

Importance of plasticity and decision-making strategies for plant resource acquisition in spatio-temporally variable environments

Gabriella Magyar^{1,2}, Ádám Kun¹, Beáta Oborny¹ and Josef F. Stuefer²

¹Department of Plant Taxonomy and Ecology, Lóránd Eötvös University, Pázmány Péter sétány 1/C, Budapest, H-1117, Hungary; ²Department of Ecology, Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, the Netherlands

Summary

Author for correspondence:

Josef F. Stuefer

Tel: +31 24 3652912

Fax: +31 24 3652409

Email: j.stuefer@science.ru.nl

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- Plants must cope with environmental variation in space and time. Phenotypic plasticity allows them to adjust their form and function to small-scale variations in habitat quality. Empirical studies have shown that stoloniferous plants can exploit heterogeneous habitats through plastic ramet specialization and internal resource exchange (division of labour).
- Here we present a spatially explicit simulation model to explore costs and benefits of plasticity in spatio-temporally heterogeneous environments. We investigated the performance of three plant strategies in pairwise competition. The nonplastic strategy was unable to specialize. The autonomous plastic strategy displayed localized responses to external resource signals. In the coordinated plastic strategy, localized responses could be modified by internal demand signals from connected modules.
- Plasticity in resource uptake proved beneficial in a broad range of environments. Modular coordination was beneficial under virtually all realistic conditions, especially if resource supplies did not closely match resource needs.
- The benefits of division of labour extend considerably beyond the parameter combination covered by empirical studies. Our model provides a general framework for evaluating the benefits, costs and limits of plasticity in spatio-temporally heterogeneous habitats.

Key words: cellular automata, changing environment, clonal plant, division of labour, modular organization, phenotypic plasticity, spatial heterogeneity, spatial population dynamics.

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Introduction

Spatio-temporal variation in environmental quality is a pervasive feature of natural habitats (Wiens, 1976; Shorrocks & Swingland, 1990; Jackson & Caldwell, 1993a, 1993b; Caldwell & Percy, 1994; Wiens, 2000). Dealing with environmental variation at different spatio-temporal scales can be considered one of the foremost ecological challenges for sessile organisms such as plants. Phenotypic plasticity allows them to adjust their form and function to small-scale variations in habitat quality. Plasticity implies that a given genotype can express multiple

phenotypes depending on the environmental conditions (Bradshaw, 1965; Schlichting, 1986, 2002; Schmid, 1990, 1992; Scheiner, 1993; van Kleunen & Fischer, 2005). Plasticity can be seen as an attempt to track environmental variations in space and time and to match plant form and function to specific environmental situations.

Plant growth requires light, water and mineral nutrients. These essential resources must be present in specific quantitative relations for plants to exhibit optimal growth and development. Most plants are able to adjust their resource-uptake capacity from above- and belowground sources by plastic adjustments

in biomass allocation to roots and to shoots (Bloom *et al.*, 1985; Garnier, 1991). Because of resource-based trade-offs, however, increased investments in one uptake function (e.g. leaf allocation to boost light capture) commonly impair complementary uptake functions (e.g. uptake of water and nutrients by roots).

Phenotypic plasticity relies on the acquisition and interpretation of environmental signals indicating the state of a plant's immediate surroundings. The induction of plastic responses requires decisions from the plant to alter its structure or functioning in response to these signals. As plants are modular organisms that lack central control (Novoplansky, 2002; Oborny, 2003), the induction of plastic responses takes place at the organizational level of modules and organs. Nevertheless, the decision to respond to local cues can be modified by plant internal signals indicating the state of connected modules and organs, as shown clearly by developmental studies (Novoplansky *et al.*, 1989; Sachs *et al.*, 1993; Novoplansky, 2003). This leads to the conclusion that 'whole-plant plasticity is the sum of all modular responses triggered by local environmental conditions plus all interaction effects that are caused by communication and behavioural integration of modules' (de Kroon *et al.*, 2005). A plant's phenotypic response to fine-grained environmental variation is thus the result of local and nonlocal decision-making rules.

Stoloniferous and rhizomatous plants produce horizontally growing shoots that root at their nodes and give rise to cloned offspring individuals. The genetic individual (genet) consists of numerous, potentially independent modular units (ramets), which remain physically interconnected for variable, often extended periods. Such ramet networks can be long-lived and may reach a considerable spatial extent under natural conditions. Stoloniferous and rhizomatous plants sample their above- and belowground environment at multiple locations, and share resources (reviewed by Pitelka & Ashmun, 1985; Marshall, 1990; Marshall & Price, 1997) and information (Gómez & Stuefer, 2006) among connected ramets. Experimental studies have shown that spatial heterogeneity in resource availability can be buffered by an internal redistribution of captured resources among interconnected ramets (Hartnett & Bazzaz, 1983; Evans, 1991; Shumway, 1995).

Individuals of nonclonal plants typically specialize in uptake of the scarcest resource to alleviate growth limitation. For example, plants exposed to a low availability of water and a high supply of light develop large root systems to enhance water uptake at the expense of shoot growth. By contrast, interconnected ramets of stoloniferous and rhizomatous plants can specialize in the uptake of a locally abundant resource and redistribute local surplus of carbohydrates, water and nutrients internally, according to supply-and-demand (source-sink) principles. This phenomenon, called spatial division of labour, has been shown experimentally in a number of species (Stuefer *et al.*, 1996; Alpert & Stuefer, 1997; Wijesinghe & Hutchings, 1997; Stuefer, 1998) and can enhance the productivity of

stoloniferous plants by up to 70% under experimental conditions (Stuefer *et al.*, 1996).

Division of labour should be most profitable if resource transport between ramets is efficient and reliable, if patches are rich in one resource (e.g. light) and poor in another (e.g. water), and if environmental resource conditions do not change rapidly over time (Stuefer, 1998). While the first criterion seems reasonable for a number of stoloniferous and rhizomatous species, strictly negative covariance and temporal constancy of resource availabilities may be rather rare in nature, or restricted to specific sites and conditions. Nevertheless, all experimental studies on division of labour have been carried out in temporally stable environments with a strongly negative spatial correlation in the abundance of two resources (light and water, Alpert & Mooney, 1986; Stuefer *et al.*, 1996; light and nitrogen, Friedman & Alpert, 1991), or with a heterogeneous supply of only one resource (Birch & Hutchings, 1994). The functional feasibility and general ecological importance of division of labour under a wider set of conditions thus remains elusive.

We have built a simulation model to explore the benefits and costs of plastic specialization and cooperation of modules (ramets) in a broad range of environments, differing in spatial and temporal aspects of habitat heterogeneity. We used a cellular automata approach and modelled a population of clonal plants exposed to spatio-temporally homogeneous or heterogeneous environments. We compared the performance of three plant strategies (*nonplastic*, *autonomous plastic* and *coordinated plastic*) differing in their responses to environmental variation. The *nonplastic* strategy does not respond to environmental variation, while the two *plastic* strategies show inducible specialization, which enhances the uptake of a locally abundant resource. We assumed that specialization for the uptake of one resource implies an opportunity cost in terms of reduced uptake capacity for the other resource. Temporal heterogeneity in resource conditions can lead to specialization costs, which originate from a mismatch between ramet specialization and resource availability if environmental conditions change after specialization has been induced. This cost is analogous to the information-reliability limit mentioned by DeWitt *et al.* (1998). The combined effect of misspecialization and opportunity cost can seriously hinder the profitability of plastic specialization in some habitats.

The two plastic strategies differ in their response to external and internal cues for specialization induction. The *autonomous plastic* strategy responds only to external signals of local resource availability, disregarding the internal resource balance in the ramet network, while the *coordinated plastic* strategy responds to both external signals of local supply and internal signals of nonlocal demand, specializing only if there is an internal demand for the locally abundant resource. The two strategies represent supply- and demand-driven types of specialization induction, respectively. For the plastic strategies, we varied the speed at which ramet specialization occurs and analysed its impact on plant performance. All strategies were assumed to

share captured resources equally among all interconnected ramets (full resource integration; Kun & Oborny, 2003).

This study aims to identify and quantify environmental conditions that favour plastic specialization for acquiring locally abundant resources in stoloniferous plant species. More specifically, we test the following hypotheses:

- 1 If phenotypic plasticity is a generally beneficial trait, *plastic* strategies should be superior to the *nonplastic* strategy in a large parameter region.
- 2 Spatial division of labour should yield the largest benefits if resources are negatively correlated in space.
- 3 Plasticity should be favoured in environments with no or little temporal heterogeneity, as highly dynamic environments impose an information reliability limit (DeWitt *et al.*, 1998) on plasticity. Because of lag-time limits (DeWitt *et al.*, 1998), plastic specialization should be beneficial only if the average life span of resource-rich patches is equal to, or longer than, the time needed for specialization. The speed at which plastic specialization occurs should thus determine the benefits of plasticity in temporally variable environments.

Description

We used a cellular automata model (Hogeweg, 1988; Czárán, 1998) in which space was represented by a square lattice of 100×100 cells with periodic boundaries. Each cell (site) represented a microhabitat for a single ramet. Vegetative propagation permitted the colonization of neighbouring sites, using a four-cell neighbourhood. The automata consisted of two layers. The population layer showed the distribution of ramets over the area. Each site could be empty or occupied by a ramet. The resource layer showed the distribution of good and bad sites for the two resources. Thus there were a total of four different resource states (Fig. 1).

The amount of resources taken up by a ramet depended on the local environment and on the degree of ramet specializa-

tion. Specializing for an abundant resource enabled the ramet to take up more from a resource compared with a nonspecialized ramet, but implied that less would be taken up from the other resource. Connected ramets were assumed to share resource surpluses and resource needs equally.

The following events took place in every time step.

1 Environmental change: the distribution of resources is changed in the resource layer. Each site could remain unchanged, or change with a quality-dependent probability to keep the overall quality frequencies constant (see below).

2 Updating the resource status: every group of interconnected ramets is evaluated according to the ability of ramets to take up resources.

3 Vegetative propagation: empty sites can be colonized by neighbours. Probabilities of vegetative propagation are dependent on the resource status. If two or more ramets are in the neighbourhood of an empty cell, they compete for the colonization of the empty site. The outcome of competition depends on resource status.

4 Updating the resource status: the resource status of every clonal plant network is re-evaluated to reflect changes caused by newly produced ramets.

5 Survival: death of ramets can occur. The probability of survival depends on plant resource status.

6 Updating the resource status: the resource status of every clonal plant network is re-evaluated to reflect changes caused by death.

7 Specialization: ramets belonging to a plastic strategy can change their degree of specialization. Note that the environment can change before the effect of specialization on vegetative propagation and survival is evaluated. After an environmental change, some ramets may be specialized for the uptake of the locally scarce resource (be misspecialized).

Steps 1–7 are repeated a given number of times (l) before event 8, winter, commences. Thus l represents the length of the growing season expressed in ramet generations.

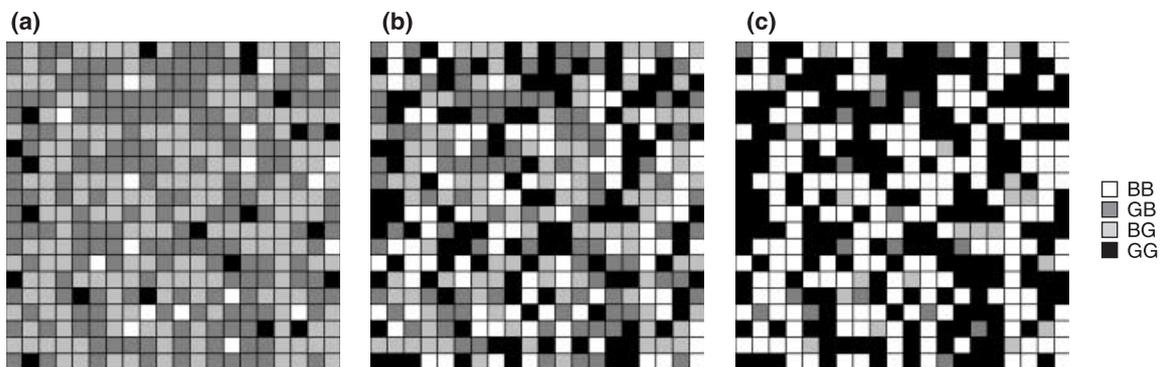


Fig. 1 Examples of heterogeneous environments: Plant growth is assumed to depend on two essential resources, R_1 and R_2 . The availability of each of them can either be high or low ('good' or 'bad', respectively). This results in four possible combinations: a site can be good for both resources (GG), good for R_1 and bad for R_2 (GB), good for R_2 and bad for R_1 (BG), or bad for both resources (BB). The total amount of resources is the same in every lattice. The overall resource richness for the two resources is equal ($p_1 = p_2 = 0.5$), and the spatial correlation between resources is different: (a) $p_{11} = 0.1$ (negative correlation); (b) $p_{11} = 0.5$ (no correlation); (c) $p_{11} = 0.9$ (positive correlation).

Table 1 Symbols and definitions

Symbol	Definition
R_1	Resource 1
R_2	Resource 2
r_i	Specialization trait of ramet i
$g_{i,1}$	Amount of R_1 available to a ramet in clonal network j
$g_{i,2}$	Amount of R_2 available to a ramet in clonal network j
a_j	Amount of the limiting resource in network j (smaller of $g_{i,1}$ and $g_{i,2}$)
b_j	Vegetative propagation probability of a ramet in network j
d_j	Death probability of a ramet in network j
$n_{i,1}$	Number of ramets in sites rich in R_1 in clonal network j
$n_{i,2}$	Number of ramets in sites rich in R_2 in clonal network j
n_j	Total number of ramets in clonal network j
$p_{GG}, p_{GB}, p_{BG}, p_{BB}$	Proportions of GG, GB, BG and BB sites in the lattice
j	Clonal network index
i	Ramet index (within a clonal network)
1,2	Resource index
Constants	
k	Scaling factor of death rate (the highest possible death rate), $k = 0.2$
m	Winter mortality, $m = 0.1$
l	Length of the growing season in ramet generations (= number of time steps within one growing season, before winter) $l = 20$
Variables	
r_{step}	Step size of specialization: the amount by which r_i can change during one time step
e	Environmental change: proportion of sites that change their quality during one time step
p_1	Overall resource richness for R_1
p_2	Overall resource richness for R_2
p_{11}	Spatial interdependence between the availability of the two resources

8 Winter: ramets can die during winter, and all fragments disintegrate. The winter mortality rate (m) is constant and independent of resource status.

Resource distribution and environmental change: event 1

The resource combinations are chosen from predetermined probabilities ($p_{GG}, p_{GB}, p_{BG}, p_{BB}$), and are randomly distributed over the simulated area in a fine-grained pattern. The probabilities are as follows:

$$p_{GG} = p_1 p_{11} \quad \text{Eqn 1}$$

$$p_{GB} = p_1 - p_{GG} \quad \text{Eqn 2}$$

$$p_{BG} = p_2 - p_{GG} \quad \text{Eqn 3}$$

$$p_{BB} = 1 - p_1 - p_2 + p_{GG} \quad \text{Eqn 4}$$

(See Table 1 for definitions of all symbols.) Consequently, the environment can be described by three parameters: p_1 , p_2 and p_{11} . p_1 and p_2 express the probabilities at which a randomly chosen site is good for R_1 or R_2 , respectively. Thus p_1 and p_2 describe the overall availabilities of the two resources. The third parameter, p_{11} , is a conditional probability expressing the chance of a random site being good for R_2 under the condition that it is also good for R_1 . Therefore p_{11} characterizes

the spatial correlation between the two resources. If $p_{11} = 0.5$ there is no spatial correlation between the two resources (randomness); if $0.5 < p_{11} \leq 1$ there is a positive correlation; and if $0 \leq p_{11} < 0.5$ there is a negative spatial correlation.

Simulations start by randomly choosing a resource combination for each site in the lattice, according to equations 1–4 (Fig. 1). Then the environment is updated in every time step (event 1). The overall frequency of change is e . This is the proportion of sites in the habitat that will change quality during one time step. Environmental change rearranges site qualities but does not change their frequency distribution. To keep frequencies ($p_{GG}, p_{GB}, p_{BG}, p_{BB}$) and spatial correlation of resources (p_{11}) constant, not all values of e are possible, which is reflected in the nonrectangular shape of graphs in Fig. 4. We used a technique in which sites are changed with probabilities that depend on site quality. For each given value of e , sites of different qualities have different probabilities of changing during a time step. Persistence is defined as the probability of a site with a given quality staying the same from one time step to the next. Patch persistence depends on both the frequencies of patches ($p_{GG}, p_{GB}, p_{BG}, p_{BB}$) and the overall temporal change (e). Cells along diagonal lines in Fig. 4 are characterized by the same values of patch persistence. (See Supplementary Material for a formal definition and details.)

We assume nondepletable resources, implying that the presence of our species does not have any long-term effect on the resource availability at a site.

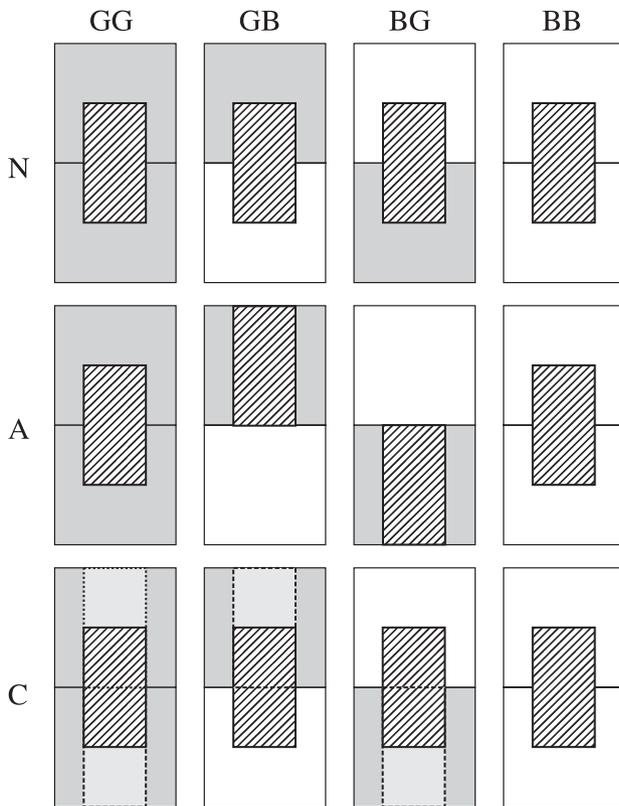


Fig. 2 Resource-uptake capacity of the three modelled strategies in each site quality. N, *nonplastic*; A, *autonomous*; C, *coordinated*. The hatched bar in the middle of each diagram represents the uptake capacity of a ramet. The upper and lower parts in the background of each hatched bar refer to the above- and belowground environments, respectively. High and low resource availability is indicated by shaded (good site, G) and open (bad site, B) background areas. All diagrams show ramets with maximum specialization. Specialization is absent in N. Specialization depends only on the local resource availability for A (always specializes for the locally abundant in GB and BG sites). For C ramets, specialization depends on plant internal resource demands (specialize on internally less available but locally abundant) and hence can have different values in GG, GB and BG sites. No specialization for C is depicted by striped bars with solid borders; specialization by light grey bars with broken borders.

Specialization: event 7

The state of a ramet i is characterized by its degree of specialization r_i , which ranges from -1 to $+1$. Positive values correspond to specialization for the acquisition of R_1 ($+1$ means full specialization for R_1) and negative values for R_2 . $r_i = 0$ indicates no specialization. *Nonplastic* (N) ramets cannot specialize. *Plastic* ramets can increase or decrease their degree of specialization by r_{step} in every time step. If $r_{\text{step}} < 1$, ramets cannot achieve full specialization within a single time step.

Figure 2 summarizes the behaviour of the strategies in all possible sites. Specialization occurs only for the locally abundant resource. No specialization can occur in BB sites, and only *coordinated* ramets can specialize on GG sites, depending on the internal needs of the clonal network.

The *coordinated plastic* strategy employs more sophisticated decision-making rules than the *autonomous plastic* strategy, as it compares internal needs with external supplies before deciding to specialize. Consider the example of a *coordinated* ramet group consisting of three nonspecialized ramets situated in GB, GB and GG sites, respectively. The ramet group as a whole experiences higher availability of R_1 than R_2 , which implies that R_2 limits its growth. The ramet in the GG site will consequently counteract the internal resource imbalance by enhancing the uptake of R_2 through specialization.

Ramets of both the *coordinated* and *autonomous* strategy decrease their degree of specialization when specialized for the uptake of the locally scarce resource: $|r_i|$ is decreased by r_{step} and ramets develop towards a nonspecialized state. (For technical details see Supplementary Material.)

Updating the resource status: events 2, 4 and 6

The amount of resources taken up by a ramet i depends on the local environment (G or B) and on the degree of specialization, r_i . Unspecialized ramets located in GG sites take up one unit of each of the two resources. The resource taken up is divided into two parts. One part is used for self-maintenance and the remainder is shared with the rest of the network. The model assumes that one unit of each resource is needed for self-maintenance within each time step. The resource need is also shared equally among ramets. In case of insufficient uptake, local resource deficits have to be balanced by resource imports from connected ramets. We assume that both resources can be distributed evenly among ramets: after redistributing surpluses and deficiencies, the resource status of every connected ramet is the same. This implies that the two resources are transported independently from each other. We did not consider storage in this model: high resource supply at one time hence does not enhance survival and vegetative propagation in the next time step.

A plastic ramet i takes up a maximum amount of $1 + r_i$ of R_1 , and $1 - r_i$ of R_2 , which implies a linear trade-off between uptake of the two resources. This trade-off is a representation of the opportunity costs of specialization. Since each ramet uses one unit of each resource for self-maintenance, the net uptake on GG sites is r_i for R_1 and $-r_i$ for R_2 (Fig. 3). The opportunity cost is not present on GB and BG sites. On a bad site, ramets cannot take up any resource, which implies that bad sites are extremely poor, and we simulate environments with a high contrast (difference in resource availability) between good and bad sites. In a bad site, the net resource availability (demand) is -1 , indicating that the ramet needs supply from the rest of the network. In temporally variable environments, the cost of misspecialization appears on all GG, GB and BG sites that are changed because of temporal heterogeneity.

Because of physiological integration, the resource status of a ramet depends not only on its local environment, but also on the environments of all other connected ramets. For a

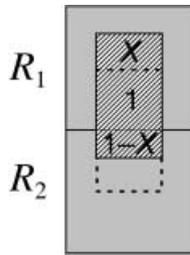


Fig. 3 Example for a ramet that specializes for R_1 to the degree x . Notations as in Fig. 2. The dashed line in the middle outlines the uptake capacity of a nonspecialized ramet (one unit from R_1 and one unit from R_2). The solid line marks actual uptake: more $(1 + x)$ is available from R_1 , and less $(1 - x)$ from R_2 . After paying the cost of self-maintenance (one unit from R_1 and one unit from R_2), there is a net gain (x) for R_1 and a net demand ($-x$) for R_2 .

clonal network j consisting of n_j ramets, with $n_{j,1}$ ramets in good sites for R_1 , and $n_{j,2}$ ramets in good sites for R_2 , the resource status of each ramet can be calculated as follows:

$$g_{j,1} = \frac{(n_{j,1} - n_j) + \sum_{i=1}^{n_{j,1}} r_i}{n_j} \quad \text{Eqn 5}$$

$$g_{j,2} = \frac{(n_{j,2} - n_j) - \sum_{i=1}^{n_{j,2}} r_i}{n_j} \quad \text{Eqn 6}$$

Vegetative propagation and survival: events 3 and 5 In accordance with the minimum law (Liebig, 1840), we assume that survival and vegetative propagation are limited by the resource available in the lowest quantity relative to the needs:

$$a_j = \min(g_{j,1}, g_{j,2}) \quad \text{Eqn 7}$$

a_j is the amount of the limiting resource in clonal network j and its range is $[-1, 0]$. Negative values indicate a need for the resource. The probabilities of death (d_j) and vegetative propagation (b_j) are assumed to depend linearly on the amount of limiting resource. The probability for vegetative propagation increases, death probability decreasing with decreasing resource limitation (smaller $|a_j|$):

$$b_j = 1 - |a_j| \quad \text{Eqn 8}$$

$$d_j = |a_j| \cdot k \quad \text{Eqn 9}$$

where k is a scaling factor, which determines the relative importance of the resource for survival vs vegetative propagation.

During vegetative propagation, all neighbours of an empty site are checked as to whether they can produce an offspring according to their b_j probabilities. If an empty site is neigh-

boured by more than one potential parent ramet, competition occurs, and only the winner can colonize the empty site. The probabilities of winning the competition are proportional to the vegetative propagation probabilities and thus dependent on the resource status. They are given by $1/4b_j$, and add up to 1 only if there are four neighbours with optimal resource balance, otherwise there is a probability of no ramet being produced. Newly produced ramets are not specialized ($r_i = 0$). During the survival event, each ramet in network j has probability d_j of dying ($1 - d_j$ probability of survival).

Winter: event 8

Ramets can die during winter with probability m . The surviving ramets are disconnected and their specialization is reset to zero, reflecting that all active plant parts die during winter and a new, nonspecialized plant grows out in spring. This simulates plants from temperate environments with annual ramet networks such as *Potentilla anserina*, *Potentilla reptans*, *Glechoma hederacea*, *Ranunculus reptans* and others. The number of cycles (iterations of events 1–7) before winter was $l = 20$ in all simulations. (For technical details see Supplementary Material.)

Parameter values, initial conditions and output

We ran simulations in environments with equal ($p_1 = p_2 = 0.5$) and unequal ($p_1 = 0.6$, $p_2 = 0.4$) resource availabilities. We tested three values of specialization speed, r_{step} (0.1, 0.5, 1) covering a wide range from slow to instantaneous specialization. Within each combination of resource availability and r_{step} , we scanned all possible values of p_{11} and e by intervals of 0.1, leaving out the extremes for p_{11} ($p_{11} = 0$ and $p_{11} = 1$).

The strategies were investigated separately (N, A or C) and in all possible pairs, simulating competition between the different strategies. Here we present the results of the two *non-plastic-plastic* strategy pairs (N–C and N–A). Competition experiments between the two *plastic* strategies yielded complex results and will be addressed separately elsewhere. The single-strategy simulations were initiated with 50 ramets and the competition runs started from 100 ramets (50 of each strategy). The ramets were distributed randomly over the lattice. The initial step represented the beginning of a growing season after winter. We did not consider disintegration of ramet networks caused by shoot death, networks broke up only during winter. We did not model ageing or age-related ramet and genet demography. The equilibrium ramet density of single-strategy simulations was used to distinguish between extinction (density = 0) or survival (density > 0) of a strategy at a given parameter combination.

The competition runs were checked every 100 time steps, and the simulation was terminated when one or both of the strategies had died out. Coexistence did not occur, resulting in the following three possible outcomes: the *plastic* strategy

won; the *nonplastic* strategy won; or both strategies died out (this outcome was very rare). We conducted 51 replicate simulations for each parameter combination, and characterized them by the percentage of repetitions in which one of the *plastic* strategies won the competition.

We used Kruskal–Wallis tests to compare the times to exclusion at different specialization speeds of the plastic strategies. In cases of significant difference, we used *post hoc* comparisons of mean ranks to identify the groups differing in exclusion times. The time to exclusion varied largely between parameter combinations (about 1000–100 000 steps).

Results

For all simulations reported here, we chose values for the constant parameters k , m and l that ensured the viability of monocultures (no competition) in the widest possible range of environments ($k = 0.2$, $m = 0.1$, $l = 20$). Nevertheless, the *nonplastic* strategy was not viable in a small region of the parameter space in which the spatial correlation between the resources was negative ($p_{11} \leq 0.2$, for both resource contents) and the environment was temporally variable ($e > 0$). Both *plastic* strategies could survive in these environments. The general viability of strategies implies that extinction of a strategy in competition was caused by competitive exclusion.

The two *plastic* strategies (A and C) won the competition against the *nonplastic* strategy (N) in a large parameter region (Fig. 4). In environments with equal availabilities of the two resources, the *plastic* strategies outcompeted the *nonplastic* strategy in a similar parameter region, indicating that the ability for specialization was the major factor determining the outcome of competition. Overall, the *coordinated* strategy was more successful in outcompeting the *nonplastic* contestant than the *autonomous* strategy (Fig. 4).

In environments with a negative spatial correlation between the availability of the two resources (left-hand side of all graphs in Fig. 4), the *plastic* strategies consistently outcompeted the nonplastic strategy. This is caused by the following two facts. (1) Opportunity costs of specialization are limited under these conditions: in stable environments, opportunity costs appear only for ramets of the *coordinated* strategy growing in GG sites. These sites are rare when resources show a strong negative correlation in space. At higher values of environmental change (e), both *plastic* strategies incur mis-specialization costs in sites of all qualities. (2) The proportions of GB and BG sites increase with an increasing negative correlation between resource availabilities (decreasing p_{11}). These sites induce specialization and provide *plastic* strategies with the opportunity to benefit from their ability to functionally respond to environmental variation.

The *plastic* strategies won the competition against the *nonplastic* strategy in all stable environments (first row of all graphs in Fig. 4). Conversely, the *nonplastic* strategy won at higher degrees of temporal change (e), suggesting a reversal

of the cost–benefit balance of plasticity with increasing small-scale environmental fluctuations. However, this transition (borderline between the winning regions for *plastic* and *nonplastic*) also depended on the spatial correlation between resources (see below).

The rate at which ramets could change their root–shoot allocation in response to environmental quality (r_{step}) did not affect the outcome of competition between the strategies (compare the three rows of graphs in Fig. 4). However, this parameter did determine the speed of competitive exclusion in *plastic–nonplastic* competition runs (Kruskal–Wallis tests, $P < 0.01$ in all cases). At small values of r_{step} (slow specialization response), it took significantly longer to decide the outcome of competition than at higher values of r_{step} (fast specialization). This was revealed by *post hoc* comparisons of mean ranks (in 84 from 89 cases for C–N competition and 86 from 89 cases for A–N competition).

In environments with unequal resource content, the *autonomous* strategy won the competition against the *nonplastic* strategy in a smaller parameter region (at lower e at given values of p_{11}) than in habitats with equal availabilities of the two resources. The overall pattern, however, was similar (compare Fig. 4d–f, j–l). In contrast to the *autonomous* strategy, resource inequality did not affect the parameter region within which the *coordinated* strategy outcompeted the nonplastic contestant (compare Fig. 4a–c, g–i). This can be explained by the fact that the performance of *autonomous* plants is always limited by the globally least abundant resource, while this is not true for *coordinated* plants. Modular coordination of plastic responses allows for a compensation of resource imbalances in the environment by unequal specialization for the two resources, making this strategy robust against changes in relative resource abundances. As a consequence, *coordinated* is a much more successful competitor against *nonplastic* than *autonomous* in environments with unequal resource content. The difference in performances between the two *plastic* strategies was also greatest at unequal resource content (Fig. 4).

The borderline between the winning regions of *plastic* and *nonplastic* strategies was not vertical (as expected if spatial correlation of resources is the decisive factor), nor horizontal (as expected if temporal patch dynamics were the dominating factor), but diagonal, reflecting an interplay between spatio-temporal effects. Patch persistence (proportion of sites unchanged from a given quality) is a good predictor for the outcome of competition between the *plastic* and *nonplastic* strategies. *Plastic* wins if patches inducing specialization (high-resource sites) are persistent in time. The superiority of the *plastic* strategies declines with decreasing patch persistence. Patch persistence changes along diagonal lines in Fig. 4 and, for some qualities, coincides with the borderlines between the winning regions of *nonplastic* and *plastic* strategies (see Supplementary Material).

Patch persistence allows for an exact quantification of the conditions characterizing the transition between the parameter

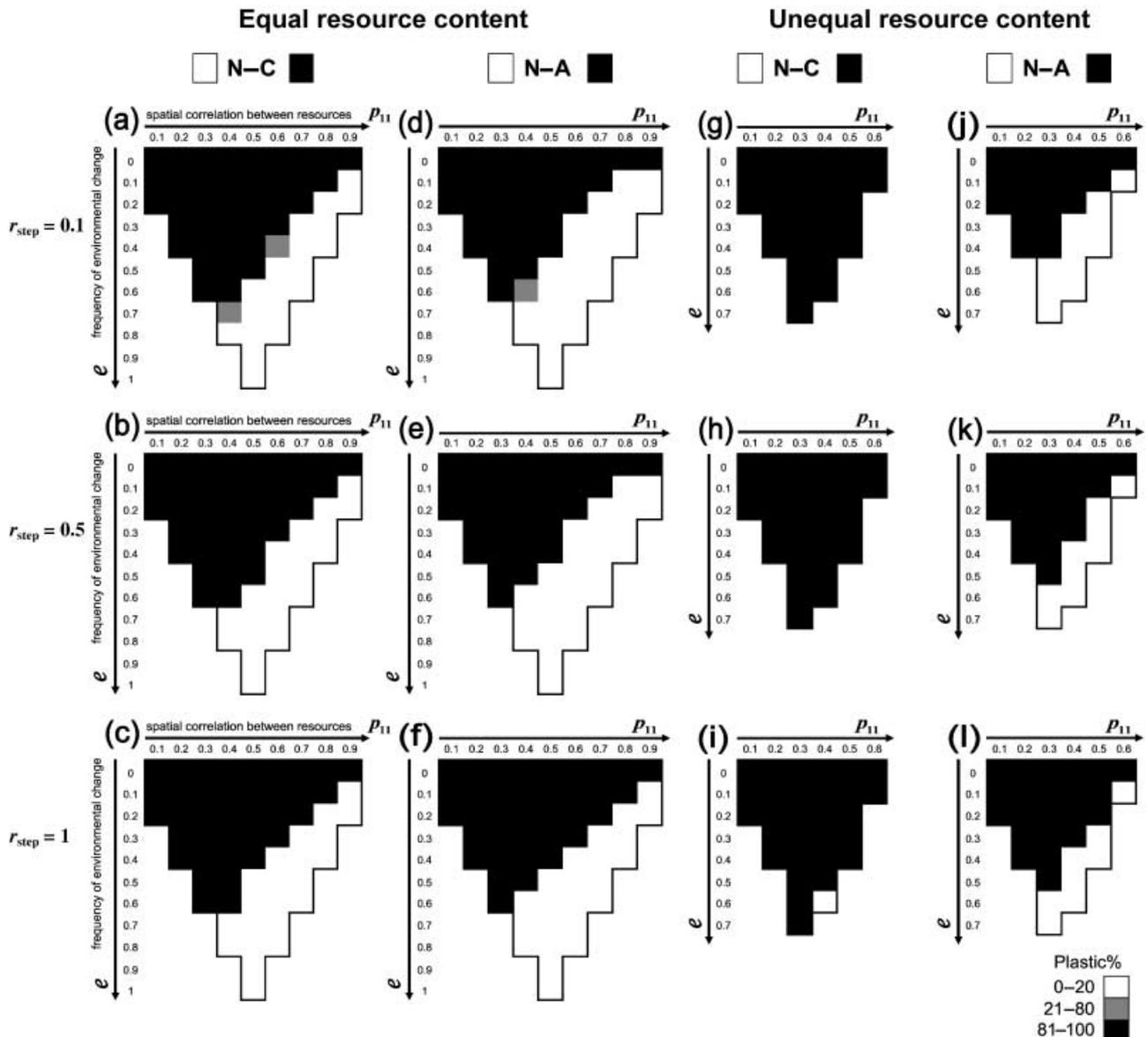


Fig. 4 Results of the pairwise competition runs. The two competing strategies are marked in the caption of each column. Each parameter combination is characterized by the winning percentage of the plastic strategy from 51 replicate runs. Black, the plastic strategy (*coordinated*, C or *autonomous*, A) wins; white, the nonplastic strategy (N) wins; grey, intermediate outcome.

regions in which *nonplastic* or *plastic* strategies are more successful competitors. At equal resource content, *nonplastic* wins over *coordinated* if < 50% of GB and BG sites remain unchanged during one time step. In these cases, patch persistence of GB and BG sites is < 50%. The same pattern holds for the *autonomous* strategy, but with slightly more variation around the 50% borderline. At unequal resource content, *nonplastic* wins against *autonomous* if persistence of BG sites is < 50%. In other words, persistence of those sites that are rich in the generally least abundant resource correlates best with the outcome of competition. The *coordinated* strategy is not sensitive to such changes in rare, rich sites, and thus wins

in all parameter combinations if resources are unequally abundant. Nevertheless it should be noted that persistence of GB sites is > 50% in all possible unequal environments.

Discussion

Our study clearly demonstrates that modular plasticity is beneficial in many heterogeneous habitats, and that patch persistence plays a key role in determining the success of plastic vs nonplastic strategies. Our results also highlight potential constraints and limitations of plasticity for enhancing plant performance in patchy environments. In a wide range of

the investigated parameter space, plastic specialization for local resource acquisition proved to be a superior strategy to not responding to environmental variation. This was especially conspicuous for relatively stable environments with some degree of negative spatial correlation between the two resources. The results of our study show that coordination of modules is beneficial in virtually all realistic settings, that is, whenever resource supplies in the environment do not closely match the internal resource demands of the plant.

Our model is strategic (*sensu* Czárán, 1998) or rule-based (*sensu* Molofsky & Bever, 2004), as opposed to tactical (*sensu* Czárán, 1998), implying that its primary aim is to obtain a better conceptual understanding of the modelled mechanisms and phenomena, rather than to simulate natural processes as realistically as possible. The focus of this approach is on qualitative predictions and the generation of hypotheses, rather than on quantitative analyses of complex interactions. Results and predictions of strategic models should therefore be interpreted qualitatively rather than quantitatively. For instance, the general success of plastic strategies in our model does not mean that plasticity should be universal, but it suggests that plasticity is likely to be favoured by natural selection in a broad range of heterogeneous habitats. Factors not included or not screened in the model (e.g. the speed of resource exchange between ramets, the contrast in resource availability between good and bad sites) are likely to quantitatively modify the patterns predicted by the model.

Our results confirm the general expectation (Stuefer & Hutchings, 1994; Stuefer *et al.*, 1996; Alpert & Stuefer, 1997) that plastic division of labour in clonal plant networks is beneficial in environments with fine-grained resource complementarity. Our study undoubtedly indicates that the beneficial effects of division of labour extend beyond the parameter combination covered by empirical studies ($p_{11} = 0$, $e = 0$) and suggests a considerable ecological potential of this strategy in several types of environment. Natural habitats with a negative correlation in the availability of two resources include systems in which water and light supplies are complementary as a consequence of a shade-caused reduction of transpiration rates (Stuefer & Hutchings, 1994; Stuefer *et al.*, 1996; Sampaio *et al.*, 2004); nutrient-poor habitats with nitrogen-fixing bushes that both enrich the soil locally and reduce light availability (Alpert, 1991; Friedman & Alpert, 1991; Alpert, 1996; Alpert & Mooney, 1996); and salt marshes where high-light and competition-free patches tend to show higher salt concentrations than more shaded patches (Evans, 1991, 1992; Evans & Whitney, 1992; Pennings *et al.*, 2005).

Our findings corroborate the prediction that benefits of plasticity should be highest in spatially variable, but temporally stable environments, while these benefits should decrease at higher rates of environmental change (Schlichting, 1986; Scheiner, 1993; Coleman *et al.*, 1994; Ackerly, 1997). This trend is indicated by the fact that the nonplastic strategy consistently outcompetes plastic strategies in highly dynamic

environments (Fig. 4). DeWitt *et al.*, (1998) identified two phenomena relevant to our model to constrain the profitability of plasticity in temporally variable environments. The 'information reliability limit' implies that plastic organisms may produce maladapted phenotypes when the environmental cues inducing plastic responses do not reliably predict the quality of the microhabitat (Ackerly, 1997; DeWitt *et al.*, 1998; Wong & Ackerly, 2005). Our simulations clearly confirm the existence of an information reliability limit as the nonplastic strategy outcompetes plastic contesters in temporally highly variable environments in which plasticity-inducing cues become unreliable.

The 'lag-time limit' on plasticity implies that the benefits of plasticity decrease or disappear as temporal variation approaches the maximum rate at which plants can express plasticity (Ackerly, 1997; DeWitt *et al.*, 1998). The lag-time limit should be most conspicuous for slow developmental processes such as changes in biomass allocation. To obtain a functional response, patches should last longer than the response time of modules, indicating a pivotal role of patch persistence for determining the profitability of plasticity. Contrary to our prediction (hypothesis 3), we could only partially confirm the existence of a lag-time limit in our system. The speed of specialization affected the time to competitive exclusion, but had a negligible effect on the final outcome of competition between *plastic* and *nonplastic* strategies.

The most important factor determining performance in competition was patch persistence. Spatial division of labour proves unprofitable whenever the patches inducing specialization (GB and BG sites) have a high chance of immediate change (persistence < 50%). Under these conditions, the costs of misspecialization combined with opportunity costs outweigh the benefits of phenotypic responses to environmental variation, and hence cause plasticity to become an inferior strategy. Environments with transient patches will favour nonplastic strategies and impose selection pressures for ignoring the unreliable cues of the environment.

Plastic plant responses may differ with regard to decision-making rules, ranging from primarily supply-driven to primarily demand-driven responses. The decision to specialize for the acquisition of a locally abundant resource can be made at the level of either individual modules or interconnected module groups. The results of our model indicate that the *autonomous* strategy performs nearly as well as the *coordinated* if (and only if) resource abundances in the environment closely match the resource ratio necessary for optimal growth and development. As the model assumes optimal plant performance at equal availabilities of the two resources, all environments with unequal resource supply (Fig. 4g–l) represent a deviation from ideal ratios. Under these conditions, *autonomous* outcompetes *nonplastic* in a more limited range than the *coordinated* strategy does. These results suggest that coordination of ramet behaviour may almost always be beneficial and necessary in nature, as environmental supply and plant demand

ratios for resources such as water, light and mineral nutrients are very unlikely to coincide under field conditions.

Our *coordinated* strategy does not specialize in response to local cues only, but a ramet's decision-making is influenced by the needs of interconnected ramets. This type of specialization has been shown empirically both for trees (between branches of *Pinus sylvestris*, Stoll & Schmid, 1998) and for stoloniferous herbs (*G. hederacea*, Birch & Hutchings, 1994). Birch & Hutchings (1994) grew individuals of *Glechoma* in a spatially heterogeneous environment, where soil resources were concentrated in a small, resource-rich patch, while light availability was spatially constant. Ramets rooted inside and outside the resource-rich patch showed clear functional specialization. Ramets inside the patch allocated a high proportion of biomass to roots, while those outside the patch allocated almost all biomass to shoots. In the context of our model, Birch & Hutchings (1994) created an environment with GB and GG sites for light and nutrients. Ramets of *Glechoma* specialized for the generally most scarce (and hence growth-limiting), but locally abundant resource, as ramets of our *coordinated* strategy do. In both cases, specialization on GG sites is driven by demands of interconnected ramets in the clonal network. Real plants are likely to signal resource demands through source-sink relationships and match supplies to demands by hormonal integration (Taiz & Zeiger, 2002). However, the spatio-temporal degree of this coordination is not clear from empirical studies available to date. In a recent review, de Kroon *et al.* (2005) postulated that modular interaction effects may be common and of central importance in determining a plant's response to environmental variation.

Spatial division of labour in stoloniferous plants can be compared with resource acquisition and commodity exchange in simple economic bartering systems. Two or more trading partners may specialize in the exploitation of locally rich sources, and exchange the surplus of commodities, thereby increasing the efficiency of resource extraction and resource use (Bloom *et al.*, 1985). Space-economic models suggest (Weber, 1927; Isard, 1956; Lloyd & Dicken, 1977; Stuefer *et al.*, 1996) that the benefits of local specialization and cooperation depend on the presence of an efficient and reliable transport system between trading partners, on the temporal stability of resource-distribution patterns, and on a negative spatial correlation between local supply rates of exchanged resources. With the exception of transport reliability, which was not included in the current study, the results of our model support these predictions by showing that plastic division of labour dominates in environments with low temporal variability and with a negative spatial correlation between two essential resources. Our model further shows that the profitability of specialization and cooperation (trading) benefits from the consideration of internal information on nonlocal demands, whenever resource abundances do not match resource needs. This prediction holds for both plants and economic systems.

Stoloniferous and rhizomatous plants are common in

nature and successfully dominate a number of biomes (van Groenendael & de Kroon, 1990; Klimes *et al.*, 1997). Empirical studies have yielded suggestions of what traits could be responsible for this success, and plastic division of labour in response to habitat heterogeneity has been mentioned as one of them (Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997). Our results show that plasticity and modular coordination in resource acquisition is beneficial in a broad range of spatially and temporally heterogeneous environments, suggesting that stoloniferous and rhizomatous plants may benefit from plastic specialization. Our model provides a general framework for the study of benefits, costs and limits of plastic division of labour in a broad range of spatio-temporally heterogeneous habitats.

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Supplementary Material

The following supplementary material is available for this article online.

Details about the simulated environments:

Appendix S1 Method details – some technical details of the model

Appendix S2 Frequency distribution of site types – a proof that the current implementation of environmental change keeps the frequency distributions of site qualities constant over time

Appendix S3 Other possibilities for the implementation of e (temporal change).

Appendix S4 Constraints for e – the formulae for constraints of temporal change

Appendix S5 Proportions of site qualities in different environments

Appendix S6 Persistence of site qualities in different environments

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