Fight or flight: plastic behavior under self-generated heterogeneity

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Abstract Plants are able to plastically respond to their ubiquitously heterogeneous environments; however, little is known about the conditions under which plants are expected to avoid or confront their neighbors in dense stands, where heterogeneity is self-generated by non-uniform growth and feedback between plant interactions and stand heterogeneity. We studied the role of plasticity for spatial pattern-formation and the resulting stand-level fitness of clonal plants, assuming variable types of plastic behavior. Specifically, the adaptive values of behavior ranging from pure avoidance, to neutral and pure confrontation were assessed using a simulation model of stands of clonally growing plants with varying capacity of plastic behavior. The results demonstrated significant effects of the type of competitive behavior on mean final densities of single-species stands at equilibrium. Density was the lowest and aggregation was the highest in stands of purely confrontational plants, and density was highest in stands of neutral and purely avoiding plants. When competing against a neutral photometer (i.e. non-plastic but otherwise identical plant), the best competitors were plants that avoided their neighbors in 0.33–0.50 of the cases and were neutral otherwise. Differences in adaptive values of individual behaviors depended both on the distance over which the environmental structure (i.e. local density) was perceived, and on overall density. Density-independent ramet mortality profoundly changed the effectiveness of competitive behaviors. Under high levels of mortality, avoidance was the most effective and confrontation the least effective behavior. The results indicate that individual-based behaviors might affect higher organizational levels, and that their reciprocal interactions with resource levels and patchiness, and

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responsiveness to density-independent mortality might generate higher-order feedbacks that intricately affect the fate of individual ramets and the patterning of whole stands and communities.

Keywords Architecture · Avoidance · Behavior · Confrontation ·
Density-independent mortality · Natality · Perception distance · Simulation model

Introduction

The immediate environments of naturally growing plants are invariably heterogeneous in both space and time (Bradshaw 1965; Levins 1968; Sultan 1987; Hutchings and de Kroon 1994; Caldwell and Pearcy 1994). Environmental heterogeneity might result from biological interactions such as competition (e.g. Chesson et al. 2004, Novoplansky 2009), herbivory (Parker and Salzman 1985) and pathogens (Stuefer et al. 2004), or from abiotic factors such as resource patchiness (e.g. Wijesinghe and Hutchings 1997; Crick and Grime 1987; Farley and Fitter 1999; Hodge 2004) and physical stresses (e.g. Salzman and Parker 1985). Due to their limited motility, plants have acquired a wide array of deterministic and plastic adaptations to their ever-changing growth conditions (Bradshaw 1965; Levins 1968; Schlichting 1986; Sultan 1987; Schlichting and Pigliucci 1998; Trewavas 2003).

However, the adaptive value of phenotypic plasticity is limited by various environmental and developmental factors (Levins 1968; DeWitt et al. 1998). An important limitation is the time required for the execution of adaptive plastic changes, which may, under high levels of environmental heterogeneity, render plastic responses maladaptive by the time their products are fully functional (DeWitt et al. 1998). Therefore, natural selection is expected to promote the responsiveness to environmental cues that bear information regarding probable future growth conditions (Aphalo and Ballare 1995; Novoplansky 2009). Perhaps the best known example of plants' ability to anticipated future growth conditions is their responsiveness to spectral red/far-red cues, which are strongly correlated with future levels of light competition (Smith 2000). In addition, plants have been demonstrated to respond to anticipatory signals related to herbivory (Kessler and Baldwin 2002), nutrient supply (Forde and Zhang 1998; Zhang and Forde 1998), physical stresses (Ackerson and Youngner 1975; Passioura 1988), and competition (Novoplansky 2009).

Under competition, plants are able to utilize different categories of competitive behaviors based on their expected adaptive values (Novoplansky 2009). Perhaps the least costly and typically most beneficial (in absolute terms) is *competitive avoidance* whereby plants or plant parts grow in ways that minimize competitive interactions with their neighbors. However, commonly plants may also benefit from active aggressive *confrontation,* or simply cannot avoid their neighbors and are thus bound to confront them. Under such conditions plants are selected to increase their dominance via maximizing resource uptake and allelopathy, which commonly result in competitive arms races and significant (absolute) costs (Cohen 1969; Novoplansky et al. 1990a; O'Brien et al. 2005). These interactions often generate size and vigor inequalities that are self-amplified by the increased ability of a few dominant individuals to preempt resources and suppress their weaker neighbors (Weiner et al. 2001). Additionally, smaller or competitively-weak plants are selected to increase their tolerance to lower resource levels (Valladares and Niinemets 2008; Chambers and Aarssen 2009; Novoplansky 2009).

Almost invariably, different parts of the same plant develop under variable availabilities of light, water, nutrients, and various stresses (Snow 1931; Drew 1975; Jones and Harper

1987; Salzman and Parker 1985; Went 1973). Due to their emphasized horizontal spreading, clonal plants are subjected to great spatial variation in competitive interactions (Purves and Law 2002). The response of clonal plants to environmental heterogeneity has been studied extensively (Caraco and Kelly 1991; Hutchings and de Kroon 1994; Oborny and Cain 1997; Oborny and Kun 2001). It has been shown that the adaptive value of plastic responses to environmental heterogeneity is dependent on frequency, spatial arrangement, contrast and grain of favorable and poor patches. It has been suggested that under field conditions, plastic responsiveness might be relatively rare, mainly due to limited predictability of resource distributions and resolution mismatches between environmental heterogeneities and plant responsiveness (Oborny 1994a, b; Novoplansky 1996, Dong et al. 2002; de Kroon et al. 2009).

All existing studies, however, have been based on the assumption that environmental heterogeneity is external and independent from the effects of the responding plant on the environment. However, any realistic depiction of plant growth must take into account a non-uniform placement of plant organs and individuals in space and time due to developmental and competitive constraints on plant growth, and their key contributions to the heterogeneity experienced by the plant (e.g. Chesson et al. 2004, Novoplansky 2009). This is exemplified by the existence of different encroachment strategies such as phalanx (short internodes and dominant intra-clone interactions) vs. guerrilla (long internodes and weak direct intra-clone interactions); (Lovett-Doust 1981). Such self-imposed heterogeneities may further complicate growth responses through interactive feedbacks (e.g. Lafarge et al. 2005, Sheffer et al. 2007; Gilad et al. 2007) and are therefore likely to affect the adaptive values of individual response types in non-trivial ways.

The recursive and autocorrelated nature of their growth and spatial arrangement may potentially allow clonal plants to make accurate developmental decisions regarding future growth and branching that are correlated with anticipated types and levels of competition. Specifically, we hypothesize that plants are able to shift between avoidance and confrontation competition based on their anticipated adaptive value.

In the current paper, we examined the adaptive value of various types of competitive behaviors in an artificial system of clonal plants. Specifically, we examined the consequences of competitive avoidance, aggressive confrontation and lack of responsiveness (neutrality) in plant stands, where all environmental heterogeneity resulted from past growth and interactions (self-generated heterogeneity). This approach enabled studying the role of developmental feedbacks in quasi-realistic heterogeneous settings, and to specifically examine the potential significance of intrinsic feedbacks between developmental decisions and their effects on the spatial structure of the stand.

Because the adaptive value of any decision is critically dependent on the quality of the information it is based on, we examined how the adaptive values of different competitive behaviors are affected by the distance over which environmental information is perceived, relative to internode length (i.e. distance between the parent and offspring ramets). Further, we examined whether the adaptive values of the mentioned competitive behaviors varied with stand density, which we introduced by varying density-independent mortality.

To address these questions we employed a spatially explicit simulation model of plant growth (Herben and Suzuki 2001; Wildová et al. 2007; Herben and Novoplansky 2008). Growth decisions were modeled so clonal ramets were allowed to use information regarding the density and potential competitive structure of their neighborhood to determine the directions of new daughter ramets. These behaviors were examined in both single "species" stands, and in mixtures of responsive and neutral "species".

Methods

The model

The model simulates vegetative growth of clonal plants, with nodes and their immediate internode as the basic modular growth units. The model runs on a continuous plane with toroidal boundaries. The simulation plane is homogeneous; any heterogeneity is generated by the ramets themselves. The model uses traits of ramet growth, allocation, competitive ability, and spacer (rhizome) architecture to simulate long-term population dynamics. For a detailed description of the model see Herben and Suzuki (2001); Wildová et al. (2007) and Herben and Novoplansky (2008).

For the sake of simplicity modeled ramets have fixed sizes. The ramets produce "resource" that is used for rhizome growth. The resource is a virtual representation of a limiting resource that is either gathered by the ramets from the environment (e.g. water, nutrients) or synthesized by it (photosynthate), the production of which is density-dependent. The rate of resource acquisition by a ramet is a function of competition with neighboring ramets; at each time step, the amount of resource produced within each ramet is constrained by the number of ramets in its neighborhood, to account for neighborhood competition. This amount can be positive or negative, the latter if the competitive effects of neighboring ramets is strong. All ramets within the local neighborhood, i.e. a circle with the focal ramet in its center and a radius of neighborhood size are taken into account. Neighborhood size, just as all other distance measures (internode length), are expressed in arbitrary units (size of the simulation plane = 1).

The resource is supplied to the node bearing the ramet. Resource levels at each node change according to resource acquisition by the ramet attached to that node (which in turn depends on habitat productivity, see Table 1), and its allocation to growth. Unused resource is held at the node and it may be used for further growth or branching at subsequent steps; no maintenance is modeled as pilot simulations have shown that the effects of maintenance are rather additive to the effects of productivity.

Rhizomes grow by adding nodes at terminal positions; the ramet at the original node dies whenever the spacer system grows; new ramet is then formed at the newly added terminal node (i.e. only replacement growth is modeled). Therefore, ramets are by definition, attached to all growing terminal nodes. New nodes are added to terminal nodes if the quantity of the resource at the existing terminal nodes is sufficient. The resource at the node is reduced once by the cost of the newly developed internode upon its addition. Whereas the fact of growth depends on the resource available at the node, the length and angle of new internodes are drawn from a gamma distribution with CV = 0.1 (internode length) or from a normal distribution with SD = 5° (branching angle) and are independent of the amount of resource of their rhizomes and the density of ramets or rhizomes in their neighborhood. New nodes form only when the mother nodes contain sufficient resource for their formation. After a new node is added, part of the resource content of the maternal node is transferred to the daughter node. Apart from this process, no resource translocation is implemented in the model. Positive resource levels means that the ramet maintains itself to the next step but when the resource balance is negative, the node bearing the ramet loses its capacity for further growth and dies.

Further, nodes are added to a rhizome by terminal branching (i.e. by adding two instead of one terminal node to a maternal node within a single time step). Branching takes place only if the available quantity of resource at that node is sufficient. Similarly to growth, branching angles are independent of resource content of the rhizome and its neighborhood.

Table 1 Parameters of the model

Name	Units	Base values	Other values tested	Definition
Architectural parameters				
Internode length	Distance	0.01	0.03, 0.05, 0.07, 0.1	Mean internode length
Branching angle	Degrees	40		Angle between mother rhizome and its daughter branch
Node lifespan	Time	20		Lifespan of the node and the adjacent internode
Probability of branching	Time	0.01		Probability of formation of a lateral ramet from a dormant bud
Resource and competition parameters				
Productivity	Resource/time	5		Productivity of the environment
Density dependent growth	Area	0.2		Intensity of density-dependence processes on resource accumulation
Mortality	Dimensionless	0	0.1, 0.2, 0.3	Density-independent mortality of ramets per step
Resource fraction put into new daughter ramet	Dimensionless	0.7		Fraction of the internal resource available at the mother node that is translocated to the daughter node at the moment of its formation
Neighbourhood size	Distance	0.05		Radius of the neighborhood size
Branching plasticity parameter	Dimensionless	0.5	(i) series 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1 (ii) series 0, 0.25, 0.5, 0.75, 1	Probability of a new branch to be placed in a direction of lower density
Searching distance	Distance		0.005, 0.05, 0.07, 0.1	Perception distance used for branching decisions

Distances are expressed as fractions of the simulation plane

Time is expressed as time steps

Modeled plants vary in their capacity to respond to their environment when they branch. Before they branch, they scan density of other ramets in both left and right directions. This is done by projecting future direction over a specified distance (parameter "Searching distance") to a point and counting ramets in the circle with the radius of neighborhood size around that point. This information is used to make a decision which direction to take using the branching plasticity parameter which determines the probability that the new branch will be placed in the direction of lower density. Accordingly, the plasticity parameter is 0 in plants that invariably branch in the direction of higher density (confrontational), 1 in plants that invariably branch in the direction of lower density (avoiding), and 0.5 in plants that are not responsive to the information about density heterogeneity.

When a branch-bearing node dies, the branch becomes independent and the rhizome fragments into two disconnected units.

Model parameterization and simulation experiments

The model was parameterized to represent a clonally-growing plant with ramets that had no ecologically relevant variation in size. The simulation plane was assumed to represent an area sufficiently large to cover reasonably large rhizome systems of the plant. Parameter values were selected to approximate values of previously studied stands of a clonal grass (e.g. *Festuca rubra*, *Deschampsia flexuosa* or *Nardus stricta*) of a temperate mountain short-turf grassland in an area of 0.25×0.25 m (Table 1, Herben and Suzuki 2001; Wildová et al. 2007).

Simulation experiments were run to test the effect of the branching plasticity parameter and its interactions with other relevant parameters on plant performance in equilibrium stands. The effects of different combinations and levels of plasticity parameter, searching distance, internode length, resource level and density-independent mortality were examined in the single- and two-species systems (values used are detailed in Table 1). Two types of simulation experiments were conducted:

(i) *Single species experiments.* These experiments were initiated with 20 randomly distributed ramets and were run for 100 steps; pilot experiments showed this was sufficient to attain equilibrium in ramet density and architectural parameters. Data on ramet density, architectural parameters and spatial structure were collected after the end of each experiment. To calculate spatial autocorrelations, ramet densities were converted to grids of 100×100 cells and Moran's I values were calculated for lags of 1–10 cells (Upton and Fingleton 1985). Because the neighborhood size was 0.05 of the simulation plane in all runs (Table 1), a lag of one cell approximately corresponded to 0.2 of the neighborhood size and thus the range of values used covers both smaller and larger ranges than the neighborhood size. At least two hundred replicate runs were used in each experiment.

(ii) *Two-species experiments.* In these experiments, a plant with the tested value of the plasticity parameter was tested against a neutral "phytometric" plant, i.e. a plant with exactly the same values of all parameters except for the plasticity parameter, which was set to 0.5 to render it neutral. These experiments were initiated with 20 randomly distributed ramets of each plant and were run for 200 steps. Preliminary tests demonstrated the importance of longer runs to allow sufficient time for the effects of competition to occur. Pilot simulations showed that increasing the number of steps beyond 200 did not affect the qualitative behavior of the system.

Results

The plasticity parameter affected the mean final density of single-species stands at equilibrium. Confrontational plants had many fewer ramets than neutral plants and avoiding plants had slightly more ramets than neutral plants (Fig. 1). Confrontational plants also had slightly different architecture; they branched more than neutral and avoiding plants (Fig. 1).

Spatial structure of equilibrium stands was primarily determined by internode length and did not vary strongly with the plasticity parameter. There was a dominant positive spatial autocorrelation of ramet density over values of lag corresponding to internode length (Fig. 2, solid lines). Further, in short-internode plants, there was a pronounced drop
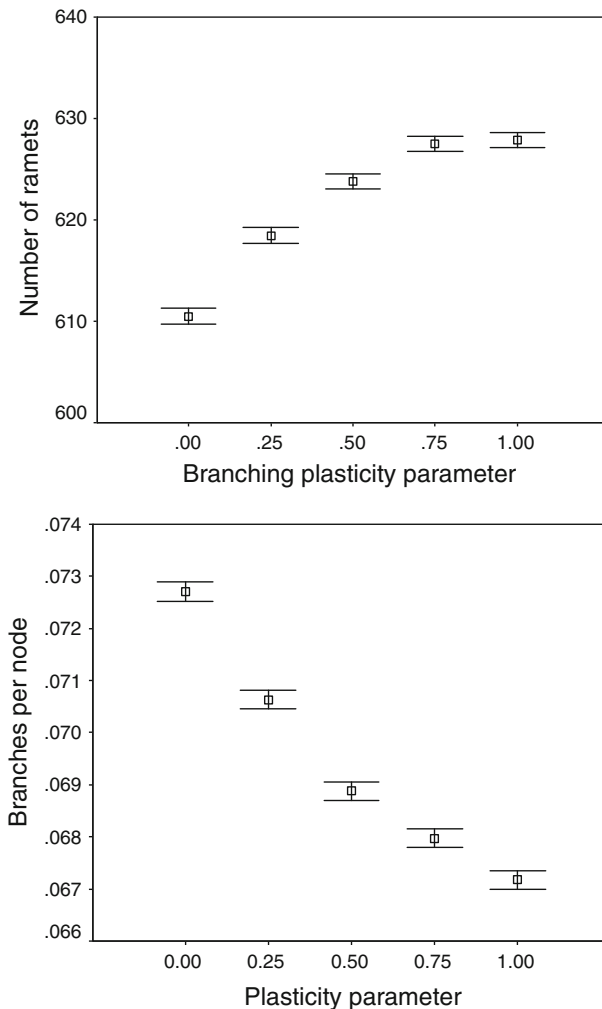

Fig. 1 Effect of branching plasticity parameter (0 means always confronting; 1—always avoiding; 0.5—neutral plants) on number of ramets and architecture of the short-internode plant. Mean and standard error of 1,000 replicate runs of 100 steps; internode length 0.01 (arbitrary units)
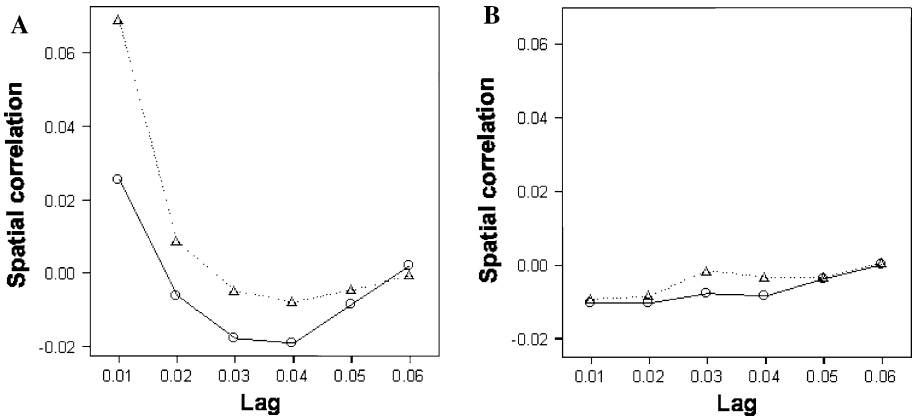
A

B

Fig. 2 Spatial structure of stands of neutral plants of two internode lengths (**A**—internode length 0.01, **B**—internode length 0.05) under two levels of density-independent mortality (*circles*—no mortality; *triangles*—0.3 mortality per ramet per step). Internode length and spatial lag are expressed in the same arbitrary units. Moran's I is used as a measure of spatial correlation. Means of 200 replicate runs, 100 simulation steps

Fig. 3 Effect of branching plasticity parameter on spatial structure of stands after 100 time steps of single short internode (0.01) plant species. Moran's I is used as a measure of spatial correlation. Spatial lag and internode length are expressed in same arbitrary units. Means of 200 replicate runs. Plasticity parameter of 0 means confrontational plants, 1 avoiding plants, and 0.5 neutral plants
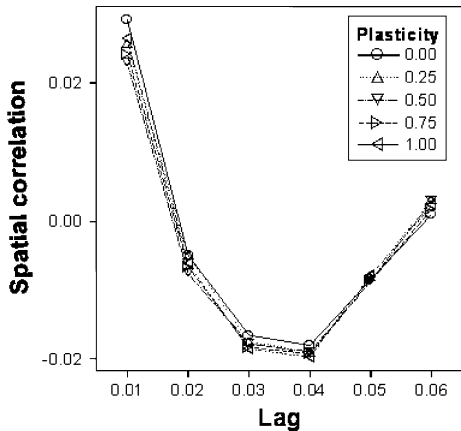
in spatial autocorrelation of ramet densities to negative values in lags larger than internode length and smaller than the interaction distance, thus demonstrating the predominance of cluster size. However, the plasticity parameter did have some, albeit minor, effects on the fine-scale spatial structure of the stand. Densities of confrontational plants showed slightly greater aggregation than those of avoiding and neutral plants at shorter autocorrelation distances (Fig. 3).

The effect of the plasticity parameter on plant performance strongly interacted with the plant's spatial growth parameters, internode length and searching distance (Fig. 4). The differences between plant behaviors were most pronounced when the values of these parameters matched: confrontational plants then invariably had the lowest performance, and in most cases, the avoiding plants performed slightly better than the neutral plants. The differences between plant behaviors were greater when both internode length and searching distance were smaller than the neighborhood size. When searching distance was much
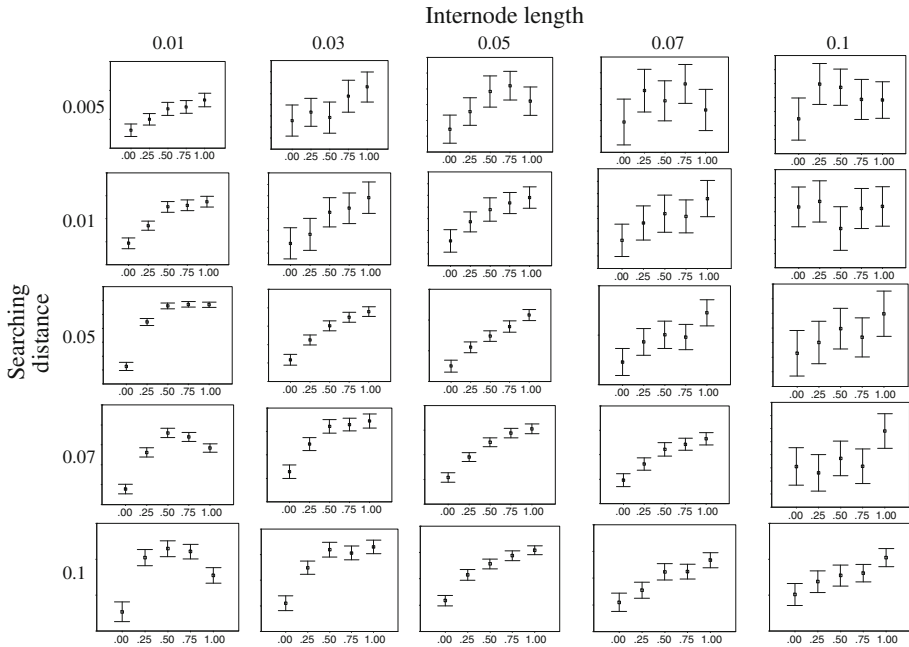
Fig. 4 Total number of ramets after 100 steps of monocultures of identical plants differing in plasticity, internode length and searching distance. Each block depicts five plants with increasing values of the plasticity parameter: 0—invariably confrontational; 0.5—invariably neutral; 1.0—invariably avoiding. Both internode length and searching distance are expressed using the same arbitrary units. Means and standard errors of ramet numbers from 100 replicate runs

shorter than the internode length, essentially no significant differences could be found between the performances of the different plastic behaviors. In contrast, when the searching distance was greater than the internode length, the differences between the plastic behaviors was similar in short-internode plants (i.e. where internode length was smaller than the interaction distance), but varied in long-internode plants, with neutral plants performing much better than both confrontational and avoiding plants (Fig. 4). Searching distance had no discernible effect on the spatial structure of the stands (data not shown).

Competition between plastic and neutral plants showed even more pronounced patterns than those of single species stands. Both confrontational and avoiding plants were worse competitors than neutral plants, although the difference was much higher for confrontational than for avoiding plants (Fig. 5a). A detailed analysis of the range of the plasticity parameter demonstrated an optimum value of the plasticity parameter around 0.6–0.7. Accordingly, plastic plants were the best competitors against neutral plants when they avoided their neighbors in 1/3 to 1/2 of the cases and behaved neutrally in the remaining cases.

As expected, density-independent mortality of ramets strongly decreased overall ramet density (Fig. 6) and profoundly changed the effect of the plasticity parameter. Under high mortality (i.e. more sparse stands), avoiding plants were doing significantly better, and confrontational plants much worse, relatively to neutral plants. The same effects were shown in species mixtures (Fig. 5). In contrast to competition under no density-independent mortality, where partially-avoiding plants were favored, non-zero
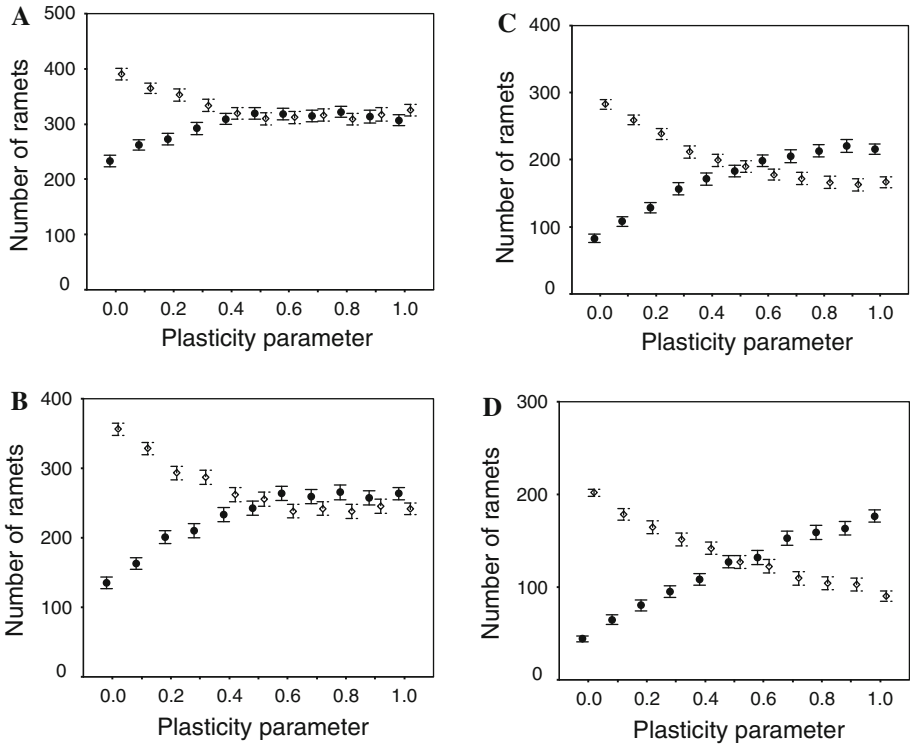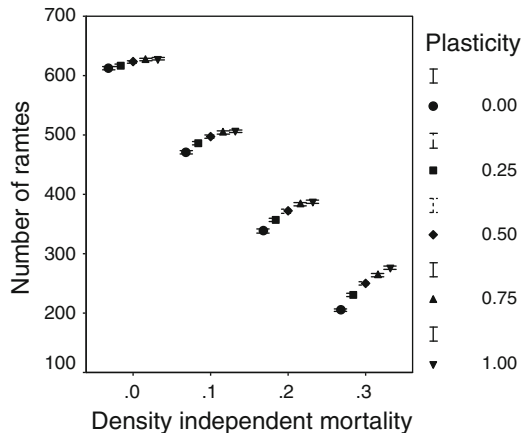
Fig. 5 Effect of density-independent mortality on the effect of the plasticity parameter in mixtures of two short-internode (0.01) species. One species (*closed circles*) has the given value of the plasticity parameter (from 0—invariably confrontational, to 1—invariably avoiding), the other is a neutral photometer (*open diamonds*) with plasticity parameter = 0.5. The system was initiated with twenty ramets of each species and ran for 200 steps. **A**—without density independent mortality, **B**—probability of density independent mortality per step = 0.1, **C**—probability of density independent mortality per step = 0.2, **D**—probability of density independent mortality per step = 0.3

Fig. 6 Effect of density-independent mortality on the effect of branching plasticity in a short-internode (0.01) plant after 100 time steps. Inserted legend indicates values of the plasticity parameter: 0—invariably confrontational; 1—invariably avoiding). Data represent means and standard errors of 200 replicate runs

mortality conferred a large advantage to strictly avoiding plants, and their advantage increased with increasing density-independent mortality (Fig. 5). The introduction of density-independent mortality also eliminated much of the negative spatial correlations, and short-range positive correlations in ramet density became more pronounced in short-internode plants (Fig. 2, dotted lines).

Discussion

Through the perception of neighbors, plants are able to anticipate competitive interactions and modify their competitive behaviors to suit their long-term gains (Aphalo and Ballare 1995). Specifically, plants may minimize competitive encounters by *avoiding* their neighbors, or maximize their competitive effects by aggressively *confront* their neighbors (Novoplansky 2009). Our results suggest a few adaptive differences between these behaviors, implying that individual plants might plastically switch between these behaviors in response to various spatial and temporal attributes of their neighborhood structure, neighbor-perception horizon and morphology.

Both density in single-species stands and competitive performance against neutral phytometers demonstrated similar trends and context dependencies. Under most scenarios, all out confrontation was the worst strategy and the optimal strategy was either full avoidance or a combination of avoidance and neutrality. Differences in the adaptive values of individual behaviors depended on both the distance over which the environmental structure (i.e. local density) was perceived, and the overall stand density. Specifically, avoidance was more successful than confrontation under low density, i.e. under high external mortality, and confrontation was relatively more successful under low mortality and high density.

These general patterns can be understood in terms of the spatial structure of the resulting stands. It has been shown that exploitative behavior (i.e. avoiding places with high density) can be adaptive only if the size of favorable patches is larger than parent-offspring distances (internode lengths) (reviewed in Oborny and Cain 1997). When dense stands develop under low mortality levels, the ranges of positive spatial correlations (i.e. sizes of favorable patches) do not exceed parent-offspring distances, which readily result in negative correlations over larger distances (Fig. 2). Therefore, developmental decisions that are predominantly based on the perception of the immediate neighborhood are prone to be maladaptive due to the plant's inability to perceive, and to efficiently and rapidly enough adapt to changes in the competitive neighborhood over greater distances. Thus, the nature of self-generated heterogeneity, derived from local interactions and spatially constrained natality, might in itself constrain the extent to which environmentally-informed decisions can be adaptive. In contrast, introducing external mortality not only lowers overall density but also changes the structure of self-generated heterogeneity, and triggers the formation of larger openings within clumps and cause larger-scale negative correlations to become much less pronounced (Fig. 2). At such spatial structures, the information perceived from the immediate neighborhood is much more predictive of the longer-range growth conditions of the ramet, making avoidance the most successful behavior.

While earlier studies (reviewed in Oborny and Cain 1997) dwelled on the effects of externally-imposed heterogeneity of variable structures, the present study deals solely with *self-generated heterogeneity,* resulting from non-uniform growth and depletion effects of the plants on their immediate environment. Such heterogeneities are sufficient to account for the generation of strong short-range spatial structures (e.g. Smethurst and Comerford

1993, Sheffer et al. 2007) and are expected to be common in stands of clonal plants, whose densities are invariably variable (Herben et al. 2007). Our results show that under some circumstances, a feedback between spatial structure and plastic behavior might exist, whereby confrontational behavior is strengthening both short-range positive- and longer-range negative spatial correlations. This was clearly demonstrated by confrontational behavior whose direct effects included the placement of new ramets in close proximity of already existing ramets.

The results demonstrate that the relative adaptive values of the competitive behaviors were strongly determined by the "perception grain" of the plants. Specifically, the adaptive differences between the competitive behaviors become more pronounced when the perception range is commensurable or larger than the distance between parent and offspring ramets. In such cases, the perceived information is most accurate and predictive of the fate of the potential offspring ramets. However, when the perception range of the parent ramet is smaller or greater than the projected future position of the offspring ramet, the differences between the adaptive values of the different competitive behaviors diminish, as the perceived information is rendered irrelevant. This result reflects the interplay between three spatial variables: neighborhood size, internode length and perception distance, whose matching leads to a net fitness difference between the competitive behaviors. Because the length of horizontal clonal spacers is often deterministic (e.g. Huber et al. 1998, Alpert and Simms 2002), it is expected that selection will mainly maximize the mentioned spatial matching by fine tuning of the perception and responsive ranges over which plants anticipate competitive interactions. Although plants are known to vary in their sensitivity to perceived cues regarding the proximity of their neighbors (e.g. Smith 1982, Schmitt et al. 2003), further work is needed to test this prediction directly.

In the studied system, confrontation was never beneficial in absolute terms, although its performance was relatively the best at high densities and relatively worst under low density/high mortality, indicating that at high density confrontation is the least selected against rather than being selected for. Under these conditions, typical to relatively productive habitats, plants are almost invariably engaged in fierce and highly costly arms race for the domination of limited resources (Novoplansky 2009). Nevertheless, the numerous examples for both direct and indirect "effect competition" (sensu Goldberg 1990) suggest that confrontational behavior is widespread and serves as an important selective force in a variety of ecosystems (Goldberg and Barton 1992; Keddy 2001). Accordingly, we suggest that its poor performance (in absolute terms) in the modeled system is most likely resulting from the two-dimensional nature of the model, which did not allow plants to confront each other in the vertical dimension. As horizontal interactions can only be symmetric, even relatively vigorous plants that assume aggressive (confrontational) behavior cannot take advantage of the potential benefits conferred by their asymmetrical overtopping of their weaker neighbors (Novoplansky 2009), although the current results indicate its success would depend, inter alia, on parameters regulating overall density, such as external mortality and background stress levels. Nevertheless, although such a two-dimensional model might reasonably depict the dynamics and expected behavior of short-statured plants and bryophytes (During and Lloret 2001), a more elaborate model, which also captures plant structure and development in the vertical axis is needed to study taller-statured plants which are often engaged in strong competition for light. More careful examination of competitive behaviors may also benefit from the inclusion of more structured translocation patterns.

Although self-generated heterogeneity is ubiquitous, its effects are expected to depend on the disturbance frequency and thus the successional stage. In early successional stands and under high disturbance frequencies (corresponding to high mortality in our system),

stands are inherently sparse and patchy at the level of the individual plant. In such cases, avoidance behavior is likely to be favored due to the high predictability of the open patches and the relatively high reliability of the environmental information regarding the expected openness of unpopulated patches (Novoplansky et al. 1990b). In contrast, in late successional stages and low disturbance frequencies and mortality rates, stands are commonly highly crowded and thus plant growth is expected to more directly reflect the default growth rules or architectural model of the plant, rendering the adaptive effects of fine-grained developmental behaviors more difficult to follow and generalize (Novoplansky 1996). However, under these conditions, plants are still expected to be highly perceptive (as predicted by the model), and plastic in their choice of competitive behavior, given the occasional emergence of novel opportunities created by various disturbances and demographic changes (Purves and Law 2002, Herben et al. 2007). Although supportive evidence for the presented expectations are scarce, earlier experimental studies and field observations provide examples of horizontal competitive avoidance as expressed in biased directional growth and branching in competitively-opportunistic plants such as *Portulaca oleracea* (Portulacaceae); (Novoplansky et al. 1990b, Novoplansky 1991), *Heliotropium supinum* (Boraginaceae) and *Malvella sherardiana* (Malvaceae); (Novoplansky, unpublished data), typical to highly disturbed and open habitats. In contrast, plants typical to dense and competitive environments such as *Onobrychis squarrosa* (Novoplansky 1996), *Trifolium resupinatum* (Papilionaceae) and *Avena sterilis* (Gramineae); (Novoplansky, unpublished data), and a few stoloniferous plants (Leeflang 1999, 2000) were found to be unresponsive to horizontal heterogeneity in light availability and spectral shade cues. Therefore, our findings call for comparative studies which explicitly take into consideration not only the immediate environmental contrasts in resource availabilities, but also their average predictabilities at timescales relevant to the life and turnover of the responding organs.

The importance of bottom-up processes for community-level processes is well established and heatedly debated (Hairston et al. 1960; Pearson and Callaway 2003; Bukovinszky et al. 2008; Turkington 2009), but recent studies also demonstrate that intimate interactions and behaviors at the individual plant and organ levels might affect higher-scale population- and community-level processes (e.g. Callaway et al. 2003; Karban 2008; Novoplansky 2009). For example, the current results show that confrontational behavior may lead to higher stand clumpiness. Interestingly, previous findings suggest that another low-level mechanism—self/nonself discrimination of ramets, may also account for clumpiness but have different community-level implications (Herben and Novoplansky 2008). While confrontational behavior increases ramet clumpiness and slightly increases the number of genets, and its effects become stronger under increased density-independent mortality, higher clumpiness due to self/nonself discrimination is expected to be much stronger and to be associated with a reduced number of genets. These theoretical observations not only imply that individual-based behaviors might affect higher organizational levels, but that their reciprocal interactions with resource levels and patchiness, and responsiveness to density-independent mortality might generate higher-order feedbacks that affect the fate of individual ramets and the patterning of whole stands and communities in highly intricate fashions.

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