



# Survival and competition of clonal plant populations in spatially and temporally heterogeneous habitats

Á. Kun and B. Oborny

Department of Plant Taxonomy and Ecology, Eötvös Loránd University, Pázmány P. sétány 1/c.  
H-1117 Budapest, Hungary. E-mail: kunadam@ludens.elte.hu and beata@ludens.elte.hu

**Keywords:** Colonization, Competitive exclusion, Habitat fragmentation, Individual-based model, Patchy environment, Physiological integration, Population dynamics, Ramet, Resource heterogeneity, Spatial ecology.

**Abstract:** Clonal populations are hierarchically organized: genetic individuals (genets) can consist of many physiological individuals (ramets). Each ramet takes up resources from its local environment, but the resource pattern can be reorganized within the clone by transport between ramets. Thus, an integrated clone is not directly subject to the pattern of resource availability in its habitat. Local shortages can be compensated, hence, the clone can 'buffer' itself against spatio-temporal heterogeneity in the habitat. We modelled a series of habitat types, assuming that one limiting resource was patchily distributed in space, and could fluctuate over time. Habitat types differed in the density, size and persistence of resource patches, and in the contrast between resource-rich patches and the resource-poor background. We applied an individual-based, spatially explicit population dynamic model to compare the performance of two plant strategies in these habitat types. In the Integrator, ramets that were interconnected distributed the resource evenly. In the Splitter, no resource translocation occurred. First we observed population growth of the two strategies separately, then in competition. We found a range of habitat types, where none of the strategies was viable, because of the scarcity of resource patches. As the density of resource patches was increased, first only the Integrator could persist. Then, at intermediate densities of resource patches, the Splitter became viable, and, being a stronger competitor, excluded the Integrator. Finally, at high resource-patch densities, the Integrator occupied the area again. Since the Splitter was viable at high density of resource patches when growing alone, its disappearance is more due to spontaneous extinction, due to competitive exclusion by the Integrator. We predict, therefore, the dominance of integrated clones both in extremely unproductive and productive environments, but for different reasons. It is important to note that this trend was observable only at high spatial and temporal variation in resource availability. Less contrast between patches of different quality, smaller patch sizes, or longer persistence of patches facilitated the dominance of the Splitter. Thus, buffering is advantageous in many but not all habitat types.

## Introduction

Terrestrial plants are sessile, so individuals have to cope with the specific conditions of the microhabitat where they are rooted. Moreover, since individual plants interact only with a limited number of neighbours, local interactions are of primary importance (Crawley 1997, Dickmann et al. 2000, Stoll and Weiner 2000). Besides seed dispersal, clonal growth offers a way to escape from locally bad conditions (c.f. Herben et al. 1994, Hutchings et al. 2000). Clonal plants produce genetically identical, vegetative offspring (ramets), each at a distance from the mother. Thus, the genetic individual (genet) can spread laterally, often spanning decimetres or meters, meeting a variety of microhabitat conditions (Cook 1985, Harper 1985, Eriksson and Jerling 1990, Wijesinghe and Hutch-

ings 1999, Hutchings et al. 2000, Pennings and Callaway 2000).<sup>1</sup> While individual ramets are still anchored in space, the genet can 'scout' its environment.<sup>2</sup>

Clonal plants are abundant members of plant communities. Some community types, like perennial grasslands, are dominated by clonal species. More than 50% of species (up to ca. 80%) have been found to be clonal in several temperate communities (Klimeš et al. 1997). Thus, species composition and spatio-temporal structure in many communities are largely determined by the processes that regulate clonal growth (de Kroon and van Groenendael 1990, Oborny and Bartha 1996, Klimeš et al. 1997). An important feature of clonal growth is the flow of resources (photoassimilates, water and mineral nutrients) from mother ramet to daughter through physiologi-

1 For example, old-aged genets of *Pteridium aquilinum* have been found to grow up to 489 meters in diameter (Oinonen 1967, cited in Cook 1985).

2 For more details about exploratory growth, see literature on plant foraging (e.g., Hutchings and de Kroon 1994, Oborny and Cain 1997).

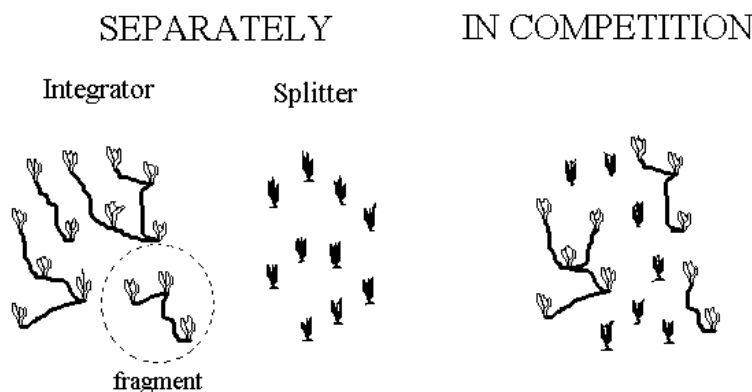
cal connections (stolons, rhizomes, etc.). In the so-called genet splitter species (Eriksson and Jerling 1990) these connections do not persist for long. Shortly after a juvenile ramet has developed its own root and shoot systems, it becomes self-supporting, and ceases to import resources from the mother. Thus, the genet splits up into autonomous ramets. Examples for this growth form are *Aster lanceolatus*, *Fragaria vesca* or *Uvularia perfoliata* (Schmid and Bazzaz 1987, Eriksson and Jerling 1990, Wijesinghe and Whigham 2001). In other species, which we may call genet integrators, the connections persist, and keep serving as pathways for the transport of resources between adult ramets. The direction of transport is determined by differences in resource concentrations relative to the local needs of ramets. (See Marshall 1990 about source-sink relations, and Sachs and Novoplansky 1997 about correlative control of growth.) It is known, however, that there is some degree of fragmentation even in typical integrator species. For example, the mean number of interconnected tillers in twenty-seven tussock forming grass species in Europe has been found to range between 3 and 75 (Wilhelm 1996). There are two basic reasons for fragmentation: [1] physiological connections between ramets die, or [2] the ramets themselves die, and thus, neighbouring ramets become disconnected (c.f. Jónsdóttir and Watson 1997).

In our study, we modelled two simplified strategies to represent the two main clonal types. [1] In the *Splitter* strategy, longevity of the connections was assumed to be much shorter than the lifespan of ramets. Each ramet became physiologically autonomous after its establishment. [2] In the *Integrator* strategy, fragmentation could occur only due to ramet death. Thus, a genet could consist of many clonal fragments, each fragment being a set of

physiologically connected ramets (Fig. 1). Clonal plant populations are hierarchically organized: both ramets and genets have their own rates of survival and reproduction (see Vourisalo et al. 1997 about hierarchical selection). In addition, we considered an intermediate level of organization in the Integrator: the fragment.

The intensity of resource transport between interconnected ramets differs greatly between clonal plant species (Pitelka and Ashmun 1985, Eriksson and Jerling 1990, Jónsdóttir and Watson 1997, Price and Marshall 1999). Patterns of integrated physiological units (*sensu* Watson 1986) and the amount of transported nitrogen, carbon, water etc. have been studied by radioactive labelling and other tracing experiments (see reviews by Jónsdóttir and Watson 1997, Price and Marshall 1999). Though the pattern of resource transport can be fairly complex, we applied simplifications in the model: we did not assume any dependence of the transport process on the age or developmental stage of the ramets, with the exception that juvenile ramets received subsidy from the mother during establishment. In the Splitter, each ramet became independent after establishment. In the Integrator, the connected ramets were fully integrated, i.e., shared their resources evenly. Thus, we contrasted two extreme cases: no integration (in the Splitter) to full integration (in the Integrator).

We hypothesized that population dynamics of the two strategies will differ significantly in heterogeneous environments, depending on the pattern of resource patches, because Splitter *versus* Integrator ramets perceive environmental heterogeneity in different ways. In the Splitter, each ramet senses its local environment. In the Integrator, ramets that belong to the same fragment sense the average resource level that is available to the whole fragment. To



**Figure 1.** A sketch of the plant strategies involved in the simulations: Integrator and Splitter. Integrator clones develop by producing interconnected ramets. Stolons or rhizomes break up only at the points where ramets die. Each set of interconnected ramets is called a fragment. Members of a fragment can share resources. The Splitter consists of autonomous ramets, i.e. resources are not shared. We compared the number of ramets in the Integrator and Splitter in two ways: when the populations were growing separately, and when they competed for the same habitat space.

study this phenomenon, we modelled a wide range of possible habitat types, and compared the performance of the strategies.

Questions about the adaptive advantage of integration in different habitats have arisen since the early clonal plant research (Harper 1978, Harper and Bell 1979, Noble and Marshall 1983, Pitelka and Ashmun 1985, Hutchings and Bradbury 1986, Slade and Hutchings 1987). As Harper put it in 1978, “When has it paid a plant that grows clonally to fragment and lose interconnection or to stay interconnected with a persistent rhizome?” In the past two decades, many studies have focused on answering this question (see reviews by Pitelka and Ashmun 1985, Hutchings and Bradbury 1986, Marshall 1990, Jónsdóttir and Watson 1997, Price and Marshall 1999). However, considering the known hypotheses and experiments geared towards understanding the effect of environmental heterogeneity in selecting for integration or splitting, it is difficult yet to make a generalization for the following reasons.

[1] The effects of different aspects of the spatial pattern (e.g., grain and contrast) are not distinguished in most empirical studies (Stuefer 1996). Greenhouse or garden experiments on clonal integration are very labor-intensive, and understandably, researchers tend to use the simplest possible design for the spatial pattern of resource-rich and poor sites. A commonly used arrangement is that one part of a set of interconnected ramets receives a uniformly resource-rich treatment while the connected part receives uniformly resource-poor conditions (e.g., watering by nutrient solution *vs.* pure water; or providing full light *vs.* shading). Very few studies have applied a mosaic of good and bad patches. In these experiments the study area was subdivided into square lattice cells, and some cells received resource-rich and others resource-poor treatment. Wijesinghe and Handel (1994) tested the effect of the proportion of rich to poor cell on clonal growth. Wijesinghe and Hutchings (1997) kept the proportion of rich and poor patches constant, and varied the size of resource patches between treatments. In addition, Wijesinghe and Hutchings (1999) tested the effect of patch size and contrast as well. To our knowledge, this is the only experiment in which the effects of grain and contrast have been separated.

[2] Another problem which hinders generalizations about the adaptive advantage of integration, is the lack of data about effects of temporal heterogeneity. Stuefer (1996) has discussed the importance of considering temporal heterogeneity when studying clonal plant responses to environment. With regard to integration, we know of no experiment where temporal changes have been included and

related to the pattern of integration, and know of only one model in which temporal variation of resource patchiness was examined (Caraco and Kelly 1991), although it can be hypothesized that variability of site quality from good to bad and *vice versa* is an important descriptor of a habitat, with relevance to the success of clonal integration.

Even with simple representations of heterogeneity, we have a suite of variables, each of which can potentially influence population growth. Naturally, experimentation with these interacting variables is difficult, because creating artificial habitats by changing these variables systematically would require a lot of space and time. Computer simulations can help by modelling a large variety of habitat types. If we have information about the local rules of interaction between ramets in good and bad patches, we can test how these rules work over several ramet generations, in a patchwork of good and bad sites.

### *The model*

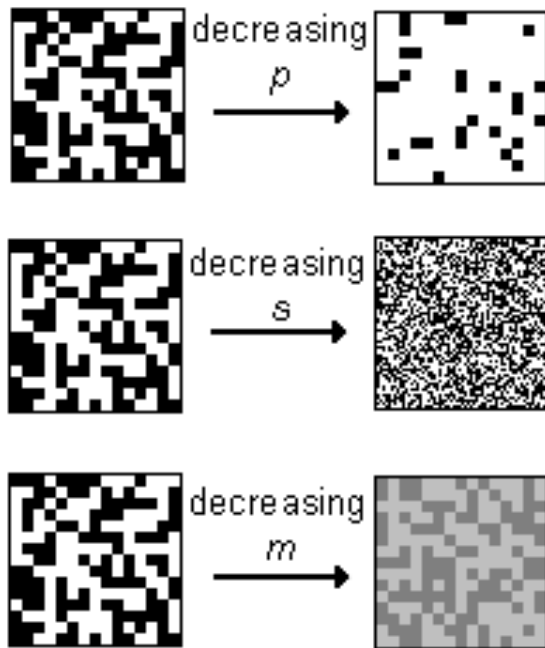
The model that we wish to present assumes a minimal representation of spatio-temporal heterogeneity. Habitat space is modelled by a square lattice. One spatial unit corresponds to the distance between neighbouring, interconnected ramets. The resource is distributed patchily. The lattice is subdivided into squares of  $s \times s$  size. Among these  $s$ -sized patches,  $p$  proportion has good quality (resource-rich), while  $1-p$  is bad (resource-poor). Contrast between good and bad sites,  $m$ , is expressed by a fitness difference (Fig. 2; see later in detail). With regard to temporal variation, we assume that the proportion of good sites,  $p$ , is stationary over time; only the locations of good patches change. Each patch ( $s \times s$  cells) changes its quality independently of the others, according to a first-order Markovian process.  $C_g$  proportion of the good patches turns into bad, and  $C_b$  of the bad patches changes into good. Since we assume that  $p$  remains unchanged, a single parameter, for example,  $C_g$  is sufficient for the characterization of patch turnover rate.

$$C_g \cdot p = (1-p) \cdot C_b. \quad (1)$$

One time unit in the temporal changes corresponds to the developmental time of a new ramet. Thus, both spatial and temporal heterogeneities are characterized according to the unit scales of plant growth. We have four parameters for the description of a habitat:  $p$ ,  $s$ ,  $m$ , and  $C_g$ .

### *Preliminaries*

The present model is part of a larger set of models, the INTEGRID model family (Oborny et al. 2000, Oborny et al. 2001, Oborny and Kun 2002). In each previous model, we have applied the same rules for producing habitat het-



**Figure 2.** Parameters of the spatial pattern, that were varied in the simulations.  $p$ : proportion of good to bad sites,  $s$ : grain,  $m$ : contrast of the pattern. Shading denotes local resource concentration from poor (white) to rich (black). In addition, a parameter of the temporal pattern was also examined,  $C_g$ : patch turnover rate. (See text for details.)

erogeneity as described above. Rules for defining the Splitter *versus* Integrator strategies were also similar.<sup>3</sup> We have compared the population growth of the Splitter and Integrator in competition (Oborny et al. 2000, Oborny et al. 2001, Oborny and Kun 2002), and also when the populations grew separately (Oborny and Kun 2002). With regard to habitat types, we have sampled only some points in the parameter space. Thus, the effects of different components of heterogeneity have not been systematically explored.

The first INTEGRID model (Oborny et al. 2000) applied three different values for each of the following parameters:  $p$ ,  $s$ , and  $m$ . Contrast between good and bad patches was assumed to be so high that each good site (cell) contained sufficient resource for the maintenance of more than one ramet. Since spatial constraints did not allow for the existence of more than one ramet at each site, this rule permitted the export of resource from a good patch, thus, gave some selective advantage to integration.

In the later models, including the present one, the quality of good sites was not so high. At the highest value of contrast ( $m = 1$ ) a good site could maintain one ramet in the best condition (0 probability for death and 1 probability for reproduction when the resource was not shared with any other ramet; see later). In the second model (Oborny et al. 2001),  $m$  was constant ( $m = 0.5$ ),  $s$  had four different values, and  $p$  had three values. In the third case (Oborny and Kun 2002), 18 different values of  $p$  were tested at  $m = 1$  and  $s = 1$ .<sup>4</sup> It is important to note that temporal changes have not been introduced into any of the models, i.e. it has been assumed that the habitat patterns were constant over time ( $C_g = 0$ ).

### Objective

The purpose of the present study is [1] to screen the effects of spatial heterogeneity parameters systematically, and [2] to introduce temporal heterogeneity.

### Methods

The methods were similar to other members of the INTEGRID family. We applied a stochastic cellular automata model. The simulation area was represented in two layers: one showed the state of the spatially and temporarily heterogeneous environment (resource layer); the other showed the states of clones (population layer). Lattice size was  $100 \times 100$  cells. We used von Neumann neighbourhood, i.e., every lattice cell had a neighbourhood of its four nearest cells. The boundaries were wrapped-around (torus), to preclude edge effects. Updating the lattice cells was synchronous.

#### Resource layer

The state of each cell - the local environment - could be either good (resource-rich) or bad (resource-poor). As we have stated in the Introduction (Fig. 2), we used the following parameters:

- (1) average resource richness of the habitat ( $p$ ),
- (2) size of patches ( $s$ ),
- (3) contrast ( $m$ ),
- (4) patch turnover rate ( $C_g$ ).

#### Population layer

In the population layer, each cell (site) could be vacant or occupied by a single ramet. A ramet in a particular cell

<sup>3</sup> The only difference was that in the first two studies (Oborny et al. 2000, 2001) fragmentation due to ramet death did not occur in the Integrator. The next study (Oborny and Kun 2002) focused exactly on the effects of presence versus absence of fragmentation.

<sup>4</sup> Naturally, not only the spatial patterns, but also the general context and questions have been different in these studies. We will return to their results only in the Discussion of the present paper.

encountered a microhabitat characterised in the resource layer at the same co-ordinates. We assumed that each ramet could take up the resource from its cell in each time step, and use it for its self-maintenance and reproduction, or could export it to other ramets. Resource depletion was assumed to be negligible. The two strategies, the Splitter and the Integrator, differed only in sharing vs. not sharing the resource; in all other respects they were the same. Those Integrator ramets that were connected, i.e., belonged to the same fragment, shared the resource evenly. Splitter ramets did not share resource. We recorded the existing connections within each fragment explicitly, knowing the identities of connected neighbours. Whenever an Integrator ramet died, all the connections to that ramet also died, so the clonal fragment broke into a number of smaller fragments. In this way, we recorded the actual branching pattern of the clones in each time step. This technical complication was necessary because we wished to know the exact locations of ramets (where they interact with their local environments) as well as their positions within the branching structure (through which they could exchange resources).

At the beginning of each simulation, we placed single ramets at random positions in the lattice. Thus, we assumed only initial seedling establishment in the population (*sensu* Eriksson 1997). When the strategies were tested separately, we introduced a starting population of 50 Integrator or 50 Splitter seeds. When grown in competition, we used 50 Integrator plus 50 Splitter seeds. All the other cells were empty.

#### Transition rules

States of the lattice cells were updated synchronously. Five updates took place in every time step: [1] change in the resource distribution, [2] evaluation of the resource level for each ramet, according to the connections between ramets, [3] birth of new ramets, [4] re-evaluation of resource levels, [5] survival of ramets.

[1] Changes in the resource layer were made only when  $C_g$  was higher than 0. A proportion,  $C_g$  of the good patches was chosen randomly, and converted to bad. At the same time, a random proportion,  $C_b$  of the bad patches was converted to good.

[2] Updating continued by evaluating the resource status,  $r_i$ , for each ramet  $i$ . Good sites contained  $e_g = 0.5 + m/2$  units of resource, and bad sites contained  $e_b = 0.5 - m/2$  units. Thus, the amounts of resource in good and bad sites changed symmetrically from equal ( $e_g = e_b = 0.5$ ) to maximally different ( $e_g = 1, e_b = 0$ ) as  $m$  increased from 0 to 1. Ramets in the Splitter did not share any resource. Accord-

ingly, the amount of resource available to a Splitter ramet was the same as the resource content of its local site:  $r_i = e_g$  in a good cell, or  $r_i = e_b$  in a bad cell. In contrast, Integrator ramets could transport the resource to and from other, interconnected ramets. Resource availability was calculated by summing the amount of resource available to all ramets in the fragment, and distributing it evenly among the ramets. If a fragment consisted of  $f$  ramets, of which  $f_g$  were situated in good sites, then every ramet received

$$r_i = \frac{e_g f_g + e_b (f - f_g)}{f}. \quad (2)$$

[3] The next step was ramet birth. Since each cell could host only a single ramet, ramet recruitment occurred only in empty sites. Dispersal of the clonal offspring was assumed to be limited to neighbouring cells. Thus, each empty cell was updated in the following way. We examined its neighbourhood, and listed all the ramets that contained more than zero resource, i.e. were capable of producing a new ramet. If there was no potential mother in the neighbourhood, then the cell remained empty, otherwise, it became occupied. If there was more than one potential mother, then competition took place. The probability that ramet  $i$  could win the competition depended on its resource status (strength) relative to other potential recruits. The voting weight of each potential mother ramet  $i$  was  $r_i$ . For example, if there were two ramets to compete for a site, ramet 1 with  $r_1 = 0.2$ , and ramet 2 with  $r_2 = 0.6$ , then ramet 1 would have a probability of 0.25 of winning the competition, and ramet 2 would have a probability of 0.75 of winning. Thus ramets with more available resource had a higher chance of producing new offspring.

If the new-born ramet was a Splitter, then the program had no further task at this point, because we assumed that the ramet became physiologically independent immediately after its establishment. If the new ramet was an Integrator, then we recorded its connection to the mother, and thus stored the information that the clonal fragment had gained a new ramet.

[4] Newly established Integrator ramets could contribute to the resource supply of other ramets. Thus, we re-evaluated the resource levels by repeating step [2].

[5] Finally, every ramet was tested for survival. The probability of each ramet  $i$  surviving was equal to its resource level,  $r_i$ . Thus, ramets that had access to more resource had a higher chance for survival. When a ramet died, its cell became empty. Connections of the dead ramet to other ramets were deleted, and the original set of interconnected ramets fell apart into smaller fragments, as in Fig. 1.

These rules imply that the amount of resource ( $r_i$ ) had a linear effect on ramet fitness. Although we have experimented with other rules (Oborny et al. 2000, and unpublished data), linearity seems to be a reasonable assumption. As Eriksson and Jerling (1990) have pointed out, if the resource utilization function is concave, which gives extra advantage to the Integrator, because any connected pair of ramets have a higher fitness than the average fitness of separate ramets. Similarly, a convex function gives advantage to integration. Therefore, linear resource utilization represents a neutral assumption.

In light of resource utilization, it is perhaps easier to explain our assumption about the resource contents of good and bad patches. Naturally, the scale of resource values is arbitrary, and the meaning of  $e_g$  and  $e_b$  can be interpreted only in relation to ramet fitness. Let us consider Splitter ramets. The statement that  $e_b = 0.5 - m/2$ , and  $e_g = 0.5 + m/2$  means that when the contrast is maximal ( $m = 1$ ), bad ramets are certain to die. Good ramets are certain to survive, and have a maximal competitive strength at reproduction. When the contrast is less extreme ( $m < 1$ ), bad ramets have some chance of surviving and reproducing ( $e_b$ ), and good ramets can die (with the same  $e_b$  probability, because  $e_g = 1 - e_b$ ). Therefore,  $m$  expresses the difference which microsite quality (good vs. bad) can have on the fate of a ramet. Of course, this applies only to Splitter ramets. Integrator ramets are not directly affected by local conditions.

#### Comparison of the strategies

We studied the difference between the strategies in two ways. [a] First, we compared population sizes when the Splitter and Integrator were growing separately to the case when growing together, in competition. [b] Secondly, we considered only competition, and recorded the winner (Splitter or Integrator). This series of runs was used for mapping the parameter space in finer resolution.

[a] *Population sizes.* The simulations were run for 20,000 time steps. Population sizes of the Splitter and the Integrator were recorded after the last time step. For each parameter combination, we made twenty repetitions for each of the three cases: Splitter alone, Integrator alone, and Splitter and Integrator in competition.

[b] *Outcome of competition.* The simulations were run for 1000 time steps. If the outcome of competition was not decidable after the 1000th step, then further steps were made up to time 40,000. We distinguished between four types of outcome:

- ‘All dead’: neither of the strategies survived;

- ‘Splitter wins’: only the Splitter survived;
- ‘Integrator wins’: only the Integrator survived;
- ‘Long-term coexistence’: both strategies survived.

Extinction was possible after 40,000 time steps, too, due to stochastic effects (when all ramets died at the same time by chance), but, extinction in such cases was extremely slow relative to the time scale of competitive exclusion. 40,000 time steps was equivalent to 40,000 ramet generations, which is a long time even if a particular species produces, say, as many as 10 ramet generations per year. Therefore, when both strategies survived to the end of the 40,000th time step, we concluded that the species could coexist over an ecological time scale.

Nine repetitions were made for each parameter combination. Usually all repetitions resulted in the same outcome, though in some cases two types of outcomes occurred. In such cases, we determined the overall outcome from the mode of the nine repetitions.

#### Parameters of the simulations

In the study of population sizes, we examined 120 combinations of  $p$ ,  $C_g$ ,  $s$ , and  $m$  values. When mapping the outcome of competition in the parameter space, we looked at 2260 parameter combinations.

[a] *Population sizes.* We considered a broad range of values for the average density of resource patches ( $p$ ), from 0.1 to 0.8. The extremes,  $p = 0$  and  $p = 1$ , were excluded, because in homogeneous environments the same amount of resource would be available to every ramet irrespective of its strategy. The value of  $p$  was increased in rather small steps, by 0.05 between simulations, because our former studies (Oborny et al. 2000, Oborny et al. 2001, Oborny and Kun 2002) have suggested that  $p$  is an important characteristic of the environment, and that a small change in a critical region can considerably influence the relative success of Splitter against Integrator. For the other parameters, we took rather extreme values: a low and a high for each, relative to the spatial and temporal scale of clonal growth. Patch turnover rate ( $C_g$ ) was 0 or 0.25; patch size ( $s$ ) 1 or 10; and contrast ( $m$ ) 0.5 or 1.

[b] *Outcome of competition.* We compared 2260 parameter combinations.  $p$  changed from 0.10 to 0.95 in 0.05 increments.  $C_g$  was 0, 0.05, 0.10, 0.15, 0.20, 0.25 or 0.30. Some combinations of  $p$  and  $C_g$  could not be realised because of the inherent constraint in equation (1):  $C_g$  could not be higher than  $(1 - p) / p$ . The size of the resource patches ( $s$ ) was 1, 2, 4 or 10. Contrast ( $m$ ) was 0.5, 0.75, 0.9 or 1.

## Results

[a] *Population sizes.* The theoretical carrying capacity of a habitat with average resource density  $p$  and contrast  $m$  can be described as

$$K(p, m) = (e_b + m \cdot p) \cdot N \quad (3)$$

where  $e_b = 0.5 - m/2$  is the amount of resource in bad cells, and  $N$  is the total number of cells.  $K$  can be interpreted as the theoretically achievable maximum population size that can be realised when any empty site is available to any mother, i.e., not only neighboring cells can be colonized. By simulating different habitat types with the same  $K$  (the same  $p$  and  $m$  values), we tested the effect of distributing the same total amount of resource in different spatio-temporal patterns. The results are presented in Figs. 3 and 4. Dashed lines show that the carrying capacity ( $K$ ) remained consistently the same within Fig. 3 and also within Fig. 4; only the size of patches into which the resource was aggregated ( $s$ ), and the turnover rate of patches ( $C_g$ ) differed.

It can be seen from Figs 3 and 4 that populations of species with both strategies deviated from the theoretical carrying capacity in most instances. This deviation follows from the fact that not every site was utilized, either because of dispersal limitation or because the site had already been occupied by the other species (in the competition case). The first graph-pair (Fig. 3.a and b) shows the results in a fine-grained habitat with no temporal change in the local resource level. The contrast is so high that bad sites are uninhabitable to Splitter ramets ( $e_b = 0$ ), while good sites provide ideal conditions for survival and reproduction ( $e_g = 1$ ). This is a repetition of a former simulation (Oborny and Kun 2002), and will serve now as an important reference for the study of other, (newly studied) habitat types. To summarize the conclusions (Oborny and Kun 2002): when the Splitter was growing alone (Fig. 3.a), we could observe a sudden decrease in its population size as the amount of resource ( $p$ ) decreased below a certain threshold (ca.  $p = 0.6$ ). In these habitat types, the population could not utilize the full carrying capacity ( $K$ ) of the habitat due to its severe dispersal limitation. Since  $m$  was maximal, Splitter ramets could not establish in bad cells at all: their survival probability was 0. Thus, spatial spreading of any Splitter clone was strictly confined to a set of good cells that was available from its site of origin (seed) by step-by-step colonization from good to good site. Thus, population size strongly depended on the percolation structure of the habitat. At low values of  $p$ , only a small fraction of the good cells could be colonised by the Splitter.

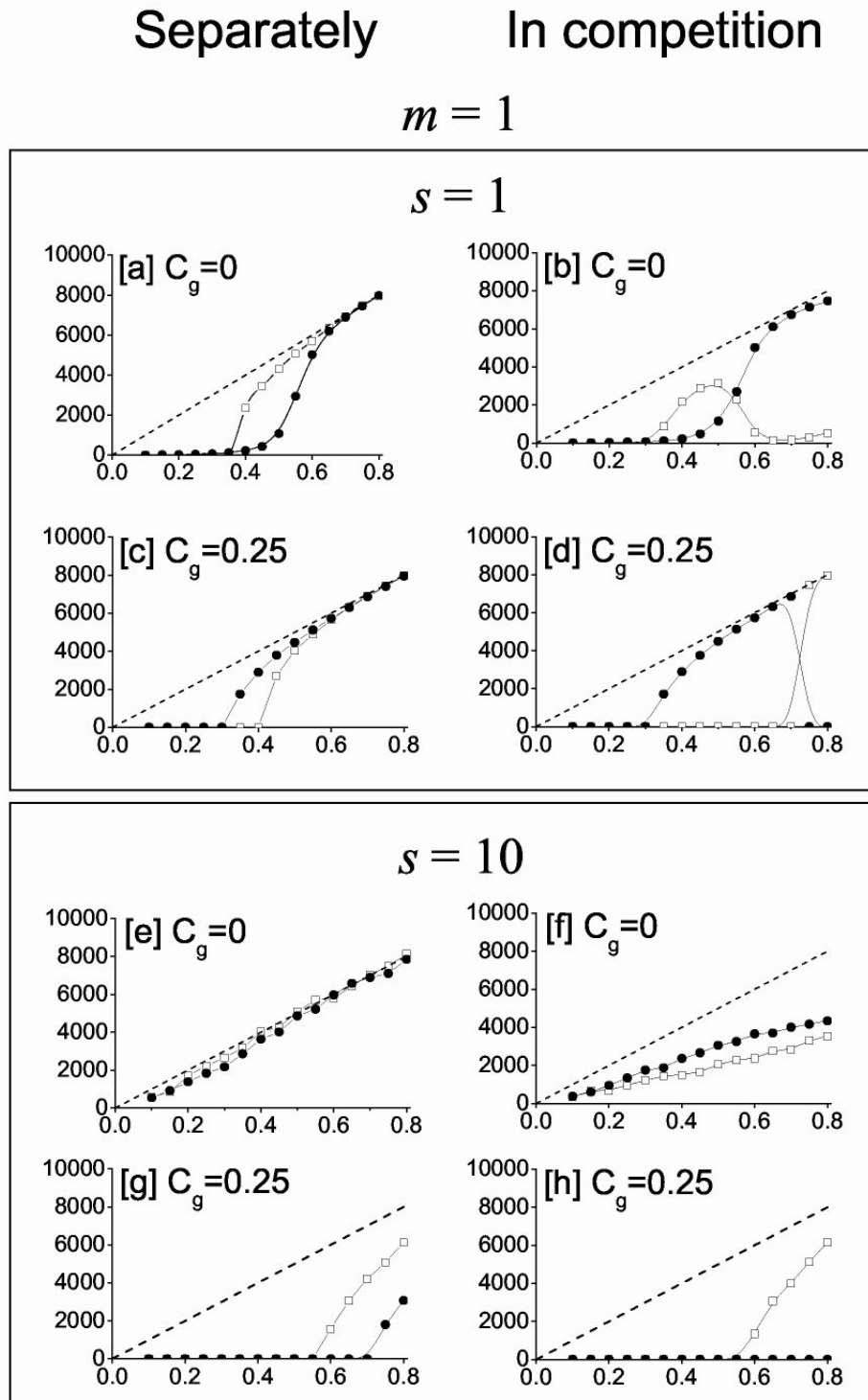
The Integrator was also affected by the discontinuity of good patches. It was possible for an Integrator ramet to colonize a bad site, using translocates from other, good ramets. Thus, the dispersal barriers were not as severe as for Splitter. This was reflected in the fact that deviation of the population size from the carrying capacity started at lower values of  $p$  (ca. at  $p = 0.5$ ). However, as scarcity of the resource patches fell further extinction occurred because the number of bad ramets that required subsidy was too high relative to the number of good ramets which could have provided subsidy.

In the competition case (Fig. 3.b), the Splitter was almost unaffected by the presence of Integrator, indicating that Splitter clones tend to be locally dominant, strong structure-forming components of plant communities. The Integrator survived in every case when the Splitter could not fully utilize the carrying capacity of the habitat ( $0.3 < p < 0.65$ ). In these habitats, the Splitter always monopolized the clusters of good cells that were reachable to its spreading, and the Integrator occupied the rest of the area. Thus, long-term coexistence between the Splitter and the Integrator became possible. The other region of coexistence at very high resource availabilities (from  $p = 0.75$ ) is only apparent: the two populations experienced similarly good resource conditions, and the Splitter could not exclude the Integrator from the field within 20,000 time steps.

After this brief summary of published results (Oborny and Kun 2002), we examine the behaviour of the system at other parameter combinations. First, we introduced fluctuation into the environment (Fig. 3.c and d). As a result, the population size of the Splitter started to increase at a lower value of  $p$  than in the non-changing environment. The Integrator showed an opposite reaction: its threshold  $p$  became higher. Thus, fluctuation of the environment was more beneficial to the Splitter than to the Integrator.

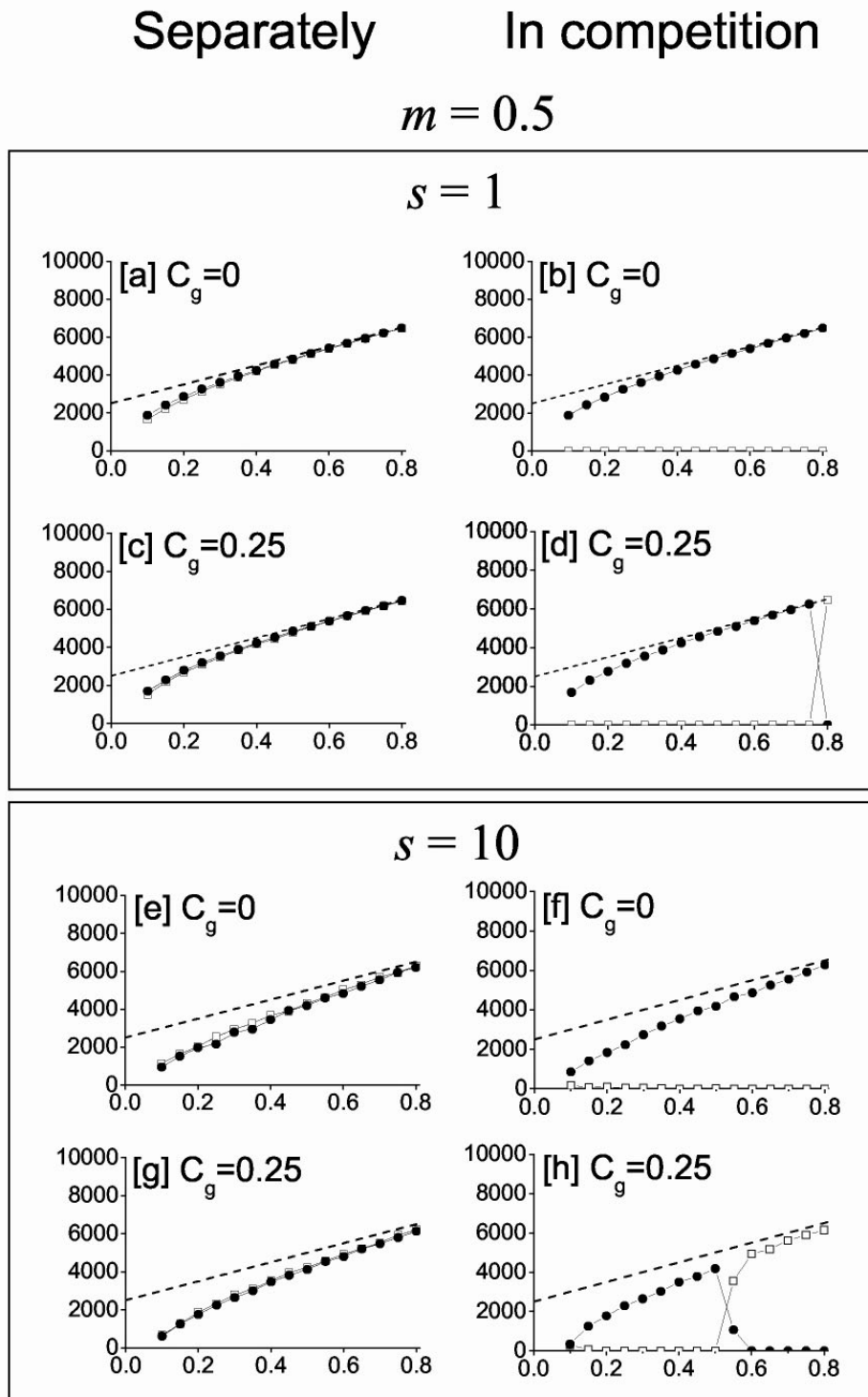
An explanation for this observation is that in the critical region, where the Splitter can survive, but is confined to small clusters of good cells, fluctuations provide temporary 'stepping stones' through which the species can spread from one cluster to another. Thus, fluctuation promotes dispersal of the Splitter.

However, fluctuation has a negative effect as well: it increases ramet mortality. Disappearance of good patches kills all the Splitter ramets that have inhabited such patches, and may also kill Integrator ramets (depending on the amount of subsidy that they receive from other parts of the clone). At the same time, a bad patch becoming good can only help the Integrator, because only Inte-



**Figure 3.** Average population size (vertical axis) at different values of  $p$ , resource richness (horizontal axis). Solid black circle: Splitter; open square: Integrator; dashed line: theoretical carrying capacity of the habitat. The left column (sub-figures a, c, e, g) presents the results when the populations were growing separately. The right column (sub-figures b, d, f, h) shows the ramets in competition. In every case, contrast was  $m = 1$ . Patch size was either  $s = 1$  or  $s = 10$  (in outlined boxes). Patch turnover rate, was  $C_g = 0$  or  $C_g = 0.25$  (shown on the top of each sub-figure).





**Figure 4.** The same as Figure 3, but patch contrast is lower:  $m = 0.5$ .

grator ramets can be found in bad patches. Thus, the second effect of fluctuation - an increase in ramet mortality - is more harmful to the Splitter than to the Integrator.

In our example (Fig. 3.c), where the resource patches were rather small ( $s = 1$ ), the first effect prevailed: Splitting enjoyed a relative advantage over Integration. This advantage was also apparent in competition (Fig. 3.d). The region where the Splitter won became significantly wider ( $0.3 < p < 0.75$ ). Only extremely resource-rich habitats ( $0.75 \leq p$ ), where the second effect of fluctuation started to prevail, benefited Integration. For example, in the extreme case when  $p$  was 0.8, every bad patch was turned into good within one time step. Only the integrator could survive momentarily bad conditions; the Splitter was certain to die. Note that the order of competitive dominance between the Splitter and the Integrator was sensitive to  $p$ . As little as a 0.05 increase in  $p$  from 0.70 to 0.75 resulted in a change in dominance.

Next, we increased the size of resource patches to  $10 \times 10$  units (Fig. 3.e-h). In the constant environment ( $C_g = 0$ ), ramets filled nearly all the good sites, even at very low values of resource availability ( $p$ ) (compare Fig. 3.a and e). Since the initial density of seeds was rather high (covering 0.5% of the area), there was a high probability that each big patch ( $10 \times 10$  units) would be colonised by at least one seed, and dispersal between patches did not play significant role in the dynamics of the populations. Moreover, a habitat with large, isolated patches is analogous to a set of homogeneous habitats. In such patches, the populations could coexist for a long time (Fig. 3.f). The Integrator was clearly inferior, because even a single ramet placed outside a good patch lowers the competitive ability of each interconnected ramet, but the difference was slight, and 20,000 time steps were still not sufficient for competitive exclusion.

In contrast, when the environment was fluctuating ( $C_g = 0.25$ ; Fig. 3.g and h), coexistence was not experienced, and the Integrator clearly dominated. Since the first effect of fluctuation, (facilitation of dispersal) was negligible, the second effect (killing ramets) prevailed. This is always more harmful to the Splitter. Moreover, a single change from good to bad quality kills more ramets when patch size is larger. The ability of the Integrator to buffer heterogeneity helped to dominate in every case when it could survive at all. This happened already at lower values of  $p$  than in the fine-grained environment (compare Fig. 3.d and h).

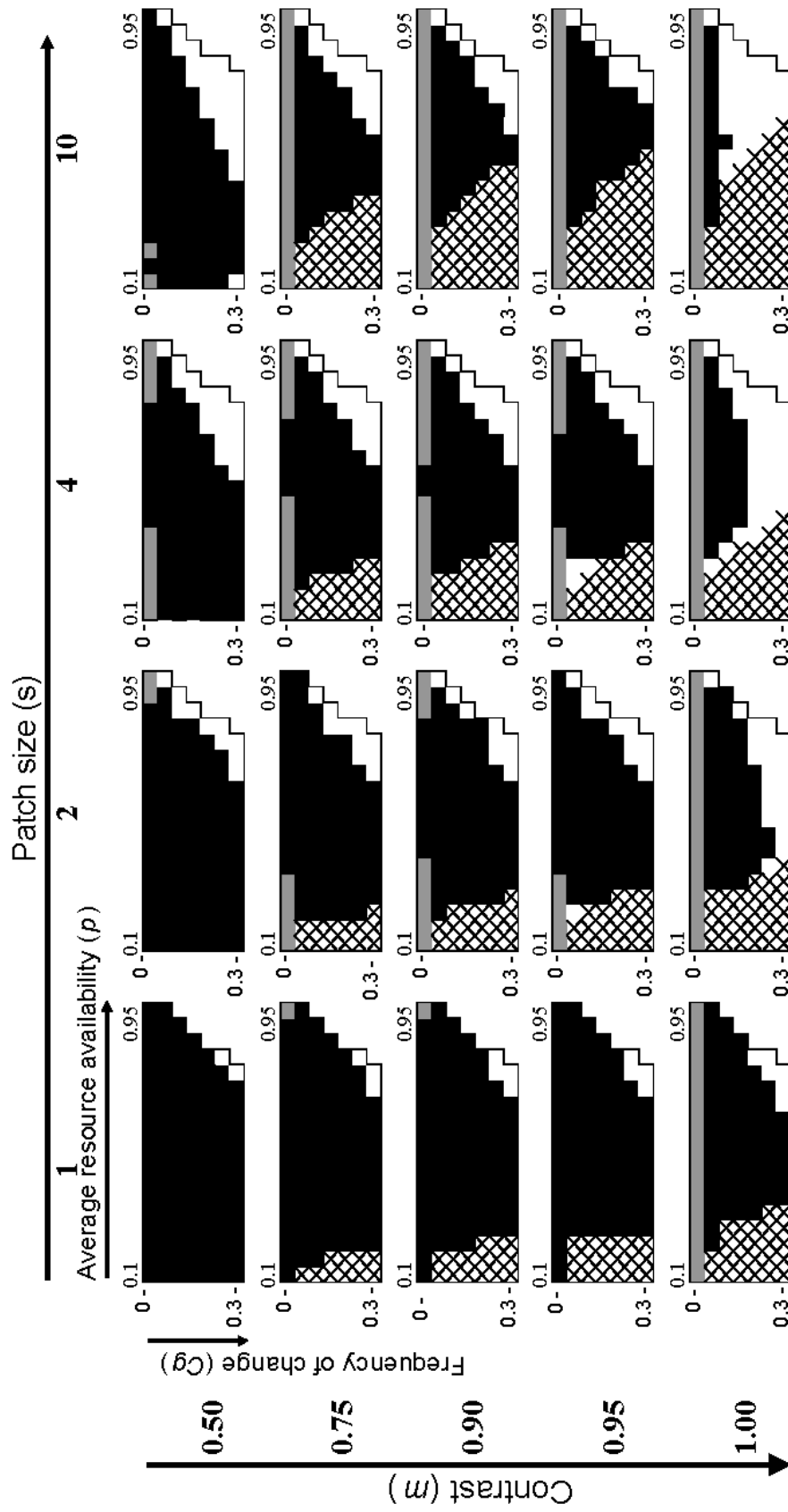
Finally, we changed the third parameter, contrast, from maximal to a moderate value ( $m = 0.5$ ; Fig. 4). Lower contrast greatly diminished the effect of all other

heterogeneity components. First, both strategies could achieve roughly the same population sizes when they grew separately (Fig. 4.a, c, e, and g). Note that the presence or absence of fluctuation made little difference to the population sizes (compare Fig. 4.a with c; and 4.e with g). Fine *versus* coarse grain also had little effect (compare Fig. 4.a with e; and 4.c with g), although population sizes were slightly smaller in the coarse grained habitats. Dispersal limitation almost disappeared, since both strategies could survive in unfavourable regions, and thus had a chance to spread from one good patch to another (compare Fig. 3.a with 4.a). When the good patches were far apart it became harder to reach new good patches. Hence population sizes were below the theoretical carrying capacity at low resource availability (low  $p$ ).

When the strategies competed, the decrease in dispersal limitation resulted in the Splitter winning in competition in all stable habitats (Fig. 4.b and f). When fluctuation occurred in a fine-grained habitat (Fig. 4.d) the Integrator could win in competition, but only at high resource availability, similar to Fig. 3.d. In coarse-grained environments, the Integrator could dominate already at moderate resource levels (from  $p = 0.55$  Fig. 4.h). The non-zero population sizes of both the Splitter and the Integrator at  $p = 0.55$  in Fig. 4.h do not indicate coexistence. In every one of the twenty repetitions, either the Splitter or the Integrator won, but the values on the figure show the average population sizes.

[b] *Outcome of competition.* Fig. 5 provides a summary of the results of competition at all simulated parameter combinations. Since there is no easy way to show the results for four parameters, instead of using a five-dimensional graph, we prepared a series of two-dimensional graphs. Each square (cell) in the sub-graphs presents the result at one particular parameter combination ('All dead', 'Splitter wins', 'Integrator wins', or 'Long-term coexistence'). The first conclusion from Fig. 5 is that none of the parameters alone could explain the outcome of competition. Either of the strategies could win at low or high contrast, in fine or coarse-grained habitats, with or without temporal fluctuation, or at different resource availabilities. This result clearly shows the importance of identifying all the components of heterogeneity when predicting the effect of integration.

The Splitter clearly dominated in habitats of extremely low contrast and fine grain (upper left sub-graphs in Fig. 5) almost irrespective of temporal change and resource availability. Even as contrast was increasing (going down in the first column), the Splitter could maintain dominance in a large proportion of the parameter space, and only a high resource level (large  $p$ ) and high fluctua-



**Figure 5.** A summary of the final outcome of competition in different habitat types. Crossed square: 'All dead'; black: 'Splitter wins'; white: 'Integrator wins'; grey: 'Long-term coexistence'. Four environmental parameters are involved. Each sub-graph shows  $p$  on the horizontal axis, and  $C_g$  on the vertical axis. In addition,  $s$  changes along the rows, and  $m$  along the columns.

tion (large  $C_g$ ) could promote dominance of the Integrator. Increasing the size of resource patches (going along the rows) diminished the competitive dominance of the Splitter, because of the larger effect of fluctuation on ramet mortality at larger patch sizes, which is selectively worse for the Splitter. In the extreme case of very coarse-grained environments with maximum contrast (lower right sub-graph), the Integrator dominated all habitats characterized by moderate to high fluctuation.

'Long-term coexistence' was experienced only in constant environments ( $C_g = 0$ ), because the Splitter clones could monopolize those good clusters that they colonised, and this pattern of patch occupancy became 'frozen' for the rest of time. The Integrator could utilize the remaining area, and thus could coexist with the Splitter. Any change in the arrangement of resource patches ( $C_g > 0$ ) was able to destroy such a 'frozen' pattern, thus,  $C_g = 0$  represents a rather specific case in the dynamics of the populations. Coexistence could occur at small values of  $p$ , because the Splitter was more constrained in space, and also at large values of  $p$ , when the average quality of the remaining area could be used by the Integrator, had improved. The final outcome, as we have stated before, was very sensitive to the initial conditions, namely, the number of good clusters initially colonised by Splitter seeds. Finally, the 'All dead' region can be characterized by low resource availability ( $p$ ), high fluctuation ( $C_g$ ), high contrast ( $m$ ), and large patch size ( $s$ ). Coincidence of these conditions increases the risk that all ramets would die at the same time.

## Discussion

### *Effects of heterogeneity components*

*Density of resource patches ( $p$ ).* Our results suggest that low density favours Integration whenever the resource pattern is highly variable in space and time (high  $C_g$ ,  $s$  and  $m$ ). In these conditions, Integration could successfully buffer individual ramets against local resource shortages. High density of good patches favoured Splitting in temporally stable environments (at 'frozen' patterns), because this helped the Splitter to spread from good to good sites, and thus to gradually exclude the Integrator from the whole area. However, when the resource pattern was not 'frozen', but fluctuated over time, the Integrator became dominant, and competitively excluded the Splitter. Buffering is advantageous when sufficient resource is available in good patches to cover the cost of growth in bad patches. It is important to note that the Integrator could win over the Splitter both in extremely productive and unproductive environments, but for different reasons. In unproductive environments (at low  $p$ ), the Splitter was not

permanently viable, and disappeared due to spontaneous extinction. In contrast, in productive habitats (at high  $p$ ) the Splitter was viable, but was outcompeted by the Integrator.

*Grain ( $s$ ).* Patch sizes were measured relative to the length of ramet-to-ramet connections. When the grain was so fine that quality of the environment at a daughter ramet's site was independent of the quality at the mother's site ( $s = 1$ ), Splitting was strongly favoured. However, when ten ramet generations were needed to cross a patch ( $s = 10$ ), Integration became more favourable in a wide range of habitat types. In particular, highly variable resource patterns were better exploited by Integrator clones, especially when the contrast between good and bad sites was also high. The explanation is that the Splitter can weakly tolerate big changes that affect large areas. Accordingly, we can hypothesize that patchy disturbances are more harmful to Splitter species than to Integrators.

*Contrast between good and bad patches ( $m$ ).* Extremely high contrast ( $m = 1$ ) promoted Integration. Otherwise, contrast had little effect on the outcome of competition. This can be explained by the sensitivity of the Splitter to barriers against spreading. Splitter ramets lack any subsidy from good sites. Therefore, when bad patches are so poor that they do not allow for survival at all, Splitter ramets are confined to good sites only. At the extreme, when the habitat pattern is 'frozen' ( $C_g = 0$ ), and the density of good patches ( $p$ ) is low, the Splitter can get stuck within small clusters of good patches, and is unable to utilize the carrying capacity of the habitat, even when there is no competitor species to limit its distribution.

*Temporal variation ( $C_g$ ).* Temporal variation of patch qualities was measured on the scale of ramet generation time. High variation favoured Integration in every case when a rather large proportion of the area was covered by resource-rich patches ( $p$  was high). Aggregation of the resource into large patches (large  $s$ ), and high contrast between good and bad sites (large  $m$ ) increased the advantage of Integration. This result can be explained, again, by the ability of the Integrator to buffer heterogeneities both in space and time.

### *Under what condition is integration successful?*

In this section, we attempt to relate our results to existing experimental data and observations in natural communities. It is not an easy task to make a straightforward comparison. First of all, our study focussed on a single effect of physiological connectedness: resource sharing. Physiological integration can imply other effects as well, depending on the species under study. For example, inter-

connecting rhizomes and stolons can store resources (see the ecological consequences of this in Pitelka and Ashmun 1985, Eriksson and Jerling 1990, Suzuki and Hutchings 1997, Suzuki and Stuefer 1999). Interconnections can also let the hormonal control of growth extend over a set of ramets (Alpert et al. 2002, see also Sachs and Novoplansky 1997) about the general ecological significance of correlative control mechanisms). In addition, as Jónsdóttir and Watson (1997) have remarked, our abilities to draw general conclusions about the effect of environmental variables are hindered by the relatively small number of habitat types that have been involved in empirical studies.

Since the units for  $s$  and  $C_g$  are species-specific, different clonal species may perceive resource availability in the same habitat in different ways. In this short review of empirical studies, we tried to estimate the environmental parameters according to the actual species in each study.

In an early, excellent review on physiological integration Pitelka and Ashmun (1985) proposed hypotheses about a suite of habitat types, where integration may have adaptive significance. We now only consider those arguments, where resource sharing was involved, because other, potential benefits from integration (such as storage) were not included in our model. Pitelka and Ashmun suggest that integration might be beneficial in disturbed habitats, because it facilitates recolonisation of empty patches. They mention that, on the other hand, there are species in which a low level of integration may be more advantageous, because ramets in good sites can more successfully maintain their positions without dependent ramets (splitting in *Aster acuminatus* was mentioned as an example). Our model fully agrees with this, demonstrating a two sided-effect of integration: it helps in colonizing new sites but makes it more difficult to persist in good positions. In agreement with Pitelka and Ashmun,  $C_g$  generally increased the success of Integration, but the spatial pattern of good and bad sites was important in determining the advantage of Integration.

In addition, Pitelka and Ashmun (1985) proposed a further habitat type in which extensive, equalized resource sharing might be beneficial. These were sites of generally good, stable resource supply over large areas (in our terms, high  $p$  and  $s$ , low  $C_g$ ). Integration was suggested to promote monopolization of the area against competitors. This hypothesis was confirmed by a study of de Kroon and Schieving (1990), in which an extensively integrated growth type, the so-called consolidator strategy, was suggested to be successful in exactly these habitat types (see the monodominant nature of *Phragmites australis* or *Solidago canadensis*). Our results confirm

that integration facilitates fast spreading, and occupation of large areas. But constantly rich, big resource patches could not be permanently monopolized by the Integrator, when there was a Splitter to compete with. Therefore, in constant habitats (where  $C_g$  was low), Integrators could only temporarily dominate (in the early successional stage). Prolonged dominance required the resource pattern to change over time (i.e.,  $C_g$  to be high).

Another strategy in the classification system of de Kroon and Schieving (1990) which has been predicted to benefit from extensive integration was the so-called conservative strategy. Plants of this type grow in resource-poor environments. A typical low- $p$  habitat which has often been mentioned in the literature to select for integration, is the tundra (c.f. Jónsdóttir and Watson 1997). Typically, a tundra environment can be characterized by poor nutrient supply in patches that are quite stable from year to year (Jónsdóttir and Watson 1997). Our simulations confirm that this habitat type (low  $p$ , and high  $m$ ) does promote Integration, provided that the patches are not too small ( $s > 2$ ), and not completely constant, i.e. can change over time to some extent ( $C_g > 0.05$ ). Considering the growth parameters of *Carex bigelowii*, that has been suggested as an example (see Table 3 in Jónsdóttir and Watson 1997), this means that the patch diameters should be larger than 20 centimetres, and more than approximately 5-20% of the good patches should change positions from year to year. Naturally, the pattern of intracolonial transport in *Carex bigelowii* is much more complex than in our simulated plant. So, other factors, like directional, acropetal transport can also contribute to the success of this species. Nevertheless, our simulations confirm that tundra-type environments can give advantage to Integration relative to Splitting.

The first proposal (high  $p$  for the consolidator) and the second (low  $p$  for the conservative strategy) are not in contradiction. The lower right graphs in Fig. 5 (at high  $m$  and  $s$  values) show that the extreme (low and high)  $p$  values favour Integration, whereas Splitting wins at intermediate  $p$  (at several values of  $C_g$ ).

A further habitat type - forest floor of deciduous forests - has also been suggested to favour extensive integration, as shown by a number of examples (*Podophyllum peltatum*, *Viola blanda*, *Maianthemum bifolium*, *Clintonia borealis*, etc.; see citations in Jónsdóttir and Watson 1997). An important factor of these environments, namely seasonal variation in the overall resource supply ( $p$ ) was not introduced into our model, so, direct comparisons cannot be made. But we can confirm that the year-to-year pattern in a deciduous forest allows for the persistence of Integrators in the understorey. With regard to

canopy gaps, availability of light can be characterized by low  $p$ , probably high  $m$  and high  $s$ . Our model predicts that extensive integration is a viable strategy in most cases, either in coexistence with Splitter species (at low  $C_g$ ) or completely monopolizing habitat space (at high  $C_g$ ).

Environments with contrasting and rather mobile patches (high  $m$  and high  $C_g$ ) have also been found to contain successful Integrators. At low patch density (low  $p$ ), sand dunes in Northern California might be mentioned as an example. Here a nitrogen-fixing shrub (*Lupinus arboreus*) has been found to reduce the light level by 80%, and at the same time, to enrich the nitrogen level by 100–200% relative to open sand 1m away. The actual distribution of resource patches depended on the population dynamics of shrubs. Therefore, the pattern showed rather high temporal variation. This habitat provided good conditions for a highly integrated clonal plant, *Fragaria chiloensis* (Alpert and Mooney 1986, Alpert 1999). High  $m$  and high  $C_g$  are not impossible at the other end of the  $p$  axis either. In productive environments, local resource scarcity may be caused by the presence of competitors. For example, in dense grasslands, herbs may find only a limited number of safe sites (gaps) which are suitable for survival. Moreover, the spatial positions of gaps depend on the actual states of individual plant in the community, therefore,  $C_g$  can be high. Our simulations suggest that if the gaps are not too small (i.e., they can sustain at least some ramets), then Integration is preferred to Splitting in these habitats. This fact might contribute to the success of integrated clonal herbs (such as *Glechoma hederacea* or *Trifolium repens*) in grasslands. However *Trifolium repens* have been found to have high benefit from reciprocal translocation of two resources (Stuefer and Hutchings 1994, Alpert and Stuefer 1997, Wijesinghe and Hutchings 1999), and *Fragaria* showed overcompensation of resource differences (Alpert 1999), so direct comparison between these species and our Integrator cannot be made (see 'Limitations of the model' later). Naturally, the value of accumulating ramets in gaps depends on interspecific competition relative to intraspecific competition for any particular species and community (c.f. Pitelka and Ashmun 1985, Schmid 1986).

Pennings and Callaway (2000) compared the performance of six clonal species in a common, natural habitat, a salt marsh. Three treatments were applied in the neighbourhoods of selected clonal fragments: [1] creating uninhabitable salt pans, [2] having competitor species, and [3] having competitor species but with clipped canopy. For each treatment, two cases were compared: intact and severed connections. Each of the treated species has

been found to be good integrator. In general, integration proved to be important for species in occupying bad patches (treatment 1), and moderately important in occupying empty but good sites (treatment 3). This is in good agreement with our results. Treatment 2 suggested that integration had no significant effect on the competitive ability of clones in interspecific competition. This treatment cannot be directly related to our simulations, because it was not known whether the patch where the competitor was growing was good or bad compared to the patch of the test species. (This depends on the relationship between intra- and interspecific competition.) But our results suggest a strong effect of integration on competitive ability, especially when the patchwork of good and bad sites is large enough to let characteristic spatial patterns of the Splitter and Integrator develop.

Klimeš and co-workers (1997) have reviewed the habitat requirements of 2760 species of Central Europe. Those growth forms of clonal plants, in which ramets typically stayed connected for more than two years were found to be frequent in forest edges, forests, and alpine vegetation, amounting more than 50% of the clonal species (confirming the hypothesis of Jónsdóttir and Watson 1997), and also occurred in high percentage in steppes and meadows, in the vegetation of rocks and high mountains, and in the synanthropic vegetation of the region. It is very difficult to draw a general conclusion from this large variety of vegetation types, but the only vegetation type where extensive integrators were relatively rare, and splitters reached approximately 25% of the clonal species, was wetland habitats. The spatial spreading of populations is relatively little limited in most wetlands (Pyšek 1997) compared to other vegetation types, because of the help of water in dispersal, and also the generally high abundance of resources in the soil, which facilitates step-by-step spreading by vegetative growth. This underlines the importance of dispersal limitation in the occurrence of Splitters, which was also emphasized by our simulation results. However, 25% as a maximum is rather low compared to the dominance of Splitting in a wide range of habitat types predicted by our model. This suggests that other advantages of integration besides resource sharing (such as the capacity for storage in rhizomes) should also be taken into account for explaining the distribution of clonal species in natural habitats.

Compared to observations, experimental studies can perhaps be better used for testing our predictions, because additional factors can be excluded, and integration *versus* no integration can be directly compared within the same species. Experiments have tested the effects of integration by severing connections between ramets, or tracing the

transport of resources by radioactive labelling or dyes (Marshall and Price 1997). Additional benefit may be gained from the fact that genotypes within species have been found to differ in the degree of integration (*Fragaria chiloensis*: Alpert 1999; *Ranunculus reptans*: van Kleunen et al. 2000; see a review in Alpert et al. 2003).

Numerous experiments have confirmed that resource translocation from relatively rich to poor ramets can effectively even out the local qualities experienced by ramets, diminishing biomass differences (Salzman 1985, Hutchings and Bradbury 1986, Schmid and Bazzaz 1987, Alpert and Stuefer 1997, Wijesinghe and Whigham 2001, Yu et al. 2002 and others). Even completely uninhabitable sites can be colonized if integration occurs (Alpert 1995, Peterson and Jones 1997), which means that the dispersal barriers at maximal contrast ( $m = 1$ ) can be successfully overcome by integration.

Further studies suggest that heterogeneous distribution of nutrients as opposed to homogeneous distribution (taking the same  $p$ , increasing  $m$ ) can even increase the total biomass of clones in a suite of clonal species (*Fragaria chiloensis*: Alpert and Mooney 1986; *Potentilla reptans* and *anserina*: Stuefer et al. 1994; *Glechoma hederacea*: Birch and Hutchings 1994; *Potentilla simplex*: Wijesinghe and Handel 1994; see also a review by Hutchings and Wijesinghe 1997). However, this high benefit from integration is not due to an economic distribution of a single resource, but probably at least two resources are involved (light and a soil nutrient) which are negatively correlated in space. Thus, integration enables reciprocal translocation of resources between ramets (see Stuefer and Hutchings 1994, Stuefer et al. 1994, Alpert and Stuefer 1997 about spatial division of labour between ramets). This is, again, an additional benefit of integration which cannot be captured by our model.

As we have mentioned earlier, experimental manipulation of environmental variables is very labour-intensive. Even the minimal representation of habitat pattern that we have applied involved four variables:  $p$ ,  $C_g$ ,  $s$ , and  $m$ . Imagine that not more than 1 m<sup>2</sup> space and a few ramet generations were devoted to each plot, and the number of repetitions was not too high. A simple test for a single species would still require unrealistically large amounts of space and time. There have been two ways to gain at least partial information about the system: [1] by computer simulations. [2] Some of the habitat patterns have been realized in experimental plots, thus, it was possible to see how real clones react to different arrangements of good and bad sites.

Wijesinghe and Handel (1994) applied various patterns of nutrient-rich and nutrient-poor sites along stolons of *Potentilla simplex*. As in our simulations, the arrangement was cellular. Discrete sites (square pots) were either good or bad in nutrient supply. The contrast ( $m$ ) was high: good cells were treated with a nutrient solution, bad pots contained pure sand. Good and bad cells were randomly placed along each stolon, and their proportion ( $p$ ) was varied: 0, 0.25, 0.5, 0.75 or 1. Size of the pots (5.7 cm) was small relative to ramet sizes, thus,  $s$  was small. Resource patterns were not changed during the time of experiment ( $C_g = 0$ ). Two cases were compared: when the stolon connections were intact, and when the connections were artificially severed 10 days after the establishment of each new ramet. Thus, an integrated clone was always compared to an (artificially) split clone, each growing in isolation. This arrangement can be compared to our Fig. 3.a. Wijesinghe and Handel (1994) used mean clone weight as a measure of the performance of clones (see Fig. 2 in their paper), whereas we used the mean number of ramets. The two approaches could be directly compared only if we assume some size difference between good and bad ramets, and weighted their numbers accordingly. Nevertheless, there are some remarkable similarities between our results. The experiment has shown that the Splitter and the Integrator (the severed and not severed case) did not differ at low values of  $p$ , each giving poor performance, but in a critical, intermediate range of  $p$ , the Integrator was significantly more successful than the Splitter. As in our results, the difference was greater at about 1:1 ratio of good and bad sites ( $p = 0.5$ ), but also observable at higher values ( $p = 0.75$ ). In accordance with our simulations, the Integrator improved its performance most between  $p = 0.25$  and 0.5 while the Splitter, improved most between  $p = 0.5$  and 0.75. Finally, at  $p = 1$ , the two strategies were the same again, achieving high performance. These results indicate that the scarcity of resource patches was limiting to *Potentilla simplex*, and it was possible to overcome these limitations in a critical range of  $p$  by clonal integration, which enabled the colonization of bad patches. This is completely in accordance with our results.

With regard to natural habitats, *P. simplex* is common in pastures and old fields (Wijesinghe and Handel 1994), therefore, intermediate  $p$  is likely to occur in its native habitats, too. Our simulations confirm the results of experiments, and we may add that more coarse-grained resource pattern than applied in the experiment (larger  $s$ ) would yield the same kind of advantage to integration, provided that the habitat pattern was not 'frozen' ( $C_g > 0$ ; Fig. 3.g). So, resource transport is likely to have adaptive advantage for *P. simplex* in a suite of habitat types. How-

ever, the simulations warn that high contrast between good and bad patches (high  $m$ ) is a prerequisite (Fig. 4).

In another experiment where habitat patterns have been explicitly represented, Wijesinghe and Hutchings (1997) tested the effect of patch size ( $s$ ). *Glechoma hederacea* was grown in a chessboard mosaic of good and bad sites. The proportion of good to bad cells was constant,  $p = 0.5$ . Contrast ( $m$ ) was high: rich cells contained potting compost, while poor cells were filled by sand. The patterns did not change over time ( $C_g = 0$ ). The size of patches ( $s$ ) was varied. In this case, our simulations would predict equally good performance of clones, because  $p = 0.5$  should be high enough to ensure almost full exploitation of the carrying capacity of the habitat for an Integrator species, irrespective of  $s$  (Fig. 3.a and e). In contrast, Wijesinghe and Hutchings found significantly larger clone weight and population size at larger patch sizes. The explanation is that *G. hederacea* has a strong morphological response to patch quality, which was enhanced by larger patch sizes. This change in growth pattern was not included in our simulation. However, the result that integration enables a species to colonize bad areas, and can bridge over wide uninhabitable regions is directly important to us. In the large-patch treatment, the bad areas were more than twice as wide as the step length of clonal growth (average ramet-to-ramet distance), and were successfully colonized by *G. hederacea* clones.

In a further experiment in the same system, Wijesinghe and Hutchings (1999) tested the effect of patch contrast as well. Six treatments of  $m$  were applied from high contrast (compost vs. sand) to no contrast ( $m = 0$ ), combined with two treatments of  $s$ . The results underline that different aspects of the pattern, grain and contrast are not independent (c.f. Stuefer 1996). For example, clone biomass was significantly increased by higher  $s$ , but only when  $m$  was sufficiently large. This finding is in agreement with our results: high  $m$  and  $s$  promoted the success of integration; changing  $s$  could compensate for the effect of  $m$ , and *vice versa*.

#### *Limitations of the model, and outlook*

Our aim was to see the effects of resource sharing by a comparison between a hypothetical Splitter and Integrator. Naturally, real species differ in many traits which can affect population dynamics beside the degree of resource sharing.

*Resource utilisation.* Species differ in the way in which the same amount of resource is utilized, i.e. how resource availability is translated into ramet fitness. We used the same resource utilization function in the two strategies.

According to our assumption, the function was linear. Eriksson and Jerling (1990) suggest that a concave function gives advantage to Integration, because it makes it worthwhile to export the resource that cannot be efficiently utilized locally. Similarly, a convex function favours Splitting. Both shapes of the function can be imagined in natural conditions. For example, a concave shape may be a consequence of limited ramet size, when further resource supply from the environment cannot increase ramet growth any further. A convex shape can be a result of asymmetric competition, when large size has extra advantages. Any deviation from linear resource utilization shifts the results to the benefit of the Splitter or Integrator. However, as our previous INTEGRID simulations have suggested, this is only a shift, and either of the strategies can dominate, depending on the habitat pattern (Oborny et al. 2000). Local advantage cannot be directly translated into global advantage, because global advantage depends on the way in which the spatial distribution of ramets relates to the spatial distribution of the resource. In accordance with this, even our simple, linear resource utilization curve lead to a non-trivial result: both the Splitter and the Integrator could win.

*Differences between ramets.* In our model, ramets of the same strategy were assumed to be identical. Their difference was caused by the local environment (good or bad), and in the case of the Integrator, by connections to other ramets. In fact, uptake and utilization of a resource can largely depend on the age and developmental stage of ramet (e.g. flowering *versus* non-flowering), and also on its position in the branching system. (See a review on source-sink relations and sectoriality in clonal plants: Marshall and Price 1997.)

*Clonal morphology and foraging.* Several species have been found to show strong morphological response to resource concentration (see a review on foraging behaviour in plants by Hutchings and de Kroon 1994). It would be important to gain a full understanding of the exploration, uptake, and internal transport of resources in clonal plants. Unfortunately, even the separate phenomena have scarcely been modelled (see review by Oborny and Cain 1997 about models on plant foraging). Cain et al. (1996) remarks that “we know of no spatially explicit models of clonal integration”. Though clear hypotheses have been proposed about the relationship between integration pattern and growth pattern (see the section “Physiological plasticity as an alternative to morphological plasticity for resource acquisition” in Hutchings and de Kroon 1994, also Alpert and Simms 2002), few studies have incorporated resource transport into models on clonal growth (to our knowledge, Caraco and Kelly 1991, Herben and



Suzuki 2002, beside the INTEGRID family). A systematic review of the relationship between foraging and integration would be an important step in understanding the ecological implications of clonality (c.f Wijesinghe and Whigham 2001). Empirical studies, like the experiments described by Wijesinghe and Hutchings (1997), Wijesinghe and Hutchings (1999); and also by Evans and Cain (1995), Alpert and Stuefer (1997), Wijesinghe and Whigham (2001), suggest that the relationship is probably very interesting, because resource can be allocated to growth at different points, both within ramets and between them, as the branching structure of the clone develops.

*Seed dispersal.* Oborny et al. (2000) has shown that a great disadvantage of Splitting is that it makes spatial spreading slower and more selective to good patches. Therefore, bad areas represent more serious barriers to Splitters than to Integrators. However, if a Splitter produces far-dispersing propagules, which can make ‘jumps’ between good patches, the Splitter can become competent against the Integrator in more habitat types. Exploration of the effects of two dispersal modes would be an interesting subject of future research.

*Additional advantages and disadvantages of integration.* Resource sharing is not the only potential advantage of keeping the ramets interconnected. Stolons and rhizomes can store resources (see Stuefer and Huber 1999). Storage, in general, buffers shortages in resource supply over time, and thus can affect the population dynamics of ramets (Suzuki and Hutchings 1997, Suzuki and Stuefer 1999). Exchange of resources can be more advantageous than simple sharing, as shown by numerous studies on division of labour between ramets (Stuefer and Hutchings 1994, Stuefer et al. 1994, Alpert and Stuefer 1997). On the other hand, there are also disadvantages: systemic diseases can spread more easily when the ramets are interconnected (D’Hertefeldt and van der Putten 1998, Wennström 1999; see also Wijesinghe 1994). Metabolic cost of maintaining interconnecting tissues can also be high. For reviews on potential costs of integration, see Pitelka and Ashmun (1985), Eriksson and Jerling (1990), Kelly (1995) and Hutchings et al. (2000).

Our simple model tested only one effect of integration: resource sharing. To overcome the limitations of the present model, it would be necessary to test each additional factor in a similar, spatially explicit way. Interactions of ramets with each other and with the environment

produce emergent phenomena, such as meso-scale structure formation. The detection of these phenomena requires a sizeable population of ramets (not only pairs or single fragments). The importance of emergent phenomena has clearly been demonstrated in a spatial model of Herben and Suzuki (2002) on clonal growth, where small changes in the parameter values for resource translocation or branching geometry could cause significant changes in equilibrium population densities. Our model shows similar conclusions. In particular, an emergent property, spatial association with the resource, and a resultant dispersal limitation, played important roles in the success or failure of the Splitter in various habitat types. In addition, success of a strategy in isolation (population size when growing alone in the area) was not a good predictor of competitive ability in the presence of the other strategy. This phenomenon has been emphasized in the model of Herben and Suzuki (2002), and found to be important in our study, too. The difference between the adaptive values of a trait in isolation *versus* in competition is, again, a consequence of spatial self-organization of the community.

## Conclusion

*Is it adaptive to buffer environmental heterogeneity?*

Numerous studies have shown that clonal integration can diminish the difference between ramets in good *versus* bad sites, and thus buffer against environmental heterogeneity.<sup>5</sup> Our study demonstrates that this buffering is not necessarily advantageous in all habitat types.

Buffering has three basic advantages. [1] It helps a species to colonize areas with sparse resource patches. The simulations have pointed out a number of habitat types where the Splitter was not viable at all, and only an Integrator could persist. These habitats were characterized by low patch density, and high spatial and temporal variation of the patches. [2] Integration helps to mobilize resources quickly. We found habitat types where the Splitter was viable when growing alone, without competition, but became extinct in competition against the Integrator. These habitats were characterized by high patch density, and high spatial and temporal variation. An advantage of the Integrator was that it could efficiently utilize the resource for subsidizing fast growth in the canopy gaps. [3] Integration helps exploration and exploitation of ‘leftover’ patches. In constant environments, where the resource patches did not change over time, the Splitter and the Integrator could coexist at intermediate values of

5 To recall a few studies: Hartnett and Bazzaz 1985, Salzman 1985, Alpert and Mooney 1986, Hutchings and Bradbury 1986, Landa et al. 1992, Wijesinghe and Handel 1994. Papers on the spatial division of labor also belong here, although the case is more complicated, because two resources are involved: Stuefer and Hutchings 1994, Stuefer et al. 1996, Alpert and Stuefer 1997.

patch density. In these cases, the Splitter could survive but could not spread over the area, being confined to clusters of good patches. The Integrator utilized the remaining area, because it could survive at lower levels of resource supply (see point [1] above). When the 'leftover' area was large, the Integrator could even exceed the Splitter in population size.

On the other hand, we have found some habitat types in which buffering was disadvantageous. These habitats were characterized by low (but non-zero) patch turnover rate, and in addition, either low contrast or fine grain of the resource pattern.

#### *Evade unfavourable patches or enter?*

Success of the Splitter *versus* Integrator in various habitat types could be explained by an important difference in the spatial behaviour of the strategies. The Splitter was locally stronger in good sites than the Integrator, but weaker in bad sites, because Splitter ramets did not share any resource. Thus, the Splitter tended to occur preferentially in good sites. Strong association with the resource patches had two potential disadvantages: [1] Dispersal was strictly constrained whenever the unfavourable region between good patches was wide. [2] Turnover from good to bad quality killed a higher proportion of more ramets.

Thus, local dominance of the Splitter in good patches did not necessarily lead to global dominance. Population dynamics of the Splitter was sensitive to the spatial and temporal pattern of the bad patches, and this determined its competitive ability against the Integrator. Clearly, Splitting and Integration represent alternative ways of coping with environmental heterogeneity: the Splitter tends to avoid bad patches, whereas the Integrator can enter them by buffering the differences between good and bad patches.

**Acknowledgements:** We thank Michael Hutchings, Josef Stuefer, Peter Alpert, Farrah Bashey, Gabriella Magyar, Ééna Jakó and an anonymous referee for their helpful comments on the manuscript. We are grateful to Géza Meszéna, Ulf Dieckmann, Krisztián Mágóri, Tamás Czárán, Miklós Kertész, György Szabó, Hajnalka Gergely and Pauline Hogeweg for the enjoyable discussions about our project. The project was subsidized by the Hungarian National Research Fund (OTKA T29789, T35009, and NWO–OTKA N34028) and the Hungarian Ministry of Education (FKFP 0187/1990, István Széchenyi Scholarship). Á. K. is grateful for support from the European Science Foundation (TBA/01) for his participation in the Young Scientist Summer Program of the International Institute for Applied Systems Analysis (Laxenburg, Austria). B. O. acknowledges support by the International Program of the Santa Fe Institute, USA.

## References

- Alpert, P. 1996. Does clonal growth increase plant performance in natural communities? In: B. Oborny and J. Podani (eds). *Clonality in Plant Communities*. Opulus Press, Uppsala. pp. 11-16.
- Alpert, P. 1999. Clonal integration in *Fragaria chiloensis* differs between populations: ramets from grassland are selfish. *Oecologia* 120:69-76.
- Alpert, P., C. Holzapfel and J.M. Benson. 2002. Hormonal control of resource sharing in the clonal plant *Fragaria chiloensis*. *Funct. Ecol.* 16:191-197.
- Alpert, P., C. Holzapfel and C. Slominski. 2003. Differences in performance between genotypes of *Fragaria chiloensis* with different degrees of resource sharing. *J. Ecol.* 91:27-35.
- Alpert, P. and H.A. Mooney. 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. *Oecologia* 70:227-233.
- Alpert, P. and E.L. Simms. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust. *Evol. Ecol.* 16:285-297.
- Alpert, P. and J. Stuefer. 1997. Division of labour in clonal plants. In: H. de Kroon and J. van Groenendael (eds). *The Evolution and Ecology of Clonal Plants*. Backhuys Publishers, Leiden. pp. 137-154.
- Birch, C.P.D. and M.J. Hutchings. 1994. Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea*. *J. Ecol.* 82:653-664.
- Cain, M.L., D. Dudle and J.P. Evans. 1996. Spatial models of foraging in clonal plant species. *Am. J. Bot.* 83:76-85.
- Caraco, T. and C.K. Kelly. 1991. On the adaptive value of physiological integration in clonal plants. *Ecology* 72:81-93.
- Cook, R.E. 1985. Growth and development in clonal plant populations. In: J.B.C. Jackson, L.W. Buss and R.E. Cook (eds). *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, Connecticut, USA. pp. 259-296.
- Crawley, M.J. 1997. Life history and environment. In: M.J. Crawley (ed.), *Plant Ecology*. Blackwell Science Ltd., pp. 73-131.
- de Kroon, H. and F. Schieving. 1990. Resource partitioning in relation to clonal growth strategy. In: J. van Groenendael and H. de Kroon (eds). *Clonal Growth in Plants: Regulation and Function*. SPB Academic Publ., Leiden. pp. 113-130.
- de Kroon, H. and J. van Groenendael. 1990. Regulation and function of clonal growth in plants: an evaluation. In: J. van Groenendael and H. de Kroon (eds). *Clonal Growth in Plants: Regulation and Function*. SPB Academic Publishing, The Hague. pp. 177-186.
- D'Hertefeldt, T. and W.H. van der Putten. 1998. Physiological integration of the clonal plant *Carex arenaria* and its response to soil-borne pathogens. *Oikos* 81:229-237.
- Dickmann, U., R. Law and J.A.J. Metz. 2000. *The Geometry of Ecological Interactions*. Cambridge University Press, Cambridge.
- Eriksson, O. 1997. Clonal life histories and the evolution of seed recruitment. In: J. van Groenendael and H. de Kroon (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishing, Leiden, The Netherlands. pp. 211-226.
- Eriksson, O. and L. Jerling. 1990. Hierarchical selection and risk spreading in clonal plants. In: J. van Groenendael and H. de Kroon (eds). *Clonal Growth in Plants: Regulation and Function*. SPB Academic Publ., The Hague. pp. 79-94.
- Evans, J.P. and M.L. Cain. 1995. A spatially explicit test of foraging behavior in a clonal plant. *Ecology* 76:1147-1155.
- Harper, J.L. 1978. The demography of plants with clonal growth. In: A.H.J. Freyden and J.W. Woldendorps (eds). *Structure and*

- Functioning of Plant Population*. North Holland, Amsterdam. pp. 27-45.
- Harper, J.L. 1985. Modules, branches, and the capture of resources. In: J.B.C. Jackson, L. W. Buss and R.E. Cook (eds). *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, Connecticut. pp. 1-33.
- Harper, J.L. and A.D. Bell. 1979. The population dynamics of growth form in organisms with modular construction. In: R.M. Anderson, B.D. Turner and L.R. Taylor (eds). *Population Dynamics*. Blackwell Scientific Publ., Oxford. pp. 29-52.
- Hartnett, C.D. and F.A. Bazzaz. 1985. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *J. Ecol.* 73:407-413.
- Herben, T., T. Hara, C. Marshall and L. Soukupová. 1994. Plant Clonality: biology and diversity. In: L. Soukupová, C. Marshall, T. Hara and T. Herben (eds). *Plant Clonality: Biology and Diversity*. Opulus Press, Uppsala. pp. 7-16.
- Herben, T. and J. Suzuki. 2002. A simulation study of the effects of architectural constraints and resource translocation on population structure and competition in clonal plant. *Evol. Ecol.* 15:403-423.
- 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. *Adv. Ecol. Research* 25:159-238.
- Hutchings, M.J. and D.K. Wijesinghe. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *TREE* 12:390-394.
- Hutchings, M.J., D.K. Wijesinghe and E. John. 2000. The effect of heterogeneous nutrient supply on plant performance: a survey of responses, with special reference to clonal herbs. In: M.J. Hutchings, E. John and A.J. Stewart (eds). *The Ecological Consequences of Environmental Heterogeneity*. Blackwell, Oxford. pp. 91-110.
- Jónsdóttir, I.S. and M.A. Watson. 1997. Extensive physiological integration: an adaptive trait in resource-poor environments? In: H. de Kroon and J. van Groenendael (eds). *The Evolution and Ecology of Clonal Plants*. Backhuys Publishers, Leiden. pp. 109-136.
- Kelly, C.K. 1995. Thoughts on clonal integration: facing the evolutionary context. *Evol. Ecol.* 9:575-585.
- Klímeš, L., J. Klimešová, R. Hendriks and J. van Groenendael. 1997. Clonal plant architecture: a comparative analysis of form and function. In: H. de Kroon and J. van Groenendael (eds). *The Evolution and Ecology of Clonal Plants*. Backhuys Publishers, Leiden. pp. 1-30.
- 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. In: J. van Groenendael and H. de Kroon (eds). *Clonal Growth in Plants: Regulation and Function*. SPB Academic Publ., The Hague. pp. 23-42.
- Marshall, C. and E.A.C. Price. 1997. Sectoriality and its implications for physiological integration. In: H. de Kroon and J. van Groenendael (eds). *The Evolution and Ecology of Clonal Plants*. Backhuys Publishers, Leiden. pp. 79-107.
- Noble, J.C. and C. Marshall. 1983. The population biology of plants with clonal growth II. The nutrient strategy and modular physiology of *Carex arenaria*. *J. Ecol.* 71:865-877.
- Oborny, B. and S. Bartha. 1996. Clonality in plant communities: an overview. In: B. Oborny and J. Podani (eds). *Clonality in Plant Communities*. Opulus Press, Uppsala. pp. 115-127.
- Oborny, B. and M.L. Cain. 1997. Models of spatial spread and foraging in clonal plants. In: H. de Kroon and J. van Groenendael (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publ., Leiden, The Netherlands. pp. 115-127.
- Oborny, B., T. Czárán and Á. Kun. 2001. Exploration of resource patches by clonal growth: a spatial model on the effect of transport between modules. *Ecol. Model.* 141:151-169.
- Oborny, B. and Á. Kun. 2002. Fragmentation of clones: How does it influence dispersal and competitive ability? *Evol. Ecol.* 15:319-346.
- Oborny, B., Á. Kun, T. Czárán and S. Bokros. 2000. The effect of clonal integration on plant competition for mosaic habitat space. *Ecology* 81:3291-3304.
- Pennings, S.C. and R.M. Callaway. 2000. The advantage of clonal integration under different ecological conditions: a community-wide test. *Ecology* 81:709-716.
- Peterson, C.J. and R.H. Jones. 1997. Clonality in woody plants: a review and comparison with clonal herbs. In: J. van Groenendael and H. de Kroon (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, The Netherlands. pp. 263-290.
- Pitelka, L.F. and J.W. Ashmun. 1985. Physiology and integration of ramets in clonal plants. In: J.B.C. Jackson, L. W. Buss and R.E. Cook (eds). *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, Connecticut, USA. pp. 399-435.
- Price, E.A.C. and C. Marshall. 1999. Clonal plants and environmental heterogeneity. *Plant Ecology* 141:3-7.
- Pyšek, P. 1997. Clonality and plant invasion: can a trait make a difference? In: J. van Groenendael and H. de Kroon (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, The Netherlands. pp. 405-427.
- Sachs, T. and A. Novoplansky. 1997. What does a clonal organisation suggest concerning clonal plants? In: J. van Groenendael and H. de Kroon (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, The Netherlands. pp. 55-78.
- Salzman, A.G. 1985. Habitat selection in a clonal plant. *Science* 228:603-604.
- Schmid, B. 1986. Spatial dynamics and integration within clones of grassland perennials with different growth form. *Proc. Roy. Soc. Lond. B* 228:173-186.
- Schmid, B. and F.A. Bazzaz. 1987. Clonal integration and population structure in perennials: effects of severing rhizome connections. *Ecology* 68:2016-2022.
- Slade, A.J. and M.J. Hutchings. 1987. Clonal integration and plasticity in foraging behavior in *Glechoma hederacea*. *J. Ecol.* 75:1023-1036.
- Stoll, P. and J. Weiner. 2000. A neighborhood view of interactions among individual plants. In: U. Dieckmann, R. Law and J.A.J. Metz (eds). *The Geometry of Ecological Interactions*. Cambridge University Press, pp. 11-27.
- Stuefer, J. and H. Huber. 1999. The role of stolon internodes for ramet survival after clone fragmentation in *Potentilla anserina*. *Ecology Letters* 2:135-139.
- Stuefer, J. and M.J. Hutchings. 1994. Environmental heterogeneity and clonal growth - a study of the capacity for reciprocal translocation in *Glechoma hederacea* L. *Oecologia* 100:302-308.

- 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. *Funct. Ecol.* 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. *J. Ecol.* 82:511-518.
- 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. In: H. de Kroon and J. van Groenendael (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden. pp. 311-330.
- Suzuki, J. and J. Stuefer. 1999. On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology* 14:11-17.
- van Kleunen, M., M. Fischer and B. Schmid. 2000. Clonal integration in *Ranunculus reptans*: by-product or adaptation? *J. Evol. Biol.* 13:237-248.
- Vourisalo, T., J. Tuomi, B. Pedersen and P. Käär. 1997. Hierarchical selection in clonal plants. In: H. De Kroon and J. van Groenendael (eds), *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, The Netherlands. pp. 243-262.
- Watson, M.A. 1986. Integrated physiological units in plants. *TREE* 1:119-123.
- Wennström, A. 1999. The effect of systematic rusts and smuts on clonal plants in natural systems. *Plant Ecology* 141:93-97.
- Wijesinghe, D.K. 1994. Temporal and structural components of ramet independence in the clonal perennial herb, *Potentilla simplex*. *J. Ecol.* 82:13-20.
- Wijesinghe, D.K. and S.N. Handel. 1994. Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*. *J. Ecol.* 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*. *J. Ecol.* 85:17-28.
- Wijesinghe, D.K. and M.J. Hutchings. 1999. The effect of environmental heterogeneity on the performance of *Glechoma hederacea*: the interactions between patch contrast and patch scale. *J. Ecol.* 87:860-872.
- Wijesinghe, D.K. and D.F. Whigham. 2001. Nutrient foraging in woodland herbs: a comparison of three species of *Uvularia* (Liliaceae) with contrasting belowground morphologies. *Am. J. Bot.* 88:1071-1079.
- Wilhelm, T. 1996. A comparative study of clonal fragmentation in tussock-forming grasses. In: B. Oborny and J. Podani (eds). *Clonality in Plant Communities*. Opulus Press, Uppsala. pp. 51-60.
- Yu, F., Y. Chen and M. Dong. 2002. Clonal integration enhances survival and performance of *Potentilla anserina*, suffering from partial sand burial on Ordos plateau, China. *Evol. Ecol.* 15:303-318.