cells occupied by the splitter (left) and the integrator (right). Shading and position refer to the quality of cells (light grey above the line, good; dark grey below the line, bad). The values are expressed in terms of percent cover, where 100% is the total area of the simulated field. Values that are $<5\%$ are truncated to 0.

of patterns in time. Fig. 4 shows the time course of competition in a typical habitat where the splitter wins (which is the same as in Fig. 3: C1), while Fig. 5 shows a time course with the opposite result (the same as Fig. 3: A1). We searched for typical differences in the spatial behavior of the strategists. For this purpose, we followed how they participated in the collective structure while the splitter-integrator community changed in time.

Time course: splitter wins.—Time 0 denotes the start of simulation, when 25 propagules of each strategy were randomly placed over the field. The Venn diagram in Fig. 4 clearly illustrates the randomness of spatial positions. There is no overlap between the triangles, indicating that there was no association between the two strategies or between either of the strategies and the resource. Sizes of the triangles represent the spatial heterogeneities of each component. Note that heterogeneity of the resource is maximal ($H_r = 1$), because the resource covered exactly half of the area ($p = 0.5$). The triangle representing H_r remains the same throughout the simulation, because the resource pattern was static (Fig. 4).

During the further growth of the populations, char-

acteristic changes occurred in the spatial structure. At the beginning, some of the propagules hit favorable patches. These had a good chance to survive and reproduce (being $w(1) = 0.9$; see Fig. 2). Others, getting into unfavorable patches, still had some opportunity for establishment ($w(0) = 0.1$). But if they did not reach good patches soon, then they were likely to become extinct. After the establishment, the clonal patches started to grow, and the neighboring ones reached the borderline of one another. At the 100th time step, the two competitors were nearly equally abundant, and similarly heterogeneous, as shown by the triangles H_s and H_i . The splitter had started to associate with the resource. At the same time, the integrator's association with the resource was much weaker. The integrator showed strong association with the splitter, since the two species tended to exclude each other. (Note that consistent avoidance implies strong spatial information, as well as consequent preference does.)

By the 200th time step, it became clear that the splitter dominated over the integrator. Its association with the resource increased. The splitter kept on determining the spatial positions of the integrator (see their asso-

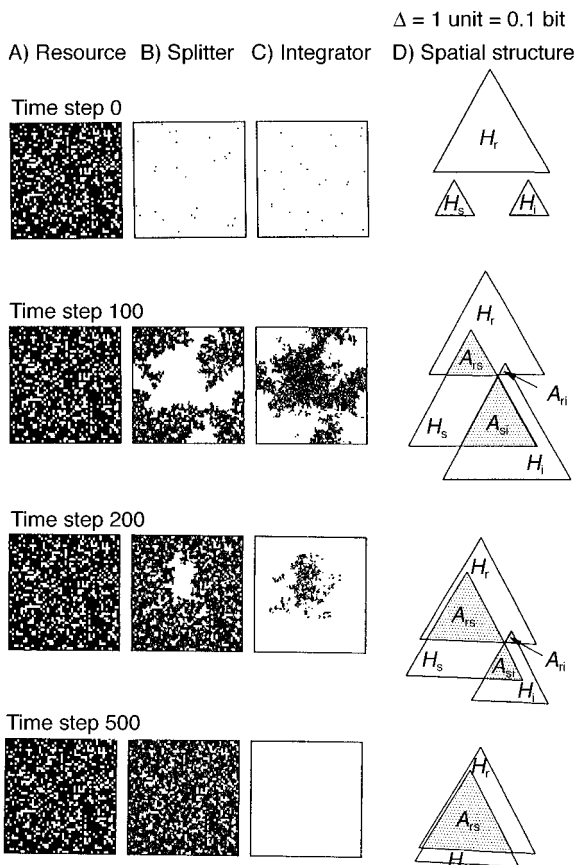


FIG. 4. Time course of competition in a typical habitat where the splitter wins (the same as C1; see Figs. 2 and 3). In each row, (A) shows the distribution of the resource (black, resource-rich site; white, poor site); (B) and (C) depict the splitter and the integrator (black, occupied site; white, empty site). (D) Venn-diagrams, calculated from 20 repetitions, showing the collective spatial structure of the resource, the splitter, and the integrator (indicated by subscripts r, s, and i). Large triangles represent species and resource heterogeneities (H_r , H_s , and H_i); overlapping areas show pairwise associations (A_{rs} , A_{si} , and A_{ri}), respectively.

ciation), excluding it from most of the area. The integrator failed to increase its association with the resource. Finally at time step 500, the integrator completely disappeared from the field. The splitter became monodominant and preserved its fairly large association with the resource patches. It significantly preferred the favorable microsites.

Time course: integrator wins.—Let us compare the above described scenario with the case when competition produces the opposite result. Fig. 5 shows the development of patterns at $p = 0.25$, when the integrator was successful against the splitter. The simulation began with placing 25 propagules of each strategy randomly over the area, similarly to the previous case (Time 0). Heterogeneity of the resource is the same as in Fig. 4, because of the following relationships:

$$m_{0(r)} = 1 - p \tag{6}$$

$$m_{1(r)} = p, \tag{7}$$

which are 0.75 and 0.25 now, and were 0.25 and 0.75 in the previous case (respectively), and H_x is symmetrical to p within the [0,1] interval (cf. Eq. 4).

By the 50th time step, the splitter had started to associate with the resource, but its propagation was quite limited. In contrast, the integrator had successfully spread over the area, but it failed to build up any association with the resource. The integrator depended only on the spatial positions of the splitter, being excluded from certain patches. Later, by time step 100, the splitter had almost disappeared, and the integrator conquered most of the field, decreasing its spatial heterogeneity. Space occupation of the integrator remained random with respect to the resource and weakly

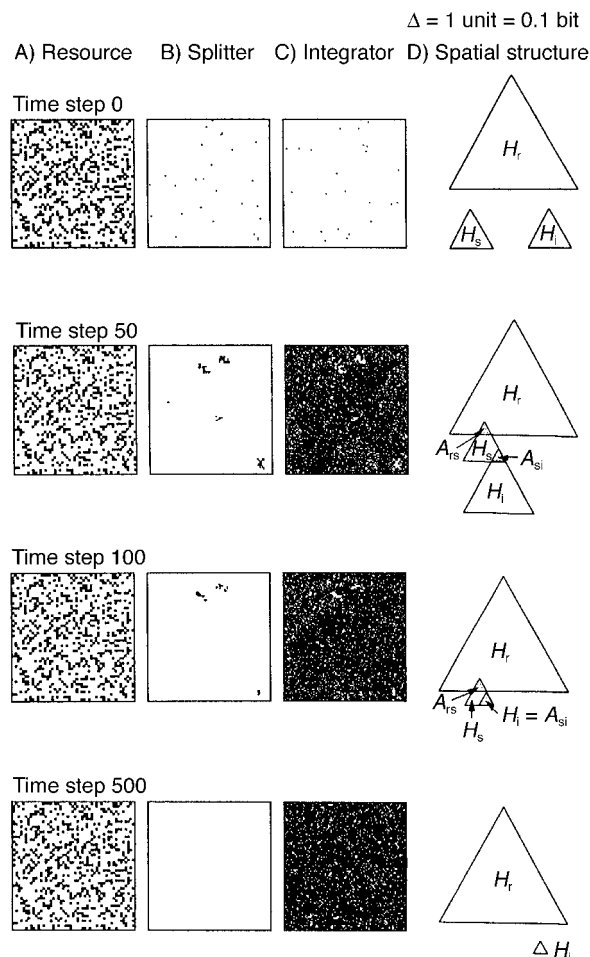


FIG. 5. Time course of competition in a habitat where the integrator wins (case A1). In each row, (A)–(C) show an example for a developing pattern, and (D) shows the corresponding Venn-diagrams gained from 20 repetitions. Notations are the same as in Fig. 4. We stopped the simulations at interesting stages, when changes occurred. This is why the time steps differ in Figs. 4 and 5.

associated to the splitter. Finally, the splitter died out, and complete spatial randomness was regained.

Comparing the two time courses, a general conclusion is that the degree of spatial association in the resource–splitter–integrator system is relatively high when the splitter wins (Fig. 4) and low when the integrator wins (Fig. 5). It is always the splitter which forms a stronger association with the resource and largely determines the spatial positions of the integrator. Interestingly, this tendency does not change even when the integrator dominates the area.

DISCUSSION

We proposed a spatially explicit approach to the study of clonal integration in heterogeneous habitats. In the model, growth of the clones and resource uptake proceeded simultaneously with internal redistribution of the resource. Thus, integration was studied together with selection of habitat patches.

Considering the spatial aspects of resource distribution fundamentally changed the predictions about the outcome of competition between a splitter and an integrator. It is worthwhile to compare the present approach to a nonspatial model of Eriksson and Jerling (1990). In that model, Eriksson and Jerling take a pair of ramets with different resource supply (a donor and a recipient) and elegantly demonstrate that the advantage of integration depends on the shape of the resource utilization curve for the ramets. The curve shows fitness as a function of physiological status (which is assumed to correlate with resource status). A general rule for the donor–recipient pair is that integration is advantageous when the curve is concave and disadvantageous when the curve is convex (see Eriksson and Jerling 1990: Fig. 7). Caraco and Kelly (1991) come to the same conclusion in a similar two-ramet (donor and recipient) system.

We adopted these results for the local rules of interaction in the cellular automata, but extended the approach by viewing a whole branching system of ramets, as it was developing in space. In contrast with the previous models, we took into account that difference in the actual performance of good and bad ramets leads to their different contribution to the next generation of ramets (in splitters). Therefore, average performance of the genet in a single time step (cf. Eriksson and Jerling 1990, Caraco and Kelly 1991) may not be a good predictor of genet fitness, because the ratio of good to bad ramets is not stationary in time. Consideration of the long-term effect of ramet demography is a novelty in this model.

According to the local rule, the concave shape of the resource utilization function ($w(q)$; see Fig. 1) gave advantage to integration: Internal transport enabled a ramet in a good patch to forward its surplus resource, increasing the average probability of survival and reproduction in the donor–recipient pair. Therefore, a nonspatial model would predict a higher rate of pop-

ulation growth with integration than without it. The integrator should exclude the splitter in all cases. In contrast, the model predicts three different outcomes of competition: (1) the integrator wins, (2) the splitter wins, or (3) long-term coexistence occurs. The outcome depended on the amount and the spatial arrangement of the resource.

When to split and when to integrate?

Integration proved more favorable than splitting when the resource was concentrated into a small number of small-sized patches. The splitter became successful when the same amount of resource was more evenly distributed among a large number of good sites. Interestingly, even a small increase in the patch sizes gave definite advantage to splitting. Not only the pattern, but also the total amount of resource influenced the outcome of competition. In slightly poorer conditions (when the good patches still provided some surplus resource), the splitter dominated. Integrators performed better at high average resource supply.

The proportion of good to bad sites (p) was important in determining the relative advantage of splitting. In a splitter clone, every ramet is “selfish” in the sense that it uses the amount of resource that is locally available in its microsite, without exporting to or importing from other parts of the clone. Consequently, splitter ramets are locally stronger than integrator ramets in good patches, but weaker in bad patches, provided that the integrator clone encounters both good and bad sites (having $w(0) < w(q) \leq w(1)$ at the actual average site quality q). As long as an integrator clone is fully inside a patch, it cannot be distinguished from the splitter. All ramets experience site quality $q = 1$. The integrator can form a temporary “inclusion” within the patch. But once the integrator reaches an edge, and the first integrator ramet is placed outside, the average amount of available resource decreases (causing $q < 1$). Therefore, every integrator ramet becomes competitively inferior to the splitter ramets. They die inside the patch faster as the ratio of favorably to unfavorably placed ramets is becoming smaller. Colonization outside a favorable patch can be successful until the ramets inside the patch subsidize the rest of the clone (maintaining $q > 0$). But after some temporary existence at the edge of the patch, the integrator clone is destined to die.

Why then does the integrator coexist with the splitter, and occasionally even win the competition, if the resource patches are scarce? As we have seen, the splitter is efficient in holding the favorable patches once found. But its ability to explore new patches is limited, because the splitter ramets cannot tolerate the bad conditions between good sites. When the good patches are abundant, the splitter is likely to percolate from one good patch to the other through the whole area. Thus, it gradually outcompetes the integrator. When the resource patches are scarce, there is a chance that the splitter cannot reach every good patch on the field.

Those patches which are isolated and initially not colonized by any splitter propagule will probably remain inaccessible to the splitter and can provide “shelters” to the integrator. If the average site quality under the integrator is good, the integrator can even win against the splitter. Dispersal limitation is crucial, because it prevents the splitter from wiping out its competitor from the area. Therefore, we can predict that longer distance dispersal (for example, by seeds) gives advantage to splitting. (Note that seed dispersal itself is an extreme form of “splitting,” combined with genetic reshuffling.)

We could achieve the dominance of splitters as well as integrators by manipulating the number of good sites (p), even though we distributed the same total amount of resource over the area. Size of the patches (s) also proved important. As spatial autocorrelation of the site quality increases (i.e., spatial predictability increases), splitter mothers in good sites have an increasing chance to place their daughters into good sites. Thus, the value of well-off mothers becomes higher. Increasing the difference between the reproductive capacity of good and bad mothers is beneficial to the whole clone. This is why splitting becomes advantageous. One unit for patch size represented the distance of one clonal growth step. Therefore, in the finest grained habitat that was used in the simulation ($s = 1$), spatial pattern of the resource was random on the scale of clonal propagation. Such extreme spatial unpredictability proved advantageous to the integrator. This result is in accordance with the traditional view that integration “buffers” habitat heterogeneity (Turkington and Harper 1979, Hartnett and Bazzaz 1985b, Alpert and Mooney 1986, Hutchings and Bradbury 1986, Slade and Hutchings 1987, Landa et al. 1992, Wijesinghe and Handel 1994, Kelly 1995). In the case of extreme unpredictability, it proved more advantageous to share the risk of mortality rather than “spreading the risk” among many ramets. It was interesting to observe that already a small deviation from randomness in resource distribution gave advantage to splitting. A patch size as small as $s = 5$ units was enough for the splitter to win. Considering the range of between-ramet distances that have been found in clonal species, $s = 5$ is still on the magnitude of centimeters or decimeters. So, this benefit from splitting due to resource patchiness is probably common in nature.

A related observation in the field is that splitting occurs even in phalanx growth forms. Wilhalm (1996) reports about frequent splitting in a number of tussock-forming grass species. For a set of tightly growing ramets, where most of the ramets have neighbors from the same clone and may experience rather similar biotic and abiotic conditions, the advantage is not readily evident. Our results do not give a general explanation but, at least, they indicate that high autocorrelation of habitat conditions is not a strong argument *against*

splitting. To the contrary, high autocorrelation can select for splitting in certain conditions.

Implications for the distribution of splitters and integrators in the field

A key question is, what types of habitats promote adaptation by integration or, alternatively, splitting? When should “poor relatives” be subsidized at the expense of the “rich,” considering that all the ramets of a clone are genetically identical? The simulations yielded some definite predictions. Integration should be adaptively advantageous in generally fertile habitats, where the resource is concentrated in small patches (having high average resource level [h] low proportion of good patches [p] and small patch size [s]). A typical example for a successful integrator may be a ruderal weed, developing in a resource-rich habitat, where the spatial positions of rich patches are unpredictable. There the clone can utilize its capacity for rapid exploration of new areas by runners at the expense of resource-rich parts of the clone. Splitting, in contrast, should be typically advantageous in more resource-limited conditions, where the resource is distributed in sizeable patches (low h , high p , and high s). An example may be a closed community with numerous (but not very rich) canopy gaps, where a stoloniferous or rhizomatous species can move from gap to gap by horizontal growth.

It is interesting to compare this general picture with other hypotheses that have been based on observations in the field. We have to restrict the comparison to those cases which do not involve temporal variation, because our habitats were constant. With regard to splitting, Pitelka and Ashmun (1985) conclude that splitting is favorable in very patchy and stressful environments (at our large s and low average h), because of selective dispersal to good sites. We can confirm this by the simulation results. A number of other studies emphasize that foraging growth is a way of coping with spatial heterogeneity (Sutherland and Stillman 1988, de Kroon and Schieving 1990, Birch and Hutchings 1994, Cain et al. 1996, Oborny and Bartha 1996, Stuefer 1996, Oborny and Cain 1997). We experienced the same, but the results emphasize that integration is an alternative way. Its success depends on the scale of heterogeneity: grain (s) and intensity (p).

With regard to integration, Eriksson and Jerling (1990) and Caraco and Kelly (1991) conclude that high average resource levels (our high h) are favorable to resource sharing. de Kroon and Schieving (1990) also suggest that consolidation growth, which involves high integration, is characteristic for resource-rich environments. Pitelka and Ashmun (1985) state the same about a space-monopolizing, extensively integrated clonal growth form. Our results confirm these hypotheses. A frequently observed tendency is that integrated clones are successful in arctic habitats. For explanation, several papers have assumed that resource sharing increas-

es genet performance in these nutrient poor and patchy areas (Callaghan 1988, Jónsdóttir and Callaghan 1988, Carlsson et al. 1990, Callaghan et al. 1997). Our results show the opposite: the lower the h and the higher the s , the more disadvantageous it became to keep the ramets connected. This suggests that resource acquisition and integration alone cannot be responsible for the observed predominance of integrators in the arctic, and other reasons should be researched. Some important factors are mentioned in the same papers (capacity for remobilization of stored nutrients, maintenance of extensive bud bank, control of growth morphology, etc.).

Comparing the dynamics of splitter vs. integrator populations, we can conclude that the integrator was always quicker in colonizing new, empty areas. If the actual habitat conditions proved advantageous to the integrator, it rapidly excluded the other strategy. The integrator ramets covered large areas rather evenly (i.e., without special preference for microsites). Thus, the integrator tended to monopolize the whole habitat. This result is in accordance with the frequent observation that integrated clones expand rather uniformly in all directions (Hartnett and Bazzaz 1985b, Solangaarachchi and Harper 1987) and occupy a wide area of ground, escaping from crowded locations (cf. Hutchings and Bradbury 1986, Schmid 1990, Hutchings and de Kroon 1994). Some extensive integrators can achieve monodominance (for example, *Clintonia borealis*, *Mercurialis perennis*, *Phragmites australis*, and *Solidago canadensis*; see Hartnett and Bazzaz 1985a, Pitelka and Ashmun 1985, de Kroon 1993, Suzuki and Hutchings 1997). Winning of the splitter over the integrator was a slower process than vice versa. The splitter did not simply tend to occupy a large area—it captured the favorable part of it. The same relationship between fragmentation (i.e., partial splitting) and microsite preference has been observed in *Ranunculus repens* and *Trifolium repens* (Hartnett and Bazzaz 1985b). Several studies support the view that integration decreases foraging efficiency (de Kroon and Schieving 1990, Hutchings and Mogie 1990, Hutchings and de Kroon 1994, Oborny and Cain 1997). In our case, we could definitely conclude that genet splitting was a precondition for microsite preference. A consequence of the efficient site selection of the splitter was its easily detectable patchy distribution. The splitter did not monopolize the field, but left the resource-poor areas largely unoccupied. These gaps remained open for any other species which can tolerate poor conditions. The information statistical analysis also demonstrated that the strategies differed in the mechanism of spatial competition. The splitter tended to dominate in the collective spatial structure, forming a strong association with the resource and with the other species. In contrast, the spatial distribution of the integrator was more independent of the distribution of the resource: the integrator did not become a strong structure-forming species even when it outnumbered the splitter. It merely filled the

gaps left open by the splitter. Integration caused a tendency for fugitive spatial behavior. This is why the two strategies could share the same habitat in our reference case.

The model yielded novel predictions concerning the spatial aspects of species coexistence. The two competing strategies in our model behave exactly alike in any homogeneous environment, since not only their demographic parameters are the same, but their local-scale spatial behaviors are also identical. This means that the only mechanism of global extinction for one of them would be random drift in any environmentally uniform and sufficiently small habitat. Increasing habitat size would increase the expected time to random exclusion. The novel feature of the splitter–integrator system becomes obvious in a patchy habitat, in which—depending on the grain and the intensity of the environmental pattern—long-term coexistence or the fast exclusion of one or the other strategy may follow. The fundamental (and only) difference between the splitter and the integrator strategies is that the former spreads the risk of low survival and low fecundity (arising from misplacement) among its ramets, whereas the latter shares it. Therefore, no previous explanations for species coexistence such as competition/colonization trade-offs, resource partitioning, local interactions, and short-range dispersal (cf. Pacala 1996, Czárán 1998) are sufficient in themselves to explain coexistence in our system. The fitness of a strategy is in most part determined by local resource accessibility and the mechanism of resource redistribution, and these are highly dependent on the actual resource pattern of the habitat. We may expect that if the typical habitat of a certain clonal plant species is not stationary in the sense that its grain and/or intensity vary in space, the species may adopt a mixed or an intermediate strategy, with an adaptive level of integration.

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LITERATURE CITED

- Alpert, P. 1990. Water sharing among ramets in a desert population of *Distichlis spicata* (Poaceae). *American Journal of Botany* **77**:1648–1651.
- Alpert, P. 1996a. Does clonal growth increase plant performance in natural communities? Pages 11–16 in B. Oborny and J. Podani, editors. *Clonality in plant communities. Special Features in Vegetation Science* 11, Opulus Press, Uppsala, Sweden.
- Alpert, P. 1996b. Nitrogen sharing in natural clonal fragments of *Fragaria chiloensis*. *Journal of Ecology* **84**:395–406.
- Alpert, P., and H. A. Mooney. 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. *Oecologia* **70**:227–233.

- Alpert, P., and J. Stuefer. 1997. Division of labour in clonal plants. Pages 137–154 in H. de Kroon and J. van Groenendael, editors. *The evolution and ecology of clonal plants*. Backhuys, Leiden, The Netherlands.
- Bartha, S., S. L. Collins, S. M. Glenn, and M. Kertész. 1995. Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. *Folia Geobotanica et Phytotaxonomica* **30**:169–184.
- Birch, C. P. D., and M. J. Hutchings. 1994. Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea*. *Journal of Ecology* **82**:653–664.
- Cain, M. L., D. Dudle, and J. P. Evans. 1996. Spatial models of foraging in clonal plant species. *American Journal of Botany* **83**:76–85.
- Callaghan, T. V. 1980. Age-related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland. *Oikos* **35**:373–386.
- Callaghan, T. V. 1988. Physiological and demographic implications of modular construction in cold environments. Pages 11–135 in A. J. Davy, M. J. Hutchings, and A. R. Watkinson, editors. *Plant population biology*. Blackwell Scientific, Oxford, UK.
- Callaghan, T. V., S. Jonasson, and R. W. Brooker. 1997. Arctic clonal plants and global change. Pages 381–404 in H. de Kroon and J. van Groenendael, editors. *The evolution and ecology of clonal plants*. Backhuys, Leiden, The Netherlands.
- Caraco, T., and C. K. Kelly. 1991. On the adaptive value of physiological integration in clonal plants. *Ecology* **72**:81–93.
- Carlsson, B. A., I. S. Jónsdóttir, B. M. Svensson, and T. V. Callaghan. 1990. Aspects of clonality in the arctic: a comparison between *Lycopodium annotinum* and *Carex bigelowii*. Pages 131–152 in J. van Groenendael and H. de Kroon, editors. *Clonal growth in plants: regulation and function*. SPB Academic, The Hague, The Netherlands.
- Crawley, M. J., and R. M. May. 1987. Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* **125**:475–489.
- Czárán, T. 1998. *Spatiotemporal models of population and community dynamics*. Chapman & Hall, London, UK.
- Czárán, T., and S. Bartha. 1989. The effect of spatial pattern on community dynamics: a comparison of simulated and field data. *Vegetatio* **83**:229–239.
- de Kroon, H. 1993. Competition between shoots in stands of clonal plants. *Plant Species Biology* **8**:85–94.
- de Kroon, H., and F. Schieving. 1990. Resource partitioning in relation to clonal growth strategy. Pages 177–186 in J. van Groenendael and H. de Kroon, editors. *Clonal growth in plants: regulation and function*. SPB Academic, The Hague, The Netherlands.
- Durrett, R., and S. A. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London* **B 343**:329–350.
- Dyson, F. 1985. *The origin of life*. Cambridge University Press, Cambridge, UK.
- Eriksson, O., and L. Jerling. 1990. Hierarchical selection and risk spreading in clonal plants. Pages 79–94 in J. van Groenendael and H. de Kroon, editors. *Clonal growth in plants: regulation and function*. SPB Academic, The Hague, The Netherlands.
- Gardner, S. N., and M. Mangel. 1999. Modeling investments in seeds, clonal offspring, and translocation in a clonal plant. *Ecology* **80**:1202–1220.
- Harper, J. L., and A. D. Bell. 1979. The population dynamics of growth form in organisms with modular construction. Pages 29–52 in R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific, Oxford, UK.
- Hartnett, D. C., and F. A. Bazzaz. 1985a. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *Journal of Ecology* **73**:407–413.
- Hartnett, D. C., and F. A. Bazzaz. 1985b. The integration of neighbourhood effects by clonal genets in *Solidago canadensis*. *Journal of Ecology* **73**:415–427.
- Headley, A. D., T. V. Callaghan, and J. A. Lee. 1988. Phosphate and nitrate movement in the clonal plants *Lycopodium annotinum* L and *Diphasiastrum complanatum* (L) Holub. *New Phytologist* **110**:497–502.
- Herben, T. 1992. Coexistence and pattern diversity in communities of clonal organisms: a model based on cellular automata. *Abstracta Botanica* **16**:49–54.
- Herben, T. 1996. Founder and dominance control: neglected concepts in the community dynamics of clonal plants. Pages 3–11 in B. Oborny and J. Podani, editors. *Clonality in plant communities*. Special Features in Vegetation Science 11, Opulus Press, Uppsala, Sweden.
- Hogeweg, P. 1988. Cellular automata as a paradigm for ecological modeling. *Applied Mathematics and Computation* **27**:81–100.
- Hutchings, M. J., and I. K. Bradbury. 1986. Ecological perspectives on clonal perennial herbs. *BioScience* **36**:178–182.
- Hutchings, M. J., and H. de Kroon. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research* **25**:159–238.
- Hutchings, M. J., and M. Mogie. 1990. The spatial structure of clonal plants: control and consequences. Pages 57–78 in J. van Groenendael and H. de Kroon, editors. *Clonal growth in plants: regulation and function*. SPB Academic, The Hague, The Netherlands.
- Hutchings, M. J., and A. J. Slade. 1988. Morphological plasticity, foraging and integration in clonal perennial herbs. Pages 83–109 in A. J. Davy, M. J. Hutchings, and A. R. Watkinson, editors. *Plant population ecology*. Blackwell Scientific, Oxford, UK.
- Inge, O. 1989. Genet and ramet survivorship under different mortality regimes—a cellular automata model. *Journal of Theoretical Biology* **138**:257–270.
- Jackson, J. B. C., L. W. Buss, and R. E. Cook. 1985. *Population biology and evolution of clonal organisms*. Yale University Press, New Haven, Connecticut, USA.
- Jónsdóttir, I. S., and T. V. Callaghan. 1988. Interrelationships between different generations of interconnected tillers of *Carex bigelowii*. *Oikos* **52**:120–128.
- Jónsdóttir, I. S., and M. A. Watson. 1997. Extensive physiological integration: an adaptive trait in resource-poor environments? Pages 109–136 in H. de Kroon and J. van Groenendael, editors. *The evolution and ecology of clonal plants*. Backhuys, Leiden, The Netherlands.
- Juhász-Nagy, P. 1984. Spatial dependence of plant populations. Part 2. A family of new models. *Acta Botanica Academiae Scientiarum Hungariae* **30**:363–402.
- Juhász-Nagy, P., and J. Podani. 1983. Information theory methods for the study of spatial processes and succession. *Vegetatio* **51**:129–140.
- Karlson, R. H., and L. W. Buss. 1984. Competition, disturbance and local diversity patterns of substratum bound clonal organisms: a simulation. *Ecological Modelling* **23**:243–255.
- Karlson, R. H., and J. B. C. Jackson. 1981. Competitive networks and community structure: a simulation study. *Ecology* **62**:670–678.
- Kelly, C. K. 1995. Thoughts on clonal integration: facing the evolutionary context. *Evolutionary Ecology* **9**:575–585.
- Klimes, L., J. Klimesova, R. Hendriks, and J. van Groenendael. 1997. Clonal plant architecture: a comparative anal-

- ysis of form and function. Pages 1–30 in H. de Kroon and J. van Groenendael, editors. The evolution and ecology of clonal plants. Backhuys, Leiden, The Netherlands.
- Landa, K., B. Benner, M. A. Watson, and J. Gartner. 1992. Physiological integration for carbon in mayapple (*Podophyllum peltatum*), a clonal perennial herb. *Oikos* **63**:348–356.
- Marshall, C. 1990. Source–sink relations of interconnected ramets. Pages 23–42 in J. van Groenendael and H. de Kroon, editors. Clonal growth in plants: regulation and function. SPB Academic, The Hague, The Netherlands.
- Oborny, B. 1994. Growth rules in clonal plants and environmental predictability—a simulation study. *Journal of Ecology* **82**:341–351.
- Oborny, B., and S. Bartha. 1996. Clonality in plant communities: an overview. Pages 115–127 in B. Oborny and J. Podani, editors. Clonality in plant communities. Special Features in Vegetation Science 11, Opulus Press, Uppsala, Sweden.
- Oborny, B., and M. L. Cain. 1997. Models of spatial spread and foraging in clonal plants. Pages 155–184 in H. de Kroon and J. van Groenendael, editors. The evolution and ecology of clonal plants. Backhuys, Leiden, The Netherlands.
- Pacala, S. W. 1996. Dynamics of plant communities. Pages 532–555 in M. J. Crawley, editor. Plant ecology. Blackwell Scientific, Oxford, UK.
- Pitelka, L. F., and J. W. Ashmun. 1985. Physiology and integration of ramets in clonal plants. Pages 399–435 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.
- Schmid, B. 1990. Some ecological and evolutionary consequences of modular organization and clonal growth in plants. *Evolutionary Trends in Plants* **4**:25–34.
- Schmid, B., and F. A. Bazzaz. 1987. Clonal integration and population structure in perennials: effects of severing rhizome connections. *Ecology* **68**:2016–2022.
- Schmid, B., and F. A. Bazzaz. 1991. Growth of transplanted and native shoots in perennials with contrasting genet architecture. *Flora* **185**:335–344.
- Silvertown, J., S. Holtier, J. Johnson, and P. Dale. 1992. Cellular automaton models of interspecific competition for space: the effect of pattern on process. *Journal of Ecology* **80**:527–534.
- Slade, A. J., and M. J. Hutchings. 1987. Clonal integration and plasticity in foraging behavior in *Glechoma hederacea*. *Journal of Ecology* **75**:1023–1036.
- Solangaarachchi, S. M., and J. L. Harper. 1987. The effect of canopy filtered light on the growth of white clover *Trifolium repens* L. *Oecologia* **72**:372–376.
- Stuefer, J. F. 1996. Potential and limitations of current concepts regarding the responses of clonal plants to environmental heterogeneity. *Vegetatio* **127**:55–70.
- Stuefer, J. F., H. de Kroon, and H. J. During. 1996. Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant. *Functional Ecology* **10**:328–334.
- Stuefer, J. F., H. J. During, and H. de Kroon. 1994. High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *Journal of Ecology* **82**:511–518.
- Sutherland, W. J., and R. A. Stillman. 1988. The foraging tactics of plants. *Oikos* **52**:239–244.
- Suzuki, J., and M. J. Hutchings. 1997. Interactions between shoots in clonal plants and the effects of stored resources on the structure of shoot populations. Pages 311–330 in H. de Kroon and J. van Groenendael, editors. The evolution and ecology of clonal plants. Backhuys, Leiden, The Netherlands.
- Turkington, R., and J. L. Harper. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of Ecology* **67**:201–218.
- van Groenendael, J., and H. de Kroon, editors. 1990. Clonal growth in plants: regulation and function. SPB Academic, The Hague, The Netherlands.
- van Groenendael, J., L. Klimes, J. Klimesova, and R. J. J. Hendriks. 1996. Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society of London*, **B 351**:1331–1339.
- Watson, M. A. 1986. Integrated physiological units in plants. *Trends in Ecology & Evolution* **1**:119–123.
- Wijesinghe, D. K., and S. N. Handel. 1994. Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*. *Journal of Ecology* **82**:495–502.
- Wijesinghe, D. K., and M. J. Hutchings. 1997. The effects of spatial scale of environmental heterogeneity on the growth of a clonal plant: an experimental study with *Glechoma hederacea*. *Journal of Ecology* **85**:17–28.
- Wilhelm, T. 1996. A comparative study of clonal fragmentation in tussock-forming grasses. Pages 51–60 in B. Oborny and J. Podani, editors. Clonality in plant communities. Special Features in Vegetation Science 11, Opulus Press, Uppsala, Sweden.
- Winkler, E., and B. Schmid. 1996. Clonal strategies of herbaceous plant species: a simulation study on population growth and competition. Pages 17–28 in B. Oborny and J. Podani, editors. Clonality in plant communities. Special Features in Vegetation Science 11, Opulus Press, Uppsala, Sweden.