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# SPACER LENGTH IN CLONAL PLANTS AND THE EFFICIENCY OF RESOURCE CAPTURE IN HETEROGENEOUS ENVIRONMENTS: A MONTE CARLO SIMULATION

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**Abstract:** A stochastic, spatially explicit simulation model for clonal growth is presented which relates growth patterns to the pattern of resource availability in the environment in both space and time. The effects of two simple growth rules were examined which affect the length of spacers depending on the local environmental conditions. According to one of the rules, shorter spacers were developed in resource-rich microsites than in resource-poor microsites (growth rule G-). If the other rule acted, the spacers were lengthened in resource-rich sites (growth rule G+). The neutral reference, G0, represented a plant of rigid growth form.

A wide range of habitat types was used in the tests and characterized by an information theory model. It was found that the effectiveness of resource capture in most habitat types can be explained by spatio-temporal predictability of the environment, measured on the scale of spacer length. Shortening the spacers in resource-rich microsites, as hypothesized by "foraging theory", reduced the proportion of misplaced ramets. Lengthening the spacers never reduced this proportion. However, the degree of intraclonal competition was significantly reduced by both shortening and lengthening the spacers in response to site quality. There were certain types of environment where plastic modification of spacers had no effect on the efficiency of resource capture when compared to the reference random (non-environment-dependent) search pattern. Such habitats can be identified exactly on the basis of the information content of habitat pattern, measured here by spatio-temporal predictability.

This study emphasizes that a wide range of environmental types should be taken into consideration when examining the adaptive nature of a certain growth pattern. Generalizing from experimental results gained in temporally constant environments may strongly bias our view on morphological adaptation.

## INTRODUCTION

The morphology of clonal plants often exhibits great plasticity. The internodes that separate the individual clonal units often prove highly responsive to environmental conditions (SUTHERLAND 1990, HUTCHINGS & DE KROON 1994). Clones can be modelled as modular structures, within the general context of plant modularity (see BELL 1984, HARPER 1985, BARLOW 1989), that consist of (a) relatively autonomous **resource acquiring structures** (or "feeding sites", BELL 1984; in clonal plants "ramets", HUTCHINGS & SLADE 1988) and (b) **spacers** (typically rhizomes or stolons). These can be considered as the basic constructional components of a clonal plant body (BELL 1984).

Resources are generally non-homogeneously distributed in the environment. Regulation of spacer length may play an important role in the efficiency of resource acquisition. Several authors assume that the length of spacers itself (BELL 1984), or the rule which determines how this length is controlled by environmental conditions (SUTHERLAND & STILLMAN 1988, KELLY 1990) is a result of adaptation to resource distribution. The basics of a strategic (or tactic) concept of clonal morphology were introduced in the 1970s to 1980s (CLEGG 1978, LOVETT DOUST 1981, BELL 1984, HARPER 1985, SUTHERLAND 1987). The idea of "optimal foraging" in plants has been highly motivated by the foraging theory in animal behavior (STEPHENS & KREBS 1986). According to the concept of plant "foraging", a clear and relatively simple rule for spacer length can be hypothesized (SLADE & HUTCHINGS 1987, SUTHERLAND 1987, WATKINSON 1988, OBORNY 1991), i.e. to shorten the spacers in resource-rich sites (gaps) and/or lengthen them in poor sites (non-gaps). This growth rule is abbreviated as G-, for "shorter in gaps". There are two alternative hypotheses: to lengthen the spacers in gaps and/or shorten them in non-gaps (G+, for "longer in gaps"), and no reaction for site quality as a neutral reference (G0).

A verbal reasoning for the adaptiveness of the "foraging" rule (G-) is that by this method a plant tends to "escape" from adverse conditions and to "remain" in favourable ones. Some examples indicate that the application of G- can increase the proportion of modules allocated into resource-rich habitat patches (SUTHERLAND & STILLMAN 1988). The same rule, G-, has been detected for the supply of entirely different resources, light and nutrients, in *Glechoma hederacea* (HUTCHINGS & SLADE 1988). These facts might suggest the existence of a general growth syndrome for resource availability. However, many other studies call for a re-evaluation of the adaptiveness of G-, together with its alternatives:

(1) In the case studies when the reaction of a plant (G-, G+ or G0) was experimentally tested, no indication of the predominance of G- has been detected. SUTHERLAND & STILLMAN (1988) listed 16 experiments on 8 species, where G- operated in 3 cases, G+ in 7 cases, and G0 in 6 cases. Thus, G- seems to be rather an exception than a general rule. Similar examples on the diversity of responses can be found in HUTCHINGS & DE KROON (1994).

(2) There are alternative predictions for the existence of other growth strategies than "foraging". DE KROON & SCHIEVING (1990) described two additional strategies, G+ ("conservative growth") and G0 ("consolidation growth"). G+ was exemplified by *Carex flacca*, and G0 by *Brachypodium pinnatum*. Although in their concept the basis of optimization is not merely morphological, with several other (physiological and developmental) traits being considered, it might be interesting to examine their prediction from the present, purely morphological viewpoint too.

(3) Several clonal species have been described to show a definitely rigid architecture (BELL 1976; see, for example, the precise hexagonal rhizome system of *Alpinia speciosa*; BELL 1979). The question emerges whether an unresponsive growth pattern, G0, might be adaptive in any habitat type.

The present study lays special emphasis on growth pattern in relation to habitat pattern. The growth rules in question are tested in a wide range of environmental types, including resource-rich and poor, constant and highly variable, fine-grained and coarse-grained habitats.

A detailed quantitative characterization of the environments is attempted using an information theory model.

The first application of this information theory model has been presented in another simulation study (OBORNY 1994). There, information theory was used for analyzing spatial and temporal predictability of the availability of resources in patchy, temporally changing environments. To obtain a more realistic view of the micro-environmental conditions experienced by a developing clone, a new concept, spatio-temporal predictability is introduced in this study. Thus, instead of considering the spatial pattern and the temporal pattern of resources in separation, a general, spatio-temporal description of the environment is attempted.

In the previous study (OBORNY 1994) I used a simulation program for analyzing the effect of several environment-dependent developmental rules that affect the activity of apical and axillary meristems in clonal plants (apical dominance, re-activation of the dormant meristem bank, etc.). G- was one of the rules, but G+ was not tested.

It was found that shortening the spacers in gaps has an effect on the capture of resources in patchy environments. However, the grain of the environment (relative to the length of spacers) influences the magnitude of the effect (OBORNY 1994). In the previous simulation, the exact size of the patches was not particularly emphasized. Only three types of grain were applied: a fine, a medium and a coarse one. The possible coarsest and finest grains were not produced, thus, the extreme values on the axis of spatial predictability (see below) were not examined.

This study aims to explore the significance of both responses, G- and G+, for more types of environment, including extremely coarse and fine grained habitats. Using a new concept, spatio-temporal predictability, a more thorough discussion of the reasons for the effectiveness of resource capture is attempted.

## MODEL

### A stochastic, spatially explicit model for clonal growth in heterogeneous environments

This study is based on a simulation model, in which the growth of a hypothetical clonal plant takes place in a spatially and temporally patchy environment. The process of clonal growth is influenced by environment-dependent rules (G+ or G-), which determine the length of the spacer(s) developed by a mother ramet, according to the actual state of its micro-environment. Thus, the response to environmental quality is local and autonomous. The neutral reference is G0, which represents random search in the habitat.

The environment is modelled as a mosaic of resource-rich and poor microsites (subsequently referred to as gaps and non-gaps) (Fig. 1). For spatial representation, an elementary hexagonal grid is defined, where sides of the hexagons are 1 unit. A hexagonal grid was used instead of a square grid, because in a hexagonal grid all the neighbours are at equal distances from a central cell, and, at the same time, the neighbours entirely fill the space around the central cell. Thus, units in the model can be directly translated into a distance measure (e.g. centimetres). The elementary grid is divided by hexagonal mosaic cells (patches) of *D* units diameter. The values of *D* applied in the simulation are 1, 3, 5, 7, 9 and $\infty$ units. The spatial pattern generated by this method is random on the scale of $D$ (if $D > 1$), but it is patchy on the unit scale, where growth processes are recorded (see below). If $D$ is equal to 1 unit, the environmental pattern is random on all scales. $D = \infty$ denotes the case when the diameter of a patch (gap or non-gap) is larger than the total area available for the clonal plant, so the environment is uniform at one point of time.

The environment is characterized by the following variables:

$P_g$, relative frequency of gaps in the grid;
$P_n$, relative frequency of non-gaps ($P_n = 1 - P_g$); and
$D$, diameter of patches (in units).

As $D \rightarrow \infty$, $P_g$ (or $P_n$) can be interpreted as the probability that the total area is covered by a gap (or non-gap).

The environment changes in discrete time intervals according to a Markovian process, characterized by

$C_{gn}$, probability of a gap to turn into a non-gap per time unit (gap turnover rate); and
$C_{ng}$, probability of change in the opposite direction.

In the present simulation the relative frequency of gaps, $P_g$, is kept constant in time. In this case

$$C_{ng} = C_{gn} \cdot P_g / P_n \quad . \tag{1}$$

Thus, three variables, $D$, $P_g$ and $C_{ng}$, are enough for a full description of the environment.

The clonal plant is modelled as a branching, two-dimensional structure, which consists of ramets and spacers between the ramets. According to architectural models in clonal morphology (BELL 1984, SUTHERLAND & STILLMAN 1988), it can be characterized by:

$S$, spacer length;
$B$, branching probability; and
$A$, branching angle.

In order to focus on the effect of change in spacer length, the other two parameters, $B$ and $A$, are kept constant ($B = 0.5$ and $A = 30^o$), i.e. they are not affected by the environment. The influence of this particular choice of the value of these parameters on the expected results is a matter for closer consideration. According to the preliminary results (OBORNY 1994), $B$ is chosen to produce the maximum morphological diversity for the clones to be able to see the widest range of responses to environmental quality. The branching angle, $A$, is set at $30^o$. The literature on similar branching structures shows no agreement with regard to the question of whether altering $A$ can alter the efficiency of resource capture. Some authors suggest that branching angle has no influence on ramet aggregation in favourable microsites (SUTHERLAND & STILLMAN 1988, WATKINSON 1988). However, there are also contradictory results (FORD

1987). It is unequivocal that the cost of intraclonal competition, is strongly affected by branching angle (CALLAGHAN et al. 1990). Generalizing the effect of different morphological parameters on the geometry of the developing clone is a matter of future research. At present, constant values were used, in order to work with a model plant of relatively simple basic architecture, to clearly demonstrate the effect of plastic modifications of spacer length, $S$.

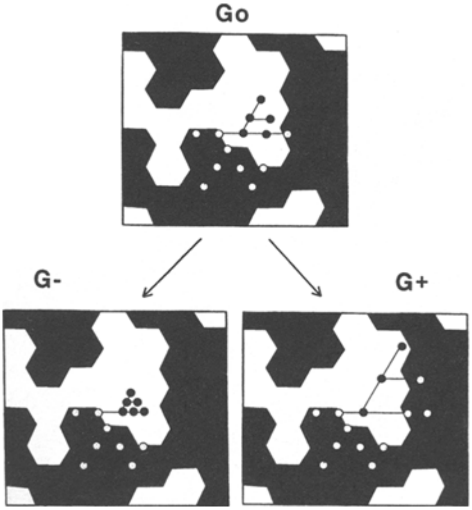


Fig. 1. Examples on the pattern of space occupation when applying G0, G- and G+. White area, gap; grey area, non-gap; black circle, ramet placed in a gap; white circle, ramet placed in a non-gap; and black line, spacer. The drawings show a particular case (which, in fact, was not used in the simulation) where all the three types of clones possess the same pattern of branching, and they are all grown in the same, constant environment.

The model plant consists of ramets and spacers. Ramets are considered as sites of interaction with the environment. These are the parts of the clone where environmental signals are perceived. The function of spacers, in the present simplified view, is only to place the ramets in space. The model is spatially discrete, i.e. the clonal plant grows in units. The growth model applied is stochastic, stationary, and spatially explicit (see WALLER & STEINGRAEBER 1985). Each ramet bears a node with an apical and a single axillary meristem. Therefore, a ramet can develop one or two spacers, and, consequently one or two daughter ramets. Meristems respond to the environmental quality in an autonomous manner. A growth rule determines the length of the spacer developed by a particular meristem. The default spacer length is 2 units. It is decreased to 1 unit in good sites if the rule G- is applied, and increased to 4 units if the rule G+ is applied. Figure 1 shows typical examples of the pattern of space occupation by model clones grown according to G0, G+ and G-.

For a closer examination of the concept of morphological adaptation, the present study focuses on two simple traits (morphological "costs") of the developing clones, that can be subject to selection:

$M$, cost of misplacement, the relative number of ramets placed into poor sites; and

$C$, cost of competition, the relative number of overlapping ramets. It refers to the degree of intraclonal interference.

Since the amount (total length) of spacers is always decreasing under G- and increasing under G+, the cost of spacing (BELL 1984) is not considered here. The above variables are formulated as follows:

$$M = (N_r - N_h)/N_r \quad , \qquad (2)$$

$$C = N_c/N_r \ , \tag{3}$$

where $N_r$ is the number of ramets, $N_h$ is the number of ramets placed into gaps (hits), and $N_c$ is the number of overlapping ramets (i.e. ramets that are placed at the same location).

Naturally, the importance of these traits, their influence on the fitness of the genet, is different in different clonal species, and several alternative evolutionary pathways are possible for minimizing one or both of the costs. The aim of this study is merely to state the value of these cost variables in different situations. In contrast to previous simulations on clonal growth in patchy environments (e.g., BELL 1984, FORD 1987, SUTHERLAND & STILLMAN 1988), the area to be explored and exploited is characterized in a detailed manner by quantitative analysis of its spatial and temporal pattern. Thus, *M*, the proportion of ramets that find favourable microsites, as compared to random search, is of special interest.

The input variables for the Monte Carlo simulation are $P_g$, $C_{ng}$, *D* and *S*, and the output variables are *M* and *C* for the G+, G- and G0 rules. The development of five generations of ramets are followed in a single genet. For one environmental type and one rule the program records 100 repetitions (i.e., the growth of 100 genets is simulated). A set of 100 repetitions will subsequently be referred to as one run. In the simulation 72 combinations of $P_g$ and $C_{ng}$ are examined at six patch diameters (*D*) for both the G+ and G- rules. This means $72 \cdot 6 \cdot 2 = 864$ runs, each with 100 repetitions.

## An information theory model for characterizing spatial and temporal heterogeneity of the environment

Parts of a clone may possess relative autonomy in their response to environmental quality (STEEVES & SUSSEX 1989), thus, local environmental signals in the close neighbourhood of a clonal part may gain special importance in the development of the total clone, and consequently, in the magnitude of the resulting "morphological costs", *M* and *C*. In the present growth model, the developmental decision (whether to change spacer length) is made on the basis of the quality of the environment in the immediate neighbourhood of a meristem. But the consequence of a decision (the fate of the newly formed daughter ramet) largely depends on the fact whether the basis of the decision is still valid at the site of the daughter ramet at another time. So predictability of the environment is of crucial importance in the adaptiveness of the growth rule.

Three questions may emerge. Knowing the quality of the environment at a point at a time, how accurately can we predict environmental quality:

(a) at the same point at the next time step;

(b) at the next point at the same time; and finally,

(c) at the next point in the next time step?

The questions inquire about (a) temporal, (b) spatial, and (c) spatio-temporal predictability of the environment (Fig. 2). "Next point" refers to a randomly chosen point at *S* units distance (spacer length) from the parent ramet. For the whole area, we can analyze the probability of changes in environmental quality (state transitions) both in space and time by a four-cell contingency table (Fig. 3). The inner cells indicate transition probabilities, and both margins show the total gap and non-gap availability ($P_g$ and $P_n$), which are kept constant.

In the case of temporal transitions - question (a) - values of the inner cells of the table are:

$$z_1 = P_g \cdot (1 - C_{gn}) \quad , \tag{4}$$
$$z_2 = P_g \cdot C_{gn} \quad , \tag{5}$$
$$z_3 = P_n \cdot C_{ng} \quad , \tag{6}$$
$$z_4 = P_n \cdot (1 - C_{ng}) \quad . \tag{7}$$

For spatial transitions - question (b) - these are:

$$z_1 = P_g \cdot (P_r + P_g \cdot P_l) \quad , \tag{8}$$
$$z_2 = P_g \cdot P_n \cdot P_l \quad , \tag{9}$$
$$z_3 = P_n \cdot P_g \cdot P_l \quad , \tag{10}$$
$$z_4 = P_n \cdot (P_r + P_n \cdot P_l) \quad , \tag{11}$$

where $P_l$ is the probability of stepping out of a mosaic cell by a step of $S$ units length (starting from a randomly chosen point of the cell), and $P_r$ is the probability of remaining within the mosaic cell. Their values can be calculated by geometric considerations. $P_l$ is a function of $D$ and $S$, and

$$P_l + P_r = 1 \; . \tag{12}$$

For spatio-temporal transitions, question (c), values of the inner cells are:

$$z_1 = P_g \cdot [P_r \cdot (1 - C_{gn}) + P_l \cdot P_g \cdot (1 - C_{gn}) + P_l \, . \, P_n \, . \, C_{ng}] \quad , \tag{13}$$
$$z_2 = P_g \cdot [P_r \cdot C_{gn} + P_l \cdot Pg \cdot C_{gn} + P_l \cdot P_n \, (1 - C_{ng})] \quad , \tag{14}$$
$$z_3 = P_n \cdot [P_r \cdot C_{ng} + P_l \cdot P_g \cdot (1 - C_{gn}) + P_l \cdot P_n \cdot C_{ng}] \quad , \tag{15}$$
$$z_4 = P_n \cdot [P_r \cdot (1 - C_{ng}) + P_l \cdot P_g \cdot C_{gn} + P_l \cdot P_n \cdot (1 - C_{ng})] \quad . \tag{16}$$

To explain the above formulae in more detail, let us take the example of $z_1$. Cell $z_1$ in the contingency table shows the probability of the event that a mother ramet was in a gap at time 1, and the daughter ramet gets into a gap as well at time 2. The probability of the event that a mother ramet was in a gap is $P_g$ (the first multiplicator on the right side of the equation). The event that its daughter ramet gets in a gap can happen in three cases: (a) the daughter is placed in the same mosaic cell, and the cell has still remained a gap [with the probability of $P_r \cdot (1 - C_{gn})$], or (b) it leaves the mother's mosaic cell, but steps into a cell which was a gap and has still remained a gap [$P_l \cdot P_g \cdot (1 - C_{gn})$], or (c) it leaves, but steps into a cell which was a non-gap, but has turned into a gap ($P_l \cdot P_n \cdot C_{ng}$). Thus, both temporal changes and the effect of moving on the plane can be incorporated into the model. Naturally, when a tip of a stolon or rhizome is advancing in a patchy environment, spatial and temporal effects take place simultaneously (as illustrated in Fig. 2).

Therefore, the aim of this formulation is to find an exact measure for environmental predictability not only in space or time, but in space-time too. Calculations are based on the family of information theory models by JUHÁSZ-NAGY (JUHÁSZ-NAGY & PODANI 1983, JUHÁSZ-NAGY 1984). In the model the most important characteristics of a contingency table are analyzed by the Shannon entropy of the cells or sets of cells of the table, with reference to their theoretical maximum and minimum. The model was originally worked out for studying spatial dependence of coexisting species in plant communities [JUHÁSZ-NAGY (1984); see BARTHA (1990) for an application].

In this paper the information theory model is used for defining the predictability of the gap/non-gap quality of the environment for the contingency tables presented above. Let us define the joint entropy of transitions, $\hat{H}$, as an estimated Shannon entropy of the inner cells,

$$\hat{H} = - \sum_{i=1}^{4} z_i \, . \log \, z_i \ , \qquad (17)$$

where log means $\log_2$, and entropy values are given in bits. The upper limit of $\hat{H}$ is the total entropy bound of the system,

$$H_{max} = 2 \ . \qquad (18)$$

Let us define **predictability**, $\hat{R}$, as

$$\hat{R} = H_{max} - \hat{H} \ . \qquad (19)$$

To illustrate this concept, let us decompose predictability into elements (JUHÁSZ-NAGY & PODANI 1983, BARTHA 1990), as shown in the Venn-diagram (Fig. 4). Let us define two measures with illustrative meaning, $\hat{M}$ and $\hat{A}$. $\hat{M}$ the marginal entropy,

$$\hat{M} = - P_g \cdot \log P_g - P_n \cdot \log P_n \ . \qquad (20)$$

$\hat{M}$ refers to **gap/non-gap diversity** of the environment. It is minimal ($\hat{M} = 0$) when $P_g = 1$ or $P_n = 1$, i.e. when the entire area is filled with gaps or non-gaps. The maximum ($\hat{M} = 1$) is achieved when $P_g = P_n = 0.5$, i.e. when the uncertainty of finding a gap (or a non-gap) in a place at a time is maximal. Since both temporal and spatial predictability is a function of total gap availability ($P_g$ and $P_n = 1 - P_g$), this entropy measure plays an important role when analyzing habitat pattern.

$\hat{A}$ is defined as the mutual information (association) between two states,

$$\hat{A} = 2 \, . \, \hat{M} - \hat{H} = -2 \, . \, (P_g \, . \log P_g + P_n \, . \log P_n) + \sum_{i=1}^{4} z_i \, . \log \, z_i \ . \qquad (21)$$

$\hat{A}$ measures the strength of interdependence of states. For the temporal and spatial contingency tables [i.e. questions (a) and (b), stated above], $\hat{A}$ has a clear meaning. In time, $\hat{A}$ characterizes non-randomness of the change of the environment. It ranges from 0 to 1. $\hat{A}$ is minimal in a randomly changing environment (where $C_{ng} = P_g$). $\hat{A}$ is maximal in a constant

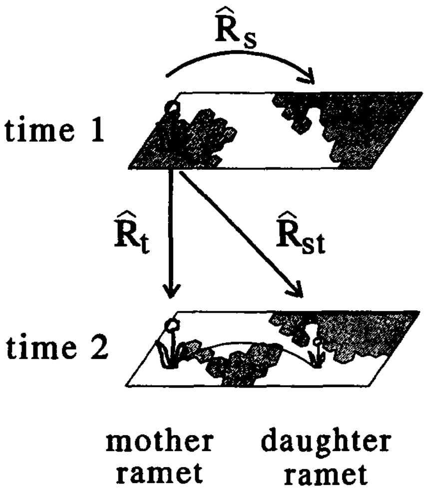
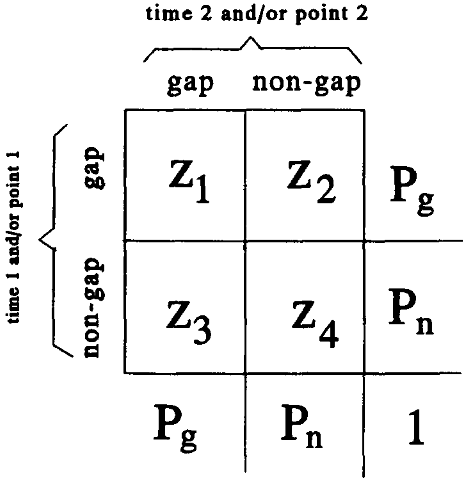


Fig. 2. An illustration of the concepts of spatial ($\hat{R}_s$), temporal ($\hat{R}_t$) and spatio-temporal ($\hat{R}_{st}$) predictability of the environment. A mother ramet of a clonal plant is developing a daughter in a spatially and temporally heterogeneous environment. State transitions of the micro-environment of the modules in space, time and space-time are indicated by arrows. Predictability of these transitions is analyzed by means of information theory. White area, gap; and grey area, non-gap.



|  |  | time 2 and/or point 2 |  |  |
|---|---|---|---|---|
|  |  | gap | non-gap |  |
| time 1 and/or point 1 | gap | $Z_1$ | $Z_2$ | $P_g$ |
|  | non-gap | $Z_3$ | $Z_4$ | $P_n$ |
|  |  | $P_g$ | $P_n$ | 1 |

Fig. 3. Contingency table representation of the probability of state transitions in time, space or space-time. See text for definition of variables. (After OBORNY 1994).

environment (where $C_{ng} = 0$) and in an environment in which the patches systematically change their quality into the opposite in each time step ($C_{ng} = 1$). If we consider only those environmental patterns that range from randomly changing to constant (i.e. where $C_{ng}$ is not greater than $P_g$), and we disregard alternating environmental patterns (where $C_{ng}$ is greater than $P_g$), $\hat{A}$ can be used as a measure of **constancy** of the environment.

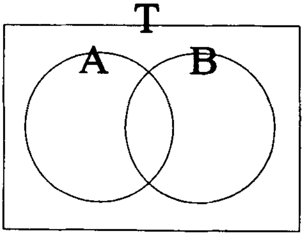
In space, $\hat{A}$ refers to the **grain** of the environment, ranging again from 0 to 1. In a fine-grained environment $\hat{A}$ is small, in a coarse-grained one it is large.

According to our definition, predictability is given as

$$\hat{R} = H_{max} - 2 \cdot \hat{M} + \hat{A} \ .$$

In the simulation model, temporal predictability, $\hat{R}_t$, is a function of two simulation parameters, $P_g$ and $C_{ng}$. Spatial predictability, $\hat{R}_s$, is a function of $P_g$ and $D$ (at a given spacer length), and finally, spatio-temporal predictability, $\hat{R}_{st}$, is a function of $P_g$, $C_{ng}$ and $D$.

Re-considering temporal and spatial predictability ($\hat{R}_t$ and $\hat{R}_s$), it can be concluded from the above decomposition that the values of $\hat{R}_t$ and $\hat{R}_s$ are related to some observable characteristics of the environment: gap/non-gap diversity, constancy (or, in general, temporal non-randomness) and grain. A simplified scheme of habitat characterization using the values of these information theory functions is shown in Fig. 5a,b,c. Considering spatio-temporal predictability, $\hat{R}_{st}$, it is clear even from its formula, that entirely



$\hat{M} \rightarrow A \equiv B$

$\hat{H} \rightarrow A \cup B$

$\hat{A} \rightarrow A \cap B$

$\hat{H}_{max} \rightarrow T$

$\hat{R} \rightarrow T - (A \cup B)$

Fig. 4. Venn-diagram representation of the information theory measures used for characterizing the environment. Set A represents the marginal entropy, $\hat{M}$, at state 1 (time 1 or point 1). B represents the marginal entropy at state 2. Since the margins of the contingency table are similar (i.e. $\hat{M}$ is constant in space and time), the area of the circles are drawn equal. Union of A and B shows the entropy of state transitions, $\hat{H}$. Intersection of A and B represents the associacion between two states of the environment, $\hat{A}$. Set T represents the total entropy bound, i.e. the maximal entropy of the system, $\hat{H}_{max}$. Predictability, $\hat{R}$, is defined as a loss of entropy from $\hat{H}_{max}$ due to non-randomness of the state transitions (after OBORNY 1994). Arrows denote the relationship "represented by".

different habitats may fall into the same category of $\hat{R}_{st}$. For example, an open habitat with few, relatively large patches of long-lived shrubs can show the same spatio-temporal predictability (e.g. from the viewpoint of light gaps experienced by a creeping clonal plant) as a more closed, quickly changing ruderal habitat with many, small patches of competitors. Comparing Fig. 5d to Fig. 5a,b,c, the value of spatio-temporal predictability, $\hat{R}_{st}$, can be related to observable characteristics (diversity, constancy and grain) of the environment, thus, it can be judged, what kind of habitats belong to a particular value of $\hat{R}_{st}$.

## Methods of data analysis

In all runs it was examined separately whether applying the growth rule G+ or G-, as compared to the neutral model G0, resulted in a change in $M$ and $C$. The values of the output parameters ($M$ and $C$) at G+/G- and G0 were compared by two-sample $t$-tests. I will subsequently refer to the result, the level of significance gained from the $t$-test, as "increase/decrease of cost" (depending on its sign). Then I examined whether any of the known environmental characteristics were related to the pattern of results. In other words: is there an environmental characteristic that explains which are the runs where the rules G+ or G- proved advantageous? Three "levels" of environmental characteristics were studied: (a) the simulation parameters ($P_g$, $C_{ng}$ and $D$) themselves; (b) temporal predictability ($R_t$) and a spatial property, patch diameter ($D$), where $\hat{R}_t$ is a function of $P_g$ and $C_{ng}$; and finally, (c) spatio-temporal predictability ($\hat{R}_{st}$), which is a function of all the three simulation parameters, $P_g$, $C_{ng}$ and $D$.

In the Results section, only a typical example for (a), and a schematic summary of the results for (b) are presented; (c) is discussed in more detail. For each run, which represents a given combination of environmental parameters, a value of $\hat{R}_{st}$ can be calculated, and a result for the increase/decrease of $M$ and $C$ can be assigned. Thus, for one type of cost ($M$ or $C$) and one growth rule (G+ or G-) two "maps" were produced in the parameter space: a map of predictability and a map of increase/decrease of cost. These maps are similar to those shown in Fig. 6a and b, but they are four-dimensional, since not simply temporal, but spatio-temporal aspects were considered. The axes of both $\hat{R}_{st}$ and of the level of significance were divided into nine ranks. Similarity of these maps was examined by the following statistical test. The results on the map of increase/decrease of cost were re-arranged according to the null hypothesis that the ranks of the results are maximally correlated with the ranks of $\hat{R}_{st}$, i.e. the similarity between the two maps is maximal. Then, the distribution of low and high ranks on the expected and the actual map were compared by $\chi^2$ test. The result of this test will be subsequently referred to as the "similarity between predictability and the increase/decrease of a cost".

## RESULTS

A wide range of environmental types was tested. Gap probability, $P_g$, ranged from 0.1 to 0.9, and gap turnover rate, $C_{ng}$, from 0 to 1, both in steps of 0.1. Patch diameter, $D$, was 1, 3, 5, 7, 9 and $\infty$. Thus, from open to closed, from temporally constant to extremely changeable, and from fine-grained to coarse-grained (even to uniform) habitats were included.

### An example on the effect of two parameters: gap probability and turnover rate

Seventy two combinations of $P_g$ and $C_{ng}$ were tested at all $D$ values. Since $\hat{R}_t$ is a function of $P_g$ and $C_{ng}$, it is possible to draw a three-dimensional figure, a map of temporal predictability (Fig. 6a). The solid grey area in the figure indicates non-realized combinations (due to the requirement of keeping $P_g$ fixed). It is noticeable that minimal predictability ($\hat{R} = 0$) is achieved, when gaps and non-gaps are in equal amounts ($P_g = P_n = 0.5$), and randomly changing in time ($C_{ng} = C_{gn} = 0.5$), because our "uncertainty" about what we find (a gap or a non-gap) in a spot at the next time step is maximal in this case. If either the total amount of gaps or the rate of their turnover changes (either increases or decreases), the environment becomes more predictable.

Let us examine a similarly constructed map for the results of runs (Fig. 6b). Shadings on the map show the change (in this case, because of its sign, the decrease) of the cost $C$ when applying the rule G-. In other words, the map shows in which runs G- proved "favourable". Shading of the map shows the level of significance, but not the sign of the difference. On this map the signs are all negative, and in general, within a map the signs proved consistently positive or negative in all cases. Comparing the two maps in Fig. 6a and b, we find similarities between the patterns. However, we do not know anything yet about the nature and degree of similarity, and the reason for it.

Before proceeding further, even this simple example shows some important features of the distribution of high and low values on the cost map (Fig. 6b). First of all, it is important that none of the simulation parameters ($P_g$ and $C_{ng}$) alone can explain the distribution of values. A test of significance of Spearman's rank correlation gives $P > 0.1$ for both simulation parameters, indicating that neither $P_g$ nor $C_{ng}$ correlates with the values on the map. Comparing Fig. 6a and 6b, it might be suggested that $\hat{R}_t$, a function of $P_g$ and $C_{ng}$, corresponds accurately to the results. This hypothesis will be tested in the next section.

Secondly, temporal predictability is equally high when a habitat is very closed (small $P_g$) or very open (large $P_g$) (Fig. 6a). For example, if there is a great mass of gaps available, at

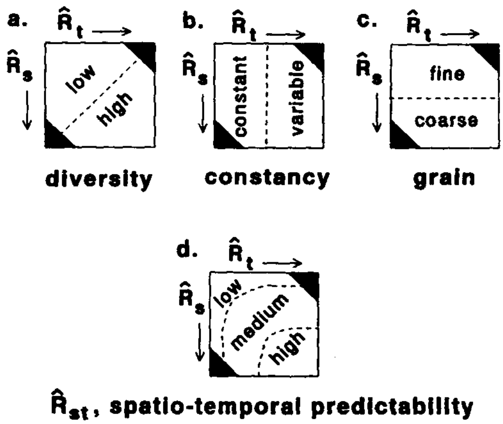


Fig. 5. Characterization of diversity, constancy and grain of the environment at different combinations of temporal and spatial predictability. (a) Gap/non-gap diversity of the environment is a function of total resource availability on the area, irrespective of its pattern in space and time. The diversity is low when gaps are very abundant or very rare ($P_g = 1$ or $P_g = 0$). The diversity is maximal when $P_g = 0.5$. (b) Constancy concerns the resource pattern in time. It is minimal when the environment is changing randomly ($C_{ng} = P_g$). It is maximal when $C_{ng} = 0$. (c) Grain concerns the resource pattern in space. The grain is the finest when sides of the hexagonal patches in the grid are 1 unit ($D = 1$), i.e. the distribution of resources is spatially random. The coarsest grain in the simulation was achieved when the patch size was larger than the size of the entire genet ($D = \infty$). (d) A schematic map of $\hat{R}_{st}$ as a function of $\hat{R}_s$ and $\hat{R}_t$. Grey areas indicate non-realized combinations of $\hat{R}_s$ and $\hat{R}_t$ due to the constraint of total gap availability, $P_g$. See text for further details.

any arrangement of these gaps we can predict with reasonable accuracy that if a ramet is in a gap at present, it is likely to get into a gap at the next time step again, and if it is in a non-gap, its environmental conditions are likely to change. This means high predictability, (see also the contingency table, Fig. 3). The same argument is true if non-gaps are very common.

Another similar observation is that $\hat{R}_t$ is equally high when $C_{ng}$ is either very high or very low, which is shown on the two vertical margins. This means that if gap/non-gap quality of a site remains the same (with the probability of 1) or changes to the opposite quality (with the probability of 1), the environment can be equally regarded as predictable. Interestingly, distribution of the low and high values of the results on the other map (Fig. 6b) follows a rather similar pattern. In order to continue with the interpretation, let us focus on $\hat{R}_t$, which has been found to be in closer relationship with the increase/decrease of cost than the simulation parameters $P_g$ and $C_{ng}$ themselves.

## The effect of temporal predictability

All the maps of the increase/decrease of costs were compared to the map of $\hat{R}_t$ in the same way as discussed above (Fig. 7). Here the "favourability" of applying a certain growth rule is shown for different combinations of temporal predictability ($\hat{R}_t$) and patch diameter ($D$). These two variables are independent. $\hat{R}_t$ refers to a temporal and $D$ to a spatial property of the environment. Now, more than one run can fall into one cell of the figure. Therefore, the "favourability" of a rule [of G- in sub-figures (a) and of G+ in sub-figures (b) in Fig. 7] was decided on the basis of all the runs falling into a cell. In Fig. 7, the blank cell indicates that more than 66% of the runs gave no significant difference at $P = 0.1$, and only the sign of the difference is shown in the other cases. Thus, "-" means that application of a growth rule proved "favourable" (because a cost was significantly reduced), "+" means "unfavourable" and a blank area means "neutral".

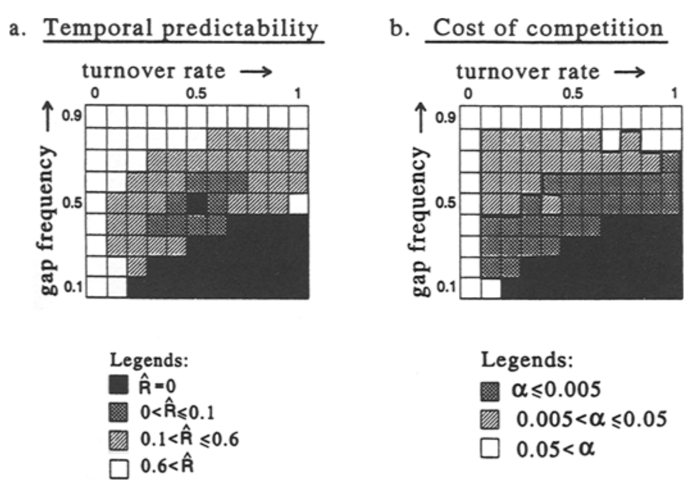


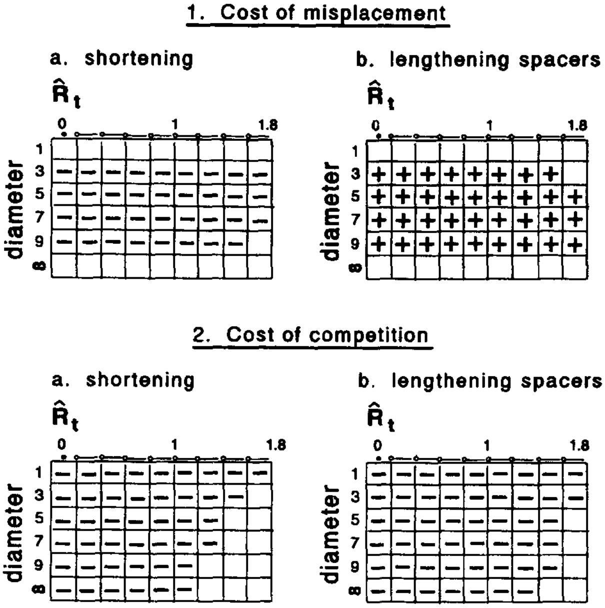
Fig.6. (a) Map of temporal predictability, $\hat{R}_t$, at different parameter combinations. Solid grey area indicates non-realized combinations. (After OBORNY 1994) (b) Map of the decrease of the cost of competition at the same parameter combinations (if $D = 5$). The shading indicates the level of significance at which the cost of competition at G- differs from that at G0.

Considering $M$, the cost of misplacement (Fig.7-1), shortening the spacers in gaps (rule G-) proves "favourable" in several environmental settings. In the other cases it is "neutral", but never "unfavourable" (Fig.7-1a). This is in accordance with the prediction of foraging theory (SUTHERLAND & STILLMAN 1988, WATKINSON 1988). Lengthening the spacers (rule G+) can be "unfavourable" or "neutral" (Fig.7-1b). Thus, this type of reaction cannot reduce $M$ in any case, as suggested by. SUTHERLAND & STILLMAN (1988). The cost of competition, $C$ (Fig.7-2), was never enhanced by any growth rule. Thus, both G+ and G- are either "favourable" or "neutral".

Considering the pattern of the occupied ("non-neutral") and blank ("neutral") cells in the sub-figures (a) and (b) in Fig. 7, it can be concluded in general that shortening (G-) and lengthening the spacers in gaps (G+) show rather similar patterns of effect (of course, the sign of the effect differs). This is in accordance with the reasonable expectation that shortening or lengthening the spacers does not imply a qualitative difference in the behaviour of the system. The growth rules cause "interesting" effects in more or less the same types of habitats (in the sense of $\hat{R}_t$ and $D$). The fact that length of the spacers can change (according to site quality) is more important than the sign of the change.

However, there are finer differences between G- and G+ both in Figs. 7-1 and 7-2. These differences, and the exact pattern of blank and occupied cells need further explanation. First, let us discuss the effect of applying the rule G- **on the decrease of the cost of misplacement** (Fig. 7-1a). The figure shows that at $D = 1$ and $\infty$ the cost of misplacement cannot be reduced at any temporal pattern of the environment. The reason for this is that if patch diameter is 1 unit, the spatial pattern of the environment can be considered as random both on the scale of default (2 units) and the shortened (1 unit) spacer size. So, shortening a spacer has no effect on the chance of placing the daughter ramet in a gap or non-gap. The probabilities of these events are exactly $P_g$ and $1 - P_g$. A similar argument is true for $D = \infty$. In this case the whole area is covered by a single, very large gap or non-gap. Site quality in any spot is exactly determined by the present status and the $C_{ng}$ turnover rate. In general, shortening a spacer has no effect on the chance of finding a good-quality microsite for the daughter ramet in all the cases when the spatial pattern of the environment is maximally unpredictable ($D$ = 1) or maximally predictable ($D = \infty$).

There is one more cell (at $D$ = 9 and very high $\hat{R}_t$) where the application of G- proves "neutral". It is an important case, because, in contrast with the previous, more or less trivial findings, this result may provide a clear example of the interdependence of the spatial and temporal properties of the environment. If the temporal predictability of the environment is very high and, at the same time, the patches are very big, the immediate neighbourhood of a ramet, i.e. the area that is potentially available within one step, "imitates" the situation of $D = \infty$. From the viewpoint of the plant, the overall habitat pattern, either temporal or spatial, is irrelevant. It detects the environment on its own scale of growth - in this particular case - as an infinite "sea" of gaps (or non-gaps). If the temporal predictability is



1. Cost of misplacement

a. shortening

| diameter \ $\hat{R}_t$ | 0 | | | | | 1 | | | 1.8 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | | |
| 3 | - | - | - | - | - | - | - | - | - |
| 5 | - | - | - | - | - | - | - | - | - |
| 7 | - | - | - | - | - | - | - | - | - |
| 9 | - | - | - | - | - | - | - | - | |
| ∞ | | | | | | | | | |

b. lengthening spacers

| diameter \ $\hat{R}_t$ | 0 | | | | | 1 | | | 1.8 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | | |
| 3 | + | + | + | + | + | + | + | + | |
| 5 | + | + | + | + | + | + | + | + | + |
| 7 | + | + | + | + | + | + | + | + | + |
| 9 | + | + | + | + | + | + | + | + | + |
| ∞ | | | | | | | | | |

2. Cost of competition

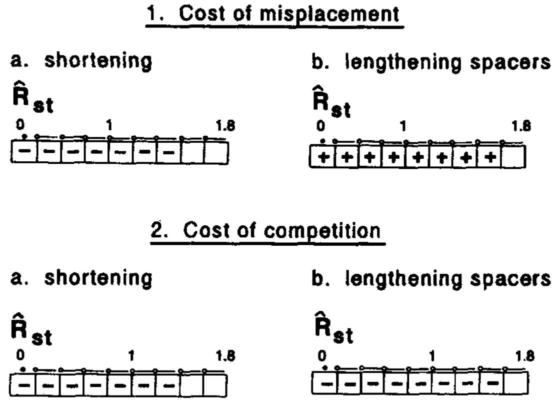
a. shortening

| diameter \ $\hat{R}_t$ | 0 | | | | | 1 | | | 1.8 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | - | - | - | - | - | - | - | - | - |
| 3 | - | - | - | - | - | - | - | - | |
| 5 | - | - | - | - | - | - | - | | |
| 7 | - | - | - | - | - | - | - | | |
| 9 | - | - | - | - | - | - | | | |
| ∞ | - | - | - | - | - | - | | | |

b. lengthening spacers

| diameter \ $\hat{R}_t$ | 0 | | | | | 1 | | | 1.8 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | - | - | - | - | - | - | - | - | - |
| 3 | - | - | - | - | - | - | - | - | - |
| 5 | - | - | - | - | - | - | - | - | |
| 7 | - | - | - | - | - | - | - | - | |
| 9 | - | - | - | - | - | - | - | - | |
| ∞ | - | - | - | - | - | - | - | | |

Fig.7. Increase or decrease of the cost of misplacement and competition when spacers shorten (G-) or lengthen (G+) in gaps. "-", the cost significantly decreases, i.e. the rule is "favourable"; "+", the cost significantly increases, i.e. the rule is "unfavourable"; and blank, no change, i.e. the rule is "neutral". Horizontal axis shows the temporal predictability, $\hat{R}_t$, vertical axis indicates patch diameter, $D$.



1. Cost of misplacement

a. shortening

| $\hat{R}_{st}$: 0 | | | | 1 | | | | 1.8 |
|---|---|---|---|---|---|---|---|---|
| - | - | - | - | - | - | - | | |

b. lengthening spacers

| $\hat{R}_{st}$: 0 | | | | 1 | | | | 1.8 |
|---|---|---|---|---|---|---|---|---|
| + | + | + | + | + | + | + | + | |

2. Cost of competition

a. shortening

| $\hat{R}_{st}$: 0 | | | | 1 | | | | 1.8 |
|---|---|---|---|---|---|---|---|---|
| - | - | - | - | - | - | - | | |

b. lengthening spacers

| $\hat{R}_{st}$: 0 | | | | 1 | | | | 1.8 |
|---|---|---|---|---|---|---|---|---|
| - | - | - | - | - | - | - | - | |

Fig. 8. The same increase/decrease of cost as indicated in Fig. 7, but shown in relation to spatio-temporal predictability, $\hat{R}_{st}$. "-", favourable; "+", unfavourable; and blank, neutral (in the sense discussed in the text).

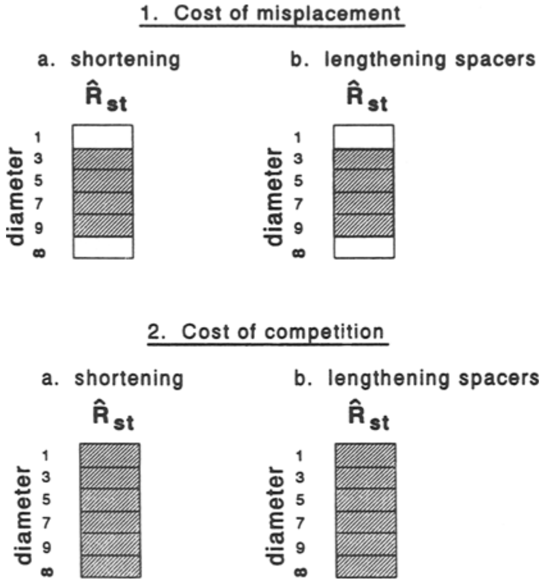


Fig. 9. Significance of "+" and "-" in Fig. 8 at different patch diameters. Hatched, significant; and white, not significant (at $P = 0.001$).

lower, or the patches are smaller, the chance of a newly produced clonal module meeting changed environmental conditions increases, so manipulations of spacer length become more effective.

A similar argument can be applied to Fig. 7-1b, the effect of G+ **on the increase of the cost of misplacement**. The reason for the blank cells at $D = 1$ and ∞ is again spatial randomness, as discussed for G-. However, the last cell in the row of $D = 9$ is not blank here, because lengthening a spacer increases the spatial scale of growth, thus a similar effect can be expected to become detectable only at a larger finite patch size (not used here).

An extra blank cell is found at $D = 3$ and very high $\hat{R}_t$. On this spatial scale the environment is detected as spatially random for the longer (4 units) spacers, thus it "imitates" $D = 1$. Again, if $D$ is larger or the environment is temporally less predictable (i.e. $\hat{R}_t$ is smaller), this effect does not arise. To draw the parallel with G- again, in Fig. 7-1a this cell is not blank, because both at the default $S = 2$ and the shortened $S = 1$ the environment is non-random at $D = 3$.

**The cost of competition** (Fig. 7-2a and b) is reduced by any change in spacer length (G- or G+) in most of the spots. An explanation for the existence of blank cells is that if the patches are quite large and/or the environment is temporally predictable, the chance increases that the clone does not meet microsites of different quality, therefore, its ability to alter spacer length can not be expressed. The blank area in Fig. 7-2a is larger than that on Fig. 7-2b, because if the spacers are shortened (G-), uniformity of the touched microsites can be more pronounced than when lengthening those (G+), thus, the same phenomenon can be detected already at smaller $D$ and lower $\hat{R}_t$ values.

## The effect of spatio-temporal predictability

The above results indicate that there is strong interdependence between the spatial and temporal characteristics of the environment. In order to make this relationship more explicit, let us focus on spatio-temporal predictability, which is a function of all the applied environmental parameters. Replacing $\hat{R}_t$ and $D$ by a single measure, $\hat{R}_{st}$, we find that the cases where application of a growth rule proves "non-neutral" ("+" or "-") are grouped on one side of the $\hat{R}_{st}$ axis (Fig. 8). $\hat{R}_{st}$ seems to be a good descriptor for the habitat types where application of a certain growth rule can be expected to affect the cost of misplacement or competition. The similarity of the maps gained for $\hat{R}_{st}$ and for the increase/decrease of costs was very high both at G- and G+ for the cost of competition. But it was not sufficiently high for the cost of misplacement to explain the pattern of results in Fig. 8-1. Spatial randomness of the environment at extremely small or large patch diameters ($D = 1$ and $D = \infty$) is ab ovo so high that the finer spatio-temporal relationships cannot be detected. Thus, the results were grouped according to patch size, and a separate test of similarity was made at each $D$ (Fig. 9).

The results in Fig. 9-1 suggest that at intermediate patch sizes, $1< D < \infty$, $\hat{R}_{st}$ does explain the distribution of cases where the cost of misplacement can be reduced by altering $S$, (hatched area). At $D = 1$ and $D = \infty$, $\hat{R}_{st}$ does not explain it, (white area). The cost of competition (Fig. 9-2) is explained by $\hat{R}_{st}$ at each patch diameter.

In summary, altering the spacer length has a strong effect on the magnitude of the cost of misplacement in spatio-temporally predictable habitats. If a habitat is extremely fine or coarse-grained, no effect can be detected. The cost of competition is always reduced irrespective of the growth rule (G- or G+) in spatio-temporally predictable habitats. $\hat{R}_{st}$ alone, without taking into account any other environmental parameter, can provide a reasonably accurate prediction for the effectiveness of a plastic response of spacers to environmental quality, provided that the patch diameter is not extremely small (smaller than the minimal spacer length) or extremely large (larger than the clonal plant itself).

## DISCUSSION

Assuming that even the simplest morphological trait, like spacer length, is adaptive needs critical consideration. When interpreting an observed pattern of growth as a "strategy", it is implicitly accepted that it is a result of an evolutionary process (CHAPLEAU et al. 1988). On the other hand, relatively few attempts have been made to relate a growth pattern, resulting from "strategic" developmental decisions, to the pattern of factors of selection in the environment.

Foraging theory provides a clear hypothesis for the optimal adjustment of spacer length according to resource supply. However, the present results suggest that in some habitat types no selection can be expected to act in favour of any environment-dependent behaviour. Opportunistic, plastic growth forms are not necessarily more advantageous than rigid structures.

Responsiveness of growth to environmental conditions (see review by HUTCHINGS & DE KROON 1994) can also be considered as a result of adaptation (SIBLY & GRIME 1986). HUTCHINGS & DE KROON (1994) raise the point that morphological and physiological plasticity may represent alternative solutions for the same problem of capturing patchily distributed resources. The present simulation suggests that responsiveness in spacer length is likely to be of relatively little importance in any highly predictable habitat. These habitats include both very rich and poor environments with relatively large, constant patches of resources.

Considering the growth rule hypothesized by "foraging" (G-) and its counterpart (G+), it was found that the set of environmental types where the application of an environment-dependent rule has any effect as compared to random search, is almost the same when either shortening or lengthening the spacers in good conditions. It is only the sign of the effect that differs, being negative at G- and positive at G+. The symmetry of G- and G+, described first by SUTHERLAND & STILLMAN (1988) in temporally constant environments, has now been confirmed in variable environments as well, not only at different patch sizes ($D$), but also at different values of temporal predictability.

Shortening the spacers in gaps reduces the proportion of ramets placed into non-gaps ($M$), while lengthening them always increases this proportion. This result supports the basic prediction of foraging theory (SUTHERLAND & STILLMAN 1988, WATKINSON 1988). However, there is a wide range of environmental types where G+ and G- do not significantly differ from G0, and this effect is probably not important.

DE KROON & SCHIEVING (1990) suggest two other alternatives to "foraging" growth: "conservative" and "consolidation" growth. Conservative growth is defined as showing G+, and consolidation growth G0. Conservative growth is expected to be characteristic for habitats of "low resource availability, high spatial and temporal patchiness" (in our terms, low $P_g$, high $D$ and high $C_{ng}$). Consolidation growth is predicted to be predominant in resource rich habitats (high $P_g$). The present simulation results do not support this prediction. At least from the viewpoint of misplacement, lengthening the spacers (G+) was never favourable. But DE KROON & SCHIEVING (1990), when defining the three strategies, consider not only morphological but several other properties (physiological, developmental, etc.). This simulation exercise can merely state that morphological arguments on the effect of spacer length on the chance of resource exploration ($M$) cannot explain the existence of other than "foraging" responses of spacers.

On the other hand, if intraclonal competition ($C$) is also considered, being a trait potentially affected by selection, G- and G+ have the same, favourable effect. Both shortening and lengthening the spacers in gaps reduce competition between ramets of the same clone. This effect is realized in all habitats which are variable enough (either in space or time) to allow the different parts of the clone to meet diverse conditions. Presumably, the reason why the importance of $M$ and $C$ have not yet been examined in one, general model, is that in temporally constant environments, as modelled previously by SUTHERLAND & STILLMAN 1988), the problem of the cost of competition does not even arise. In constant, patchy environments, as shown here, G- and G+ have no effect on the cost of competition (see the blank cells in the last column in Fig. 7-2).

Considering not only constant but variable environments too, it was detected here that even an otherwise disadvantageous growth rule (G+) may prove of advantage from the viewpoint of intraclonal competition. This is in accordance with the results of CAIN et al. (1991) who compared the effects of a deterministic and a stochastic simulation model for the clonal growth of *Solidago altissima*. If variation for clonal growth parameters, including spacer length, was allowed, the potential for intraclonal competition was found to decrease. In the present study, any inherent variation for spacer length was not programmed. However, the same effect was achieved by the plant's morphological response to site quality. In other words, environmental variability induced morphological variability within the clone, and this reduced the degree of intraclonal competition.

A possible application of considering both costs (*M* and *C*) in parallel is that if "gap/non-gap" characterization of the environment is used for describing the presence/absence of a strong competitor (or of other clones of the same species), this method of simulation can be used for relating intraclonal competition to interspecific (or interclonal) competition. The economic analogy of "costs" should always be quantitatively evaluated in the actual species. Requirements for a cost-benefit analysis for resource acquisition in clonal plants are outlined in HUTCHINGS & DE KROON (1994).

When examining the adaptive nature of a certain growth rule (like the "foraging rule"), a wide range of environmental types should be taken into consideration. Greenhouse and laboratory studies have used (almost exclusively) temporally constant patches of light, nutrients, etc. (see VAN GROENENDAEL & DE KROON 1990 and HUTCHINGS & DE KROON 1994 for review), although, as experimentally detected by SLADE & HUTCHINGS (1987) in *Glechoma hederacea*, altering the resource supply (from high to low or vice versa) can induce rapid changes in the morphology of a clone. The present simulation underlines that generalizing from the experimental results gained under temporally constant conditions may cause strong bias in our view on the adaptiveness of a growth rule.

The question emerges as what kind of environmental characteristics should be measured, so as to give a reasonably accurate prediction of the outcome of a growth rule. In other similar, spatially explicit simulations on plant growth (FORD 1987, SUTHERLAND & STILLMAN 1988, INGHE 1989) the ratio of spacer length to patch diameter has been used. However, simple simulation parameters, like the above ratio or total resource availability, are insufficient to describe the situation encountered by the clonal parts advancing in an area, because patches of the same quality (gap/non-gap) may touch each other's borderline, merging thus into a larger, more or less interconnected patchwork. It is not advisable to separate theoretically the interconnected patches, even if a grid model is used. As a possible solution, the use of an information theory measure, predictability, has been suggested (OBORNY 1994).

The previous simulation model (OBORNY 1994) treated spatial ($\hat{R}_s$) and temporal ($\hat{R}_t$) predictability separately. This was predominantly motivated by the need for an interpretable description of the habitat on the basis of information theory. In reality, however, spatial and temporal effects cannot be separated (see Fig. 2). For example, a mother ramet is in a gap, and its daughter arrives at a non-gap. There is no reason for distinguishing theoretically the case where the daughter ramet has moved "too far" from its mother from the case where the environment has changed "too quickly". A part of a clonal plant can gain no information on the overall resource pattern on the plane either in space or time. Thus, proper characterization of the environment exactly on the scale of clonal growth is of special importance.

The use of $\hat{R}_{st}$, spatio-temporal predictability, has been suggested here. An advantage of the application of the present information theory model is that $\hat{R}_s$, $\hat{R}_t$ and $\hat{R}_{st}$ can be cross-related and measured exactly on the same axis of information content (ranging from 0 to 2). An intuitive argument for introducing the concept of predictability is that modules of a clonal plant can perceive and respond to environmental signals from their own environment. However, developmental decisions, that are made on the basis of local environmental conditions at a certain time, have a strong influence on the formation of the whole clonal structure. Thus, the information content of the environmental signals that serve as a basis for decision is of great importance when examining the adaptiveness of a certain developmental rule.

Spatio-temporal predictability, $\hat{R}_{st}$, has proved to be a good "predictor"of the effectiveness of plastic growth responses of spacers. Although the same value of $\hat{R}_{st}$ can cover entirely different habitat types (see Fig. 5), it was found to be in closer relationship with the results than any of the observable, simple simulation parameters (gap probability, turnover rate and patch diameter).

This study has been based on purely morphological considerations. Including more information on additional functions of a spacing organ in a given species (like storage or assimilation), or on the interaction of spacer length with other morphological traits is essential for gaining a general view of optimal spacing of clonal modules.

**Acknowledgements:** I dedicate this paper to the memory of Prof. Pál Juhász-Nagy, founder of the information theory method, who had always provided me with advice and guidance. I thank S. Bartha, A Gulyás, T. A. Watt, H. de Kroon, T. Hara, C. Marshall and T. Herben for suggestions and technical help. This research has been supported by the OTKA (Hungarian National Scientific Research Fund), grant Nos T 936, T 5316 and I/3 2046.

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