Structural blueprint and ontogeny determine the adaptive value of the plastic response to competition in clonal plants: a modelling approach

Anne-kristel Bittebière, M. Garbey, M. Smaoui-Feki, Bernard Clément, Cendrine Mony

Structural blueprint and ontogeny determine the adaptive value of the plastic response to competition in clonal plants: A modelling approach.

AK. Bittebiere[1, 2, *], M. Garbey[3], M. Smaoui-Feki[3], B. Clément[1], C. Mony[1]

[*] corresponding author

[1]UMR 6553 Ecobio, Université de Rennes 1, Av. du Général Leclerc, 35042 Rennes Cedex, France

[2]Université de Lyon; UMR 5023 LEHNA Université de Lyon 1; CNRS; ENTPE; 69622; Villeurbanne; France

[3]Department of Computer Science, University of Houston, 501 Philipp G. Hoffman Hall, Houston, TX 77204-3010, USA

e-mails: anne-kristel.bittebiere@univ-lyon1.fr; cendrine.mony@univ-rennes1.fr; bernard.clement@univ-rennes1.fr; garbey@cs.uh.edu

Running title:

Structural and ontogenetic traits influence plastic adaptive value.

Keywords

Adaptive value; Competition intensity; Ontogeny; Plasticity; Structural blueprint.

Total word count: 7211; Abstract: 211 words; Introduction: 677 words; Material and Methods: 1903 words; Results: 546 words; Discussion: 1551 words; Acknowledgments: 27 words; Appendix: 239 words.

Number of cited references: 48

Number of figures: 5; Number of tables: 3

For online publication: Appendix A

Abstract

Local competitive interactions strongly influence plant community dynamics. To maintain their performance under competition, clonal plants may plastically modify their network architecture to grow in the direction of least interference. The adaptive value of this plastic avoidance response may depend, however, on traits linked with the plant's structural blueprint and ontogeny. We tested this hypothesis using virtual populations. We used an Individual Based Model (IBM) to simulate competitive interactions among clones within a plant population. Clonal growth was studied under three competition intensities in plastic and non-plastic individuals. Plasticity buffered the negative impacts of competition at intermediate densities of competitors by promoting clone clumping. Success despite competition was promoted by traits linked with (i) the plant's structural blueprint (weak apical dominance and sympodial growth) and (ii) ontogenetic processes, with an increasing or a decreasing dependence of the elongation process on the branch generation level or length along the competition intensity gradient respectively. The adaptive value of the plastic avoidance response depended on the same traits. This response only modulated their importance for clone success. Our results show that structural blueprint and ontogeny can be primary filters of plasticity and can have strong implications for evolutionary ecology, as they may explain why clonal plants have developed many species-specific plastic avoidance behaviours.

Introduction

Local interactions such as competition are one of the principal drivers of plant community assemblages and determine plant spatial and temporal dynamics (Rees et al 1996; Gibson 1999; Warren et al 2002; Wilson 2007). Depending on its intensity (i.e., the extent to which it decreases the quality of the individual environment), competition impacts plant individuals in terms of survival, growth or reproduction (Begon et al 1996; Weigelt and Jolliffe 2003). Nevertheless, many studies have demonstrated that plants can actively modify their architecture (Weijschedé et al 2008; Herben and Novoplansky 2010; Bittebiere et al 2012a), based on environmental signals in order to limit the effects of the presence of competitors on their performance (Sultan, 1995; Novoplansky 2009). The nature of these architectural modifications (e.g., internode elongation or shortening) can strongly influence the outcome of competitive interactions (Bittebiere et al 2012b).

Growth in clonal plants occurs through horizontal iterations that generate a network of ramets (potential descendants) (van Groenendael et al 1996). This growth is regulated by a trade-off between space occupation (producing aggregated ramets limiting competitor intrusions within the clonal territory and thus supporting the resistance to competition) and exploration (investing in long connections to infiltrate the surrounding vegetation) (Lovett Doust 1981). In heterogeneous habitats, clonal plants are able to forage for the best patches through variations in their horizontal growth traits. In the presence of competitors, this foraging capacity may enable them to develop in the direction of least interference (Ross and Harper 1972; Richards et al 2010). We would expect similar response strategies to result in similarities among architectural features in different plant species (similar mean traits). For instance, growing far from competitors (i.e., avoidance behaviour) may imply an elongation of connections. However, experimental or field studies that compare plant architecture in the presence or absence of competitors report a large range of effective (i.e., observed) responses

to competition (e.g., either an increase or a decrease in the inter-ramet distance or branching frequency) or intensities in these responses (from low to high variation in these traits) (Cheplick and Gutierrez 2000; Markuvitz and Turkington 2000; Novoplansky 2009; Bittebiere et al 2012a; Oborny et al 2012).

We argue that this gap between expected and observed architectures should be explained by the interaction between plasticity and two other processes ultimately defining the architecture: the structural blueprint and ontogeny (Huber et al 1999). The structural blueprint specifies the basic structural organisation or growth form of the species (Bell 1984) and can be viewed as a combination of phylogenetically fixed traits characterising, for example, the location and number of connection buds or the degree of apical dominance. Ontogeny includes processes that either activate or inhibit connection buds during clone development. They may both constrain the expression of the plastic avoidance response, consequently altering its adaptive value. We suggest that certain values of traits linked with the plant structural blueprint or with ontogeny may well increase or decrease this adaptive value and contribute to the selection of plastic features in clonal plants. Depending on their basic architectural traits, plants may thus evolve a variety of plastic behaviours that may be more advantageous in certain species than others. This process may have strong implications for the understanding of the reasons that certain species may be more plastic than others.

These hypotheses were addressed through a modelling approach, as trait variation effects are difficult to disentangle experimentally. Virtual clonal plant populations were simulated to manipulate the values of individual traits linked with the structural blueprint and ontogeny and to subsequently determine the resulting success of plastic and non-plastic clones under contrasted situations of competition intensity. We used an Individual Based Model (IBM) that enabled us to disentangle the effects of the different traits studied on clone success. Model simulations were performed through volunteer computing, facilitating the

extensive browsing of model parameters through large-scale simulations (Mony et al 2011). More precisely, we aimed to determine (i) under which conditions of competition intensity plastic avoidance was adaptive and (ii) which traits linked with the structural blueprint and with ontogeny promoted the adaptive value of plasticity.

Materials and methods

Principles of the model

The model simulates the growth of a clonal plant population for one growing season (colonisation of bare soil) without mortality or sexual reproduction. The elementary units of the model are clones modelled as a branched network of ramet units linked through rhizome units (non-photosynthetic connections) without any fragmentation (Fig. 1). Ramets allow the acquisition of resources, which may be considered to be equivalent to biomass, whereas rhizome units are only used for resource storage and translocation. Space is represented by a hexagonal grid offering six growing directions and balanced competitive interactions between ramets (Birch et al 2007). Plant growth is a function of the time step t. The model comprises two levels: the population model PRAIRIE, which defines interaction rules and is based on the model CLONAL, simulating the growth of the clone (for a detailed description of the model see Mony et al 2011).

Model structure

The entire model structure and simulation process is summarised in Fig. 2. Among all plasticity model versions detailed in Bittebiere et al (2012b), we chose this model version because it corresponds to exploitative behaviour based on surrounding environmental cues.

- PRAIRIE model

The initialisation phase of PRAIRIE first defines the dimensions of the virtual grassland, and the duration of the simulation in terms of the number of time steps. Second, it provides the number of elementary units (clones) to sow on the grassland and the random position of their initial ramets. At each time step, PRAIRIE applies the growing processes of CLONAL to each clone, selected individually in random order. Once all clones have grown, a new time step begins until the entire run is completed.

- CLONAL model

CLONAL governs the two-dimensional growth of each clonal plant through 19 input parameters and nine stochastic growth rules relative to the metabolism and storage of resources (Appendix A) and to the form and spatial colonisation strategy of the plant. Each combination of input parameter values defines a species.

Clonal colonisation of space relies on two processes: the elongation of existing rhizomes and the addition of new rhizomes from ramet units by branching (Fig. 1). At each time step, the spatial colonisation thus begins by determining which of these two processes occurs, following (1):

(1) $P_{el/br} = \alpha$, $\alpha \in [0; 1]$,

where $P_{el/br}$ is the probability of elongation and α is a random variable between 0 and 1. We fixed $P_{el/br(0)}$ as the threshold value for elongation vs. branching processes.

If $P_{el/br} > P_{el/br(0)}$, an elongation process occurs rather than a branching process. Equation (2) is then used to determine which rhizome (R) elongates. A new growth unit is added to the rhizome (R) characterised by the highest elongation probability P_{el}, calculated as follows:

(2) $$P_{el}(R) = \beta\left(\frac{1}{(1 + E_l G(R))(1 + E_g L(R))}\right)(F_N), \beta \in [0; 1],$$

where G(R) and L(R) are the generation level and the length of the rhizome, respectively. These components were both included in (2) to reflect that plants usually first invest in the growth of older structures (Huber et al 1999). β is a random variable ranging from 0 to 1, E_g and E_l express the dependence of elongation on generation level and the length of the rhizome, respectively, and F_N represents a plasticity function (described below and see Fig. 1a). The type of growth unit created to elongate the rhizome is defined in relation to the inter-ramet distance D_r attributed to each ramet unit (r). If the distance along the rhizome from (r) is lower than the actual inter-ramet distance, a rhizome unit is created; otherwise, a ramet unit is produced. D_r follows a stochastic law:

(3) $D_r = d_0 + \mu d_1$, $\mu \in [0; 1]$,

where d_0 and d_1 are integers representing a number of rhizome units.

If $P_{el/br} < P_{el/br(0)}$, a branching process occurs rather than an elongation, and CLONAL consequently first defines which rhizome should branch. This selection is based on the branching probability of each clone rhizome $P_{br}(R)$, calculated as follows:

(4) $P_{br}(R) = \gamma\left(\frac{(1 + B_l L(R))}{(1 + B_g G(R))}\right)$, $\gamma \in [0; 1]$ if $G(R) < 3$

$P_{br}(R) = 0$ if $G(R) \geq 3$,

where γ is a random variable ranging from 0 to 1, G(R) and L(R) are the generation level and the rhizome length, respectively, and B_l and B_g express the dependence of branching on the length and the generation level of the rhizome, respectively. We implemented branching limitation for tertiary rhizomes because previous experiments had demonstrated that clonal plants do not develop connections at higher generation levels if cultivated on a short-term basis (for a few months) (Benot et al 2008). The rhizome with the highest P_{br} is selected. This result synchronises branching decisions over the clone via physiological integration. Second, CLONAL determines which ramet (r) of the previously selected rhizome should hold the new

branch and in which direction, based on Equation (5). The new branch may develop, starting with a rhizome unit, in two possible directions, k = 1 or k = 2. The branching probability of each ramet, $P_{br}(r)$, is thus calculated for these two k values:

$$(5)\quad P_{br}(r,k) = \delta\left(\frac{1}{e + B_p\, d(r)}\right)\left(F_N(k)\right),\ \delta \in [0;\ 1],$$

where δ is a random variable ranging from 0 to 1, *e* is a constant, d(r) is the distance between ramet (r) and the base of the rhizome to which it belongs, B_p is the variable expressing the dependence of the branching process on the distance from the ramet to the base of the branch, and F_N represents a plasticity function (described below and see Fig. 1b) calculated for the two possible branching directions k. The highest $P_{br}(r, k)$ indicates which ramet of the previously selected rhizome should hold the branch and in which direction.

Two clonal populations were tested separately: (i) a control population, within which clones display no active response to competition and for which $F_N = 1$, and (ii) a plastic population composed of clones that actively orient their growth in the direction of the least competitive pressure (avoidance behaviour) (Ross and Harper 1972; Richards et al 2010) (Fig. 1). In this second case, the avoidance response was defined through the plasticity function F_N as follows:

$$(6)\quad F_N = 1 - \frac{N}{6},$$

where N is the number of ramet units present in the six neighbouring cells of the target cell (i.e., the cell that will be colonised if a branching or an elongation process occur). This definition of plastic avoidance is based on the assumption that clones can detect the presence of surrounding competitors, as demonstrated by previous experimental studies [see, e.g., Novoplansky (2009) for a review]. Plasticity costs are not implemented in the model, as experimental studies have demonstrated that they are negligible (van Kleunen and Stuefer 1999; van Kleunen et al 2000).

At each time step, the growth process of each clone ends with the calculation of the probability P_g of creating the new growth unit given the amount of resource available. This calculation is performed according to (7):

$$(7)\ P_g = \varepsilon\left[1 + \log\left(\frac{R_{IPU}}{c_g}\right)\right],\ \varepsilon \in [0; 1] \text{ if } R_{IPU} \geq c_g$$

$$P_g = 0 \text{ if } R_{IPU} < c_g,$$

where $P_g = P_{ramet}$ or $P_{rhizome}$ depending on the nature of the growth unit created, c_g is the production cost of one ramet ($c_g = 1$) or one rhizome unit ($c_g = 0.5$), ε is a random variable ranging from 0 to 1, and R_{IPU} is the total amount of available resource within the 10 growth units sharing them, i.e., composing the integrative physiological unit (IPU). The growth unit is created if $P_g > 0.6$. These parameter values were chosen according to previous results (Mony et al 2011).

Competition prevents the creation of ramets in cells already occupied by ramets but does not affect rhizome units, which can be created regardless of the cell status (empty or already occupied by a ramet or a rhizome unit). If this competition rule is fulfilled, the new growth unit is created, and the IPU is depleted of c_g; otherwise, the growth unit is not produced. A single growth unit per clone is created per time step.

Simulations

The simulated system was a virtual grassland of 200 × 200 cells. The boundary effect was avoided by the addition of an external frame of 99 × 99 cells sown at the same density as the focal grassland and where identical processes were simulated. The individual grid size was adapted to avoid the clone reaching its boundaries while growing: 199 × 199 cells for a clone without competition and 99 × 99 cells for competing clones. Three sowing densities were tested to simulate various levels of competition intensity: low (one clone, intra-clonal competition), intermediate (50 clones), and high (300 clones). As all clones on the virtual

grassland belonged to the same species, competition was intraspecific. For each sowing density, the two plastic responses were tested successively. Six modalities of competition intensity × plasticity were thus tested.

We tested the effect of 11 input parameters characterising plant space colonisation on plant performance, distinguishing between plant structural blueprint and ontogeny. Two to four input parameter values (each value corresponding to one input trait) were selected from the literature or experiments (Benot et al 2008) (Table 1), but instead of testing all combinations of parameter values for each treatment, 2,000,000 combinations of parameter values for each competition intensity × plasticity modality were randomly selected using a Monte Carlo method. Each simulation ran for 300 time steps and was replicated 1000 times for the low-density grassland and 20 times for the two others. These replicate numbers were determined by a previous analysis of the convergence of the model and are a function of the clone densities. Indeed, the output measures are means calculated per simulation on all clones growing on the virtual grassland. Because the clone number increases with the tested density, the variability of the mean result due to external noise decreases, as well as the number of required simulations. The large simulation campaigns were run on the shared software platform BOINC (Anderson 2004) using volunteer computing (Smaoui-Feki et al 2009).

Five output measures were calculated to characterise the clone performance (biomass and number of ramets) and architecture (number of rhizomes, mean lengths of the primary and secondary rhizomes). Primary rhizomes started from the initial ramet and branched in the secondary rhizomes.

Data analysis

All analyses were performed on a data subset consisting of the simulations in which clones performed best in terms of biomass production and reached 75% of the maximal per-clone

biomass recorded during a simulation for each competition intensity × plasticity modality. This threshold was fixed by a preliminary analysis per competition intensity × plasticity modality of the curve describing the maximal per clone biomass produced in all simulations and corresponded to the threshold at which the curve slope drastically decreased.

Using this data subset, we calculated, for each parameter and each competition intensity × plasticity modality, the percentage of best-performing clones sharing each parameter value (trait). For example, at low competition intensity and for non-plastic clones, we found the following distribution of percentages: 20.2% of the best-performing clones had $n_0 = 2$; 39.1% had $n_0 = 4$; and 40.7% had $n_0 = 6$. Traits shared by 100% of the best-performing clones are considered determinant for their success. Chi-square tests were then performed per parameter to compare the distributions of trait percentages (i) among the three competition intensities for plastic and non-plastic clones and (ii) among plastic and non-plastic clones for the three competition intensities. If the effect of competition intensity was significant, partial Chi-square tests were performed to detect differences among competition intensity levels. A Bonferroni correction was used to control for multiple comparisons.

Results

Adaptive value of plasticity depends on competition intensity

Clone performance decreased along the gradient of competition intensity, with mean decreases of 12% to 43% (biomass) or 22% to 43% (number of ramets) for the intermediate and high competition intensities, respectively, compared to the low competition treatment (Figs. 3a, b). Plastic avoidance compensated for these competitive effects by biomass increases of 3% and 10% for the low and intermediate competition intensities, respectively, compared with the non-plastic clones. However, at high competition intensity, biomass production per plastic clone was not maintained and even decreased by 13%. Similarly, the

number of ramets produced increased 3% and 11% in the low and intermediate competition intensity treatments, respectively, and then decreased 20% under high competition intensity.

Determinant input traits in plastic and non-plastic clone success

The effects on clone performance of seven of the 11 structural and ontogenetic parameters tested were independent of the competition intensity and plastic avoidance response: d_0, d_1, n_0, B_l, B_g, e, and B_p (Tables 2 and 3, Figs. 4 and 5). Nevertheless, particular values of these traits promoted plant performance without being involved in resistance to competition: the same trait was selected in plastic and non-plastic clones regardless of competition intensity. Indeed, 100% of the best-performing clones displayed a short and fixed inter-ramet distance ($d_0 = 1$ and $d_1 = 0$). Most performing clones (approximately 70%) also displayed intermediate B_g, B_l and B_p values, indicating that clone success tend to rely on an intermediate dependence of the branching process on the rhizome length and generation level and on the branching position. However, variations in the n_0 and e values had no consequences for clone performance.

The other four traits (n_b, $P_{el/br(0)}$, E_l, E_g) significantly depended on competition intensity (Table 2) and were modulated by the plastic response of the plant (Table 3, Figs. 4 and 5). Competition intensity increased selection for the highest number of buds ($n_b = 2$) at rhizome nodes, which was similar at low and intermediate competition intensities compared with high competition intensity in non-plastic individuals. A plastic avoidance response increased the importance of having two buds per node at intermediate competition intensity (Fig. 4). In non-plastic clones, the predominance of elongation over branching was a strong determinant for low and intermediate competition intensities (100% of performing clones had $P_{el/br(0)} = 0.2$) but was less significant at higher competition intensities (75% of the best-performing clones had $P_{el/br(0)} = 0.2$ and 25% had $P_{el/br(0)} = 0.5$). The same pattern was

observed in plastic clones at low and intermediate competition intensities. At higher competition intensities, however, plastic avoidance reduced the importance of $P_{el/br(0)} = 0.2$ (60% of clones displayed this trait, and 40% had $P_{el/br(0)} = 0.5$) (Fig. 4). Competition intensity affected the dependence of the elongation process on the rhizome length (E_l) independently of plasticity (Tables 2 and 3). The percentage of best-performing clones with an intermediate E_l value (0.2) increased with competition intensity (Fig. 5). At low competition intensity, most non-plastic clones had an extremely low dependence of elongation on the generation level of the rhizome (lowest E_g value) compared with plastic clones. In contrast, high competition intensity showed strong selection of intermediate E_g values for non-plastic clones and balanced selection between intermediate and high E_g values for plastic clones (Fig. 5).

Discussion

The resistance to competition depended primarily on the traits linked with the structural blueprint, with the ontogenetic traits playing a less strongly determining role. These traits also determined the adaptive value of plastic avoidance, which only modulated their importance for clone success.

Plastic avoidance is adaptive only under low and intermediate competition intensities

Competition induced a decrease in clone performance, which plastic avoidance only buffered at low and intermediate competitor densities. These situations generally occur in early successional stands or in highly disturbed habitats. Clone success for the intermediate competitor density was promoted by an adaptive effective architecture that differed between plastic and non-plastic clones. If both displayed relatively long rhizomes, plastic competitor avoidance induced a clumping (more rhizomes of shorter lengths, Fig. 3). This observation is consistent with experimental studies demonstrating that ramet aggregation increases clone

success under competitive conditions (Cheplick 1997; Humphrey and Pike 1998), although this phenomenon does not appear to be general (Stoll and Prati 2001; Bolker et al 2003). In such environments, plasticity promotes space preemption, limiting interspecific contacts (Lovett Doust 1981; Schmid 1986), and it lowers intraclonal interference via a better spatial arrangement of clone connections.

At higher competition intensity, plastic avoidance appears maladaptive. This outcome may be explained by two possible and non-exclusive reasons. First, clones may experience higher intraclonal interference due to their even more highly clumped architecture (Fig. 3) (Lovett Doust 1981; Schmid 1986; Humphrey and Pike 1998). Indeed, local space availability for the development of new ramets was reduced (the birth rate was spatially constrained), and clones may have been unable to reach more favourable patches because of their shorter rhizomes. In these situations, plastic responses may involve traits that may not be linked with horizontal colonisation (e.g., height, growth rate) (Goldberg 1987; Grime 2001). Novoplansky (2009) recognised two other competitive responses in plants: (i) confrontation, maximising the negative effects of plants on their neighbours; and (ii) tolerance, showing no active response but maximising plant performance under the worsened conditions generated by neighbours. Such strategies may have higher adaptive values in crowded habitats (Herben and Novoplansky, 2010; Oborny et al, 2012). Moreover, these authors suggested that plants can switch plastically between these strategies, from avoidance to tolerance, depending on their environmental competitive conditions. Second, it has been emphasised that the adaptive nature of a growth response also depends on the predictability of the environment (Oborny, 1994; Alpert and Simms, 2002). More densely populated environments may be less predictable because their density increases more rapidly, and this characteristic may be less favorable to plastic behaviours.

Competition intensity was approximated by clone density with no implementation of competition effects on plant photosynthesis (no biomass and density-dependent reduction of plant growth). Nevertheless, a study by Bittebiere et al (2012b) on competition modelling has demonstrated that even the simplest model yields realistic results. The implementation of the plastic response alone was of primary importance to obtain relevant results. The three competition intensities tested may have differed for plastic and non-plastic clones, as they compete against themselves (intraspecific competition) rather than against a standard competitor. The spatial occupation of grasslands may have been more efficient in the early time steps of simulations in the plastic population, temporarily reducing competition intensity. Nevertheless, the duration of the simulation was chosen to allow the saturation of the grassland surface. This approach should have reduced differences in spatial occupation and competition intensity between plastic and non-plastic populations over time.

Importance of ontogeny and of the structural blueprint for clone success

Clone performance was enhanced, regardless of the competition intensity and plastic ability, by a star-like architecture supported by an initial branching in six directions, by a low inter-ramet distance, and by weak effects of ontogeny on the branching process. This result confirms that in homogeneous and productive environments, the local exploitation strategy is the most efficient (Lovett Doust 1981; Humphrey and Pike 1998; Herben 2004). Under heterogeneous environmental conditions, traits linked with an exploratory strategy may have been selected.

Resistance to competition (i.e., maximisation of clone success under competition) depended on (i) the plant structural blueprint through the selection of a high number of potentially active axillary buds and a weaker apical dominance; it also depended on (ii) plant ontogeny, with an increasing or a decreasing dependence of the elongation process on the

branch generation level or length, respectively, along the competition gradient. Ontogenetic processes influence the ramet positioning within the clone and thus the intensity of intraclonal competition. Favouring the elongation of primary rhizomes limits new ramet settlement near the clone base (i.e., the initial ramet) and thus favours the spatial expansion of the clone. This mechanism allows the clone to first reach available spaces and then consolidate the occupation of these spaces via a high branching process based on a sympodial development. This tactic limits competitor invasions within the clone territory. Nevertheless, the number of axillary buds tested was limited by the grid used to model the clone environment because this grid constrains the number and angle of branches. Further studies using continuous-space models would be needed to test a wider range of number of buds (structural trait) and consequently analyse the effective architecture.

Surprisingly, competition intensity had no effect on the role of the inter-ramet distance in clone success. Clone success was always favoured by a low inter-ramet distance, although previous studies have shown that clones with long inter-ramet distances are more successful because of their higher potential to explore space at low competitor densities (Schmid and Harper 1985; Winkler and Schmid 1995; Cheplick 1997; Humphrey and Pike 1998). This divergence may be linked to the spatial distribution of resources. Under our homogeneous conditions, investing in long connections is not necessary to reach favourable sites (Lovett Doust 1981; Humphrey and Pike 1998) and would have been made at the expense of local resource exploitation and biomass production by ramets. In contrast, we would have expected a greater allocation of biomass to exploration-related organs in heterogeneous environments.

The effects of ontogenetic and structural traits on plant fitness can be altered by their own interactions and by contingent relationships with other traits (Wildová et al 2007; Oborny et al 2012). For this reason, further studies are needed to investigate the consequences for the adaptive value of plasticity.

The adaptive value of the plastic avoidance response depends on the plant species

The adaptive value of the plastic avoidance response to competition depended on the same ontogenetic and structural traits as those promoting resistance to competition. The avoidance response only modulated the importance of these traits for clone success. At low density, the best-performing plastic individuals displayed a strong development of the primary rhizomes involved in the exploration of space at the expense of the secondary and tertiary rhizomes generally used for local habitat exploitation (i.e., an increase in the dependence of the elongation process on the rhizome generation level, an ontogenetic trait) (Huber et al 1999). At intermediate competition intensity, plastic competitor avoidance stimulated branch production by increasing the importance of having two buds per node (a structural trait), thus enhancing the local exploitation of favourable patches (i.e., less densely colonised) (Cain 1994; de Kroon et al 1994). At high competition intensity, however, plastic avoidance decreased the selectivity of competition for high apical dominance, which decreased interference with other clones but promoted intraclonal competition (Lovett Doust 1981; Schmid 1986). This effect may explain the relatively poor performance of plastic individuals.

Under the modelling conditions of our study, the results obtained showed that plastic competitor avoidance was maladaptive at high competition intensity regardless of the ontogenetic and structural traits of plant species. However, such plasticity was adaptive at low and intermediate competition intensities but only for certain combinations of these traits. These findings have strong implications for evolutionary ecology, as they may explain why clonal plants develop many plastic behaviours in a species-specific manner. Indeed, Bradshaw (1965) has emphasised that plasticity is a character in itself that evolved under the pressure of three forces: selection, drift, and disruption of the genetic system (Schlichting 1986). During

evolution, the basic architectural traits of species may have altered the selection of plasticity by competitive interactions. Accordingly, our results help to determine in which species (characterised as the combination of genetically fixed traits linked with ontogeny and the structural blueprint as described above) plastic avoidance should be selected as an additional feature supporting the species' competitive ability. More precisely, horizontal competition avoidance should be observed in species with sympodial development (at least two buds of connection per node). This prediction tends to be supported by previous studies based on experiments or field studies. This type of competitor avoidance has indeed been observed in *Portulaca oleracea* (Novoplansky et al 1990) and in *Aechmea nudicaulis* (Sampaio et al 2004), which both display sympodial branching.

Concluding remarks

Our study contributed to the knowledge of the relative importance of the structural blueprint and ontogenetic processes for the adaptive value of plant responses. Previously, this topic was poorly understood (but see Geber et al 1992). The difficulty of addressing certain questions through experimentation emphasises the value of modelling approaches coupled with volunteer computing, especially those based on IBMs, which focus on local interaction between individuals. As illustrated here, modelling approaches are particularly powerful for determining and disentangling the effects of different traits on plant fitness under specified environmental conditions.

Acknowledgements

This project benefited from the grant ANR-08-SYSC-012 provided by the Agence Nationale de la Recherche (France). We thank the volunteers worldwide that contributed to the calculations.

References

Alpert P, Simms EL (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? Evol Ecol 16: 285-297

Anderson DP (2004) BOINC: a system for public-resource computing and storage. In: Proceedings of the 5th IEEE/ACM International Workshop on Grid Computing. Pittsburgh, pp 1-7

Begon M, Harper JL, Townsend CR (1996) Ecology, Blackwell Science, Oxford

Bell AD (1984) Dynamic morphology: a contribution to plant population ecology. In: Dirzo R, Sarukh´an J (eds) Perspectives in Plant Population Ecology, Sinauer, Sunderland, pp. 48-65

Benot ML, Mony C, Puijalon S et al (2008) Responses of clonal architecture to experimental defoliation: a comparative study between ten grassland species. Plant Ecol 201:257-266

Berger U, Piou C, Schiffers K (2008) Competition among plants: Concepts, individual-based modelling approaches, and a proposal for a future research strategy. Perspect Plant Ecol Evol Syst 9:121-135

Birch CPD, Oom SP, Beecham JA (2007) Rectangular and hexagonal grids used for observation, experiment and simulation in ecology. Ecol Model 206:347-359

Bittebiere AK, Mony C, Clément B et al (2012b) Modeling competition between plants using an individual based model: methods and effects on the growth of two species with contrasted growth forms. Ecol Model 234:38-50

Bittebiere AK, Renaud N, Clément B et al (2012a) Morphological response to competition for light in the clonal *Trifolium repens* (Fabaceae). Am J Bot 99:1-9

Bradshaw AD (1965) Evolutionary significance of plasticity in plants. Adv Genet 13: 115-155

Cain ML (1994) Consequences of foraging in clonal plant species. Ecology 75:933-944

Cheplick GP (1997) Responses to severe competitive stress in a clonal plant: differences between genotypes. Oikos 79:581-591

Cheplick GP, Gutierrez CM (2000) Clonal growth and storage in relation to competition in genets of the rhizomatous perennial *Amphibromus scabrivalvis*. Can J Bot 78:537-546

de Kroon H, Stuefer JF, Dong M et al (1994) On plastic and non-plastic variation in clonal plant morphology and its ecological significance. Folia Geobot 29:123-138

Geber MA, Watson MA, Furnish R (1992) Genetic differences in the clonal demography in *Eichhornia crassipes*. J Ecol 80:329-341

Gibson DJ, Connolly J, Hartnett DC et al (1999) Designs for greenhouse studies of interactions between plants. J Ecol 87:1-16

Goldberg DE (1987) Neighborhood competition in an old-field plant community. Ecology 68:1211-1223

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, John Wiley & Sons, Chichester.

Herben T (2004) Physiological integration affects growth form and competitive ability in clonal plants. Evol Ecol 18: 493-520

Herben T, Novoplansky A (2010) Fight or flight: plastic behavior under self-generated heterogeneity. Evol Ecol 24:1521-1536

Huber H, Lukács S, Watson MA (1999) Spatial structure of stoloniferous herbs: an interplay between structural blue-print, ontogeny and phenotypic plasticity. Plant Ecol 141:107-115

Humphrey LD, Pike DA (1998) Demographic and growth responses of a guerrilla and a phalanx perennial grass in competitive mixtures. J Ecol 86:854-865

Lovett-Doust L (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. J Ecol 69:743-755

Marcuvitz S, Turkington R (2000) Differential effects of light quality, provided by different grass neighbours, on the growth and morphology of *Trifolium repens* L. (white clover). Oecologia 125:293-300

Mony C, Garbey M, Smaoui M et al (2011) Large scale parameter study of an individual-based model of clonal plant with volunteer computing. Ecol Model 222:935-946

Novoplansky A (2009) Picking battles wisely: plant behaviour under competition. Plant Cell Environ 32:726-741

Novoplansky A, Cohen D, Sachs T (1990) How *Portulaca* seedlings avoid their neighbors. Oecologia 82:490-493

Oborny B (1994) Growth rules in clonal plants and environmental predictability -- A simulation study. J Ecol 82: 341-351

Oborny B, Mony C, Herben T (2012) From virtual plants to real communities: A review of modelling clonal growth. Ecol Model 234:3-19

Rees M, Grubb PJ, Kelly D (1996) Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. Am Nat 147:1-32

Richards MLA, Aitkenhead MJ, McDonald AJS (2010) Improving the effectiveness of angular dispersion in plant neighbourhood models. Ecol Model 221:1649-1654

Ross MA, Harper JL (1972) Occupation of biological space during seedling establishment. J Ecol 60:77-88

Sampaio MC, Araújo TF, Scarano FR et al (2004) Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity. Evol Ecol 18:429-442

Schlichting CD (1986) The evolution of phenotypic plasticity in plants. Ann Rev Ecol Syst 17: 667-693

Schmid B (1986) Spatial dynamics and integration within clones of grassland perennials with different growth form. P Roy Soc B 228:173-186

Schmid B, Harper JL (1985) Clonal growth in grassland perennials: I. Density and pattern-dependent competition between plants with different growth forms. J Ecol 73:793-808

Smaoui-Feki, M., Nguyen, V. H. & Garbey, M. (2009) Parallel genetic algorithm implementation for BOINC. In: Proceedings of the International Conference on Parallel Computing. Lyon

Sultan SE (1995) Phenotypic plasticity and plant adaptation. Acta Bot Neerland 44: 363-383

van Groenendael JM, Klimeš L, Klimešová J et al (1996) Comparative ecology of clonal plants. Philos T R Soc B 351:1331-1339

van Kleunen M, Fischer M (2001) Adaptive evolution of plastic foraging responses in a clonal plant. Ecology 82:3309-3319

van Kleunen M, Fischer M, Schmid B (2000) Clonal integration in *Ranunculus reptans*: by-product or adaptation? J Evol Biol 13:237-248

van Kleunen M, Stuefer JF (1999) Quantifying the effects of reciprocal assimilate and water translocation in a clonal plant by the use of steam-girdling. Oikos 85:135-145

Warren J, Wilson F, Diaz A (2002) Competitive relationships in a fertile grassland community - does size matter? Oecologia 132:125-130

Weigelt A, Jolliffe P (2003) Indices of plant competition. J Ecol 91:707-720

Weijschedé J, Berentsen R, de Kroon H et al (2008) Variation in petiole and internode length affects plant performance in *Trifolium repens* under opposing selection regimes. Evol Ecol 22:383-397

Wildová R, Gough L, Herben T et al (2007) Architectural and growth traits differ in effects on performance of clonal plants: an analysis using a field-parameterized simulation model. Oikos 116 :836-852

Wilson M (2007) Measuring the components of competition along productivity gradients. J Ecol 95:301-308

Winkler E, Schmid B (1995) Clonal strategies of herbaceous plant species: a simulation study on population growth and competition. Abs Bot 19:17-28

Appendix A. Metabolic rules of the CLONAL model.

At each time step t, the total amount of resource of the clone $R_T(t)$ was calculated according to equation (A1):

$$(A1)\ R_T(t) = R_T(t-1) + \sum_{g=1}^{g=n} R_g(t-1) - aC_g \text{ , } R(1) = 1,$$

where $R_g(t)$ is the net gain of resource (biomass accumulation for ramets or storage for rhizome units) of each growth unit g, C_g is the cost of creating one growth unit (C_g equals 1 for a ramet and 0.5 for a rhizome unit), and a is equal to zero if no new unit is added to the clone (otherwise, *a* equals one).

Biomass accumulation occurs at the ramet scale and was assumed to follow a logistic law at each time step t:

$$(A2)\ \frac{dB_r(t)}{dt} = r_p\,(1 - r_s)B_r(t)\left(1 - \frac{B_r(t)}{r_{mr}}\right),$$

where $B_r(t)$ is the biomass status of ramet r, r_p is a constant ($r_p = 0.3$) providing the biomass supplied to a ramet by photosynthesis, $1\text{-}r_s$ is the fraction of biomass allocated to long-term reserve formation ($r_s = 0.1$), and r_{mr} ($r_{mr} = 20$) is the maximum biomass achieved by a ramet.

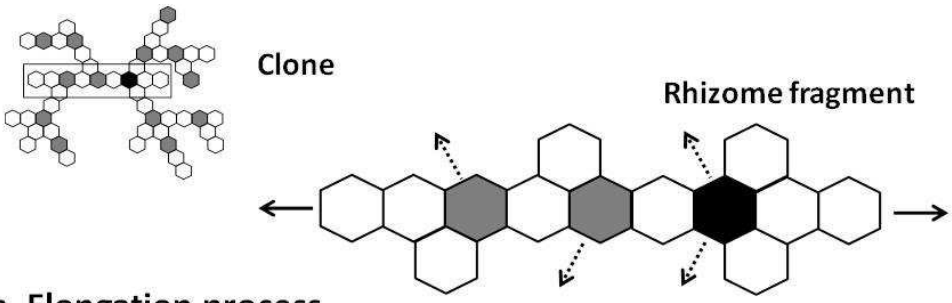
The resource available for the growth of a ramet r was calculated as the overall growth units belonging to the same integrative physiological unit (IPU) according to the following equation:

$$(A3)\ R_{IPU}(r) = \sum_{r=1}^{r=nIPU} R_g \text{ ,}$$

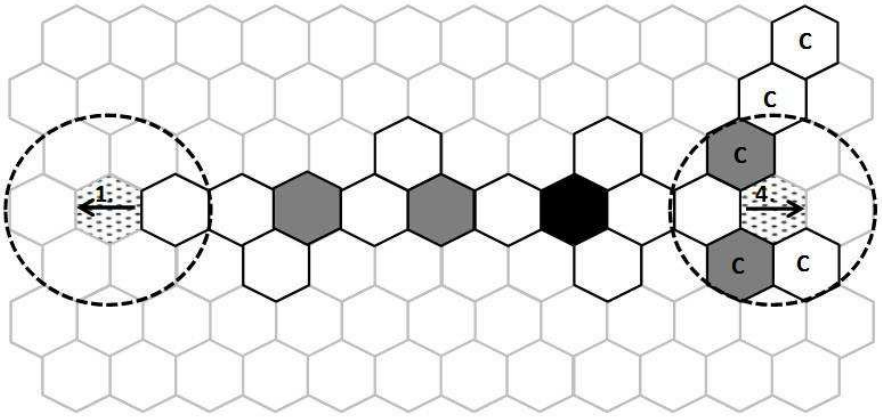
where R_g is the resource of the growth unit g and n_{IPU} (equal to 10) is the number of growth units in the IPU. R_g is null for a rhizome unit, which stores only long-term resources unavailable for growth.

Figure legends

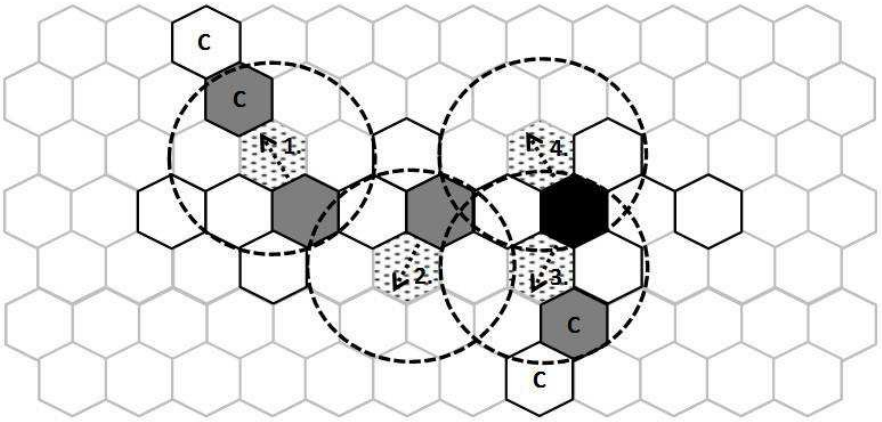
Figure 1. Clonal growth processes: elongation and branching. The plasticity function F_N is calculated for a) an elongation process, b) a branching process. 1a) Two possible directions of elongation are possible in the example. Competitor ramet number is calculated in the neighbourhood of the two target cells and introduced in the calculation of the plasticity function F_N: case 1: N = 0; 2: N = 2. 1b) Three ramets may hold the new branch, one of them in two possible directions: cases 3 (k = 1) and 4 (k = 2). Competitor ramet number is calculated in the neighbourhood of the four target cells and introduced in the calculation of the plasticity function F_N: case 1: N = 2; 2: N = 1; 3: N = 2; 4: N = 1. Elongation and branching processes are less probable in the directions of higher competitor ramet numbers.



a. Elongation process



b. Branching process



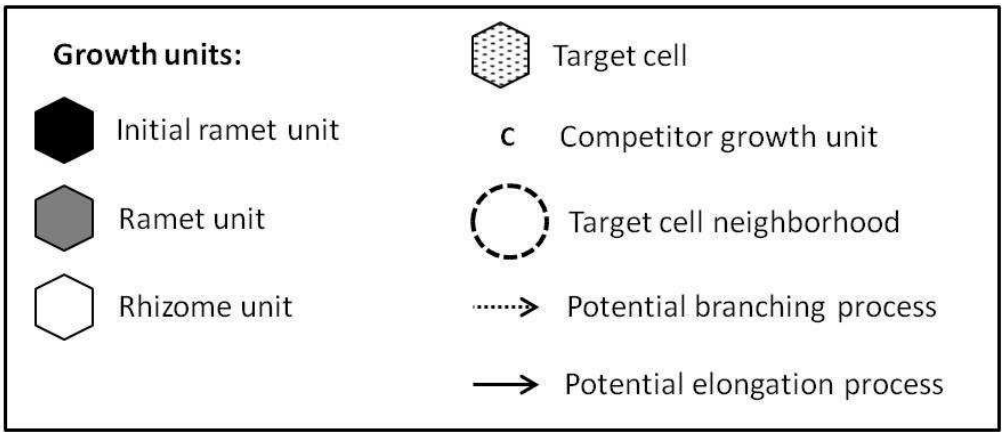


Figure 2. Virtual grassland simulation. Shaded stages are governed by the PRAIRIE model, unshaded stages by the CLONAL model.

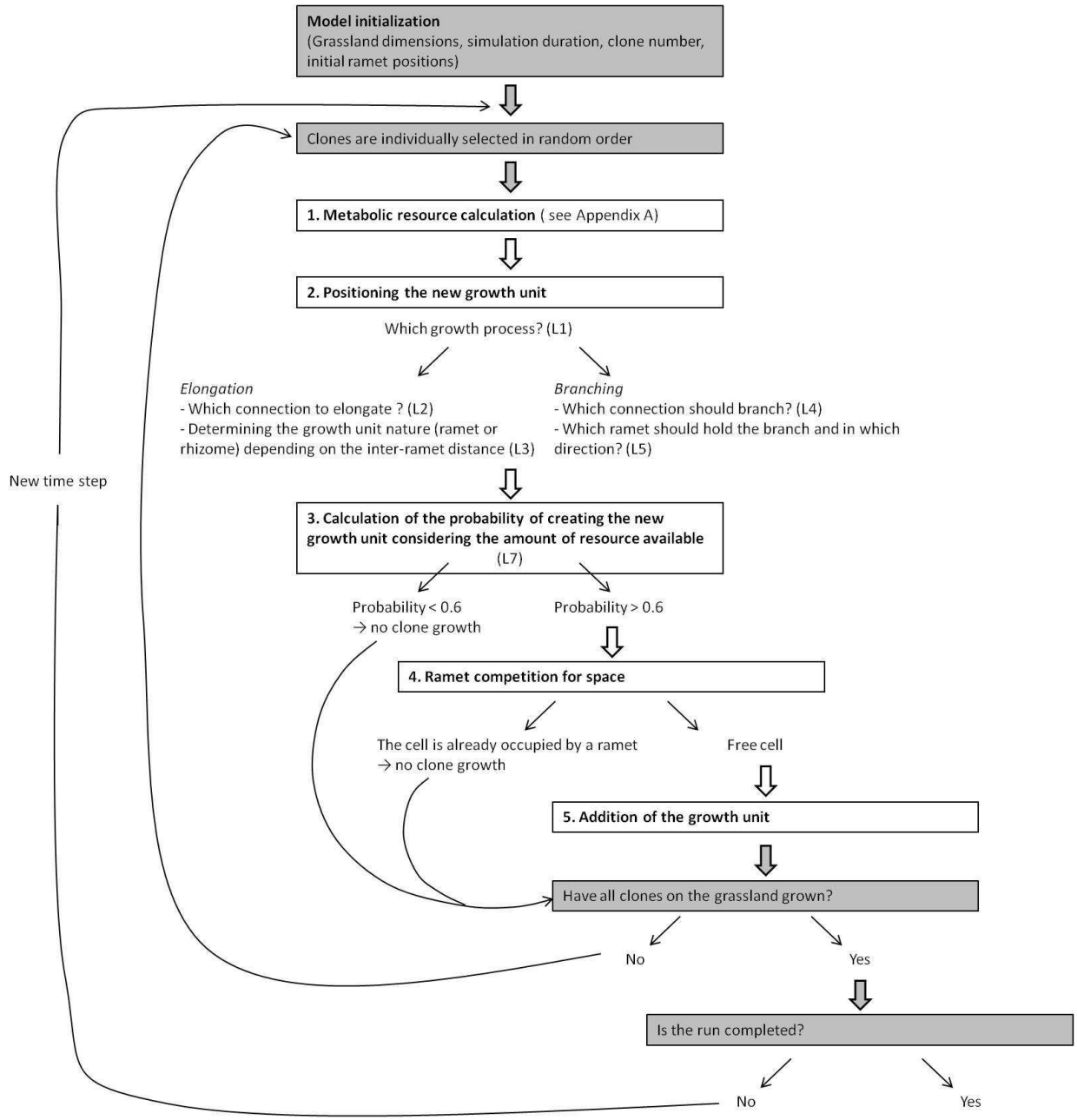


Figure 3. Mean (± SD) performance and architectural traits of plastic and non-plastic clones growing under the three competition intensities: (a) biomass, (b) number of ramets, (c) number of rhizomes, (d) mean length of primary rhizome, and (e) mean length of secondary rhizome. For each competition intensity × plasticity modality, the mean traits were calculated on the data subset comprising the simulations in which clones reached at least 75% of the maximal per clone biomass recorded.

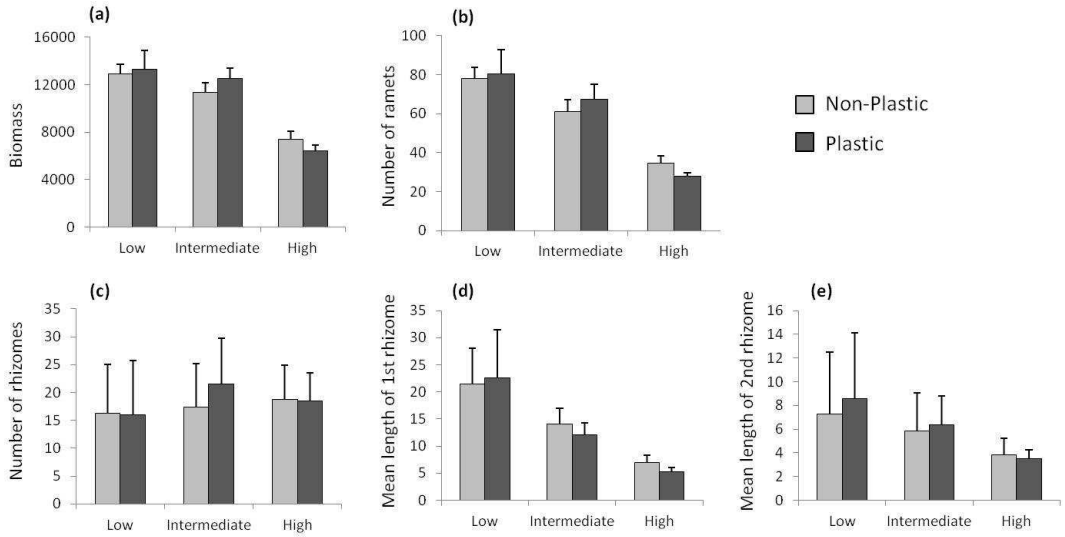


Figure 4. Structural blue-print trait percentages in the best-performing plastic and non-plastic clones growing under the three competition intensities. Plastic clones: P, black symbols; non-plastic: NP, grey symbols. Symbols of different shapes refer to different parameter values (traits). Letters and numbers indicate significant differences in percentage distribution between the three competition intensities for non-plastic or plastic clones, respectively.

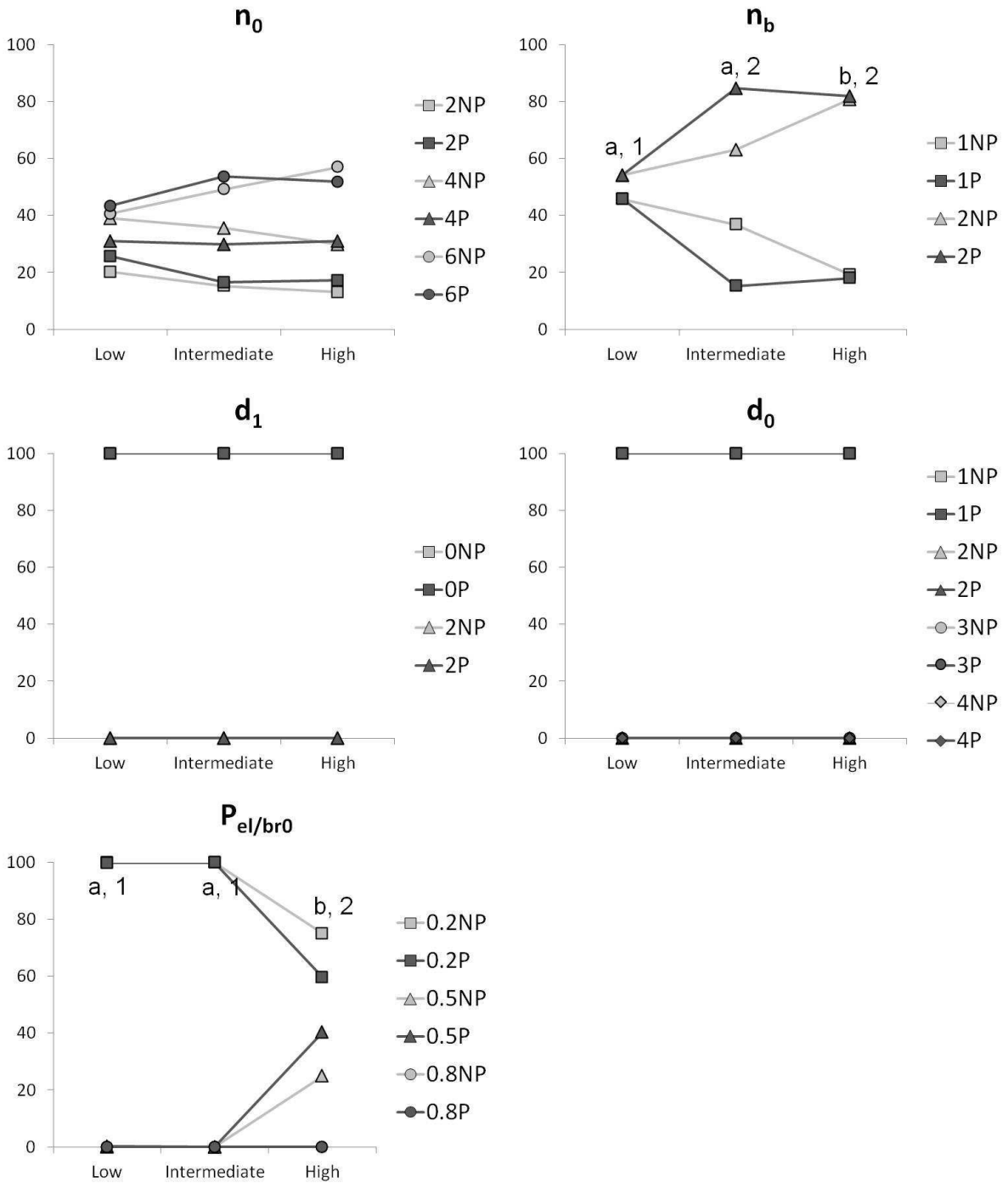

n_0
100
80
60
40
20
0
Low
Intermediate
High
2NP
2P
4NP
4P
6NP
6P
n_b
a, 2
b, 2
a, 1
1NP
1P
2NP
2P
d_1
0NP
0P
2NP
2P
d_0
1NP
1P
2NP
2P
3NP
3P
4NP
4P
$P_{el/br0}$
a, 1
a, 1
b, 2
0.2NP
0.2P
0.5NP
0.5P
0.8NP
0.8P

Figure 5. Ontogenetic trait percentages in the best-performing plastic and non-plastic clones growing under the three competition intensities. Plastic clones: P, black symbols; non-plastic: NP, grey symbols. Symbols of different shapes refer to different parameter values (traits). Letters and numbers indicate significant differences in percentage distribution between the three competition intensities for non-plastic or plastic clones, respectively.

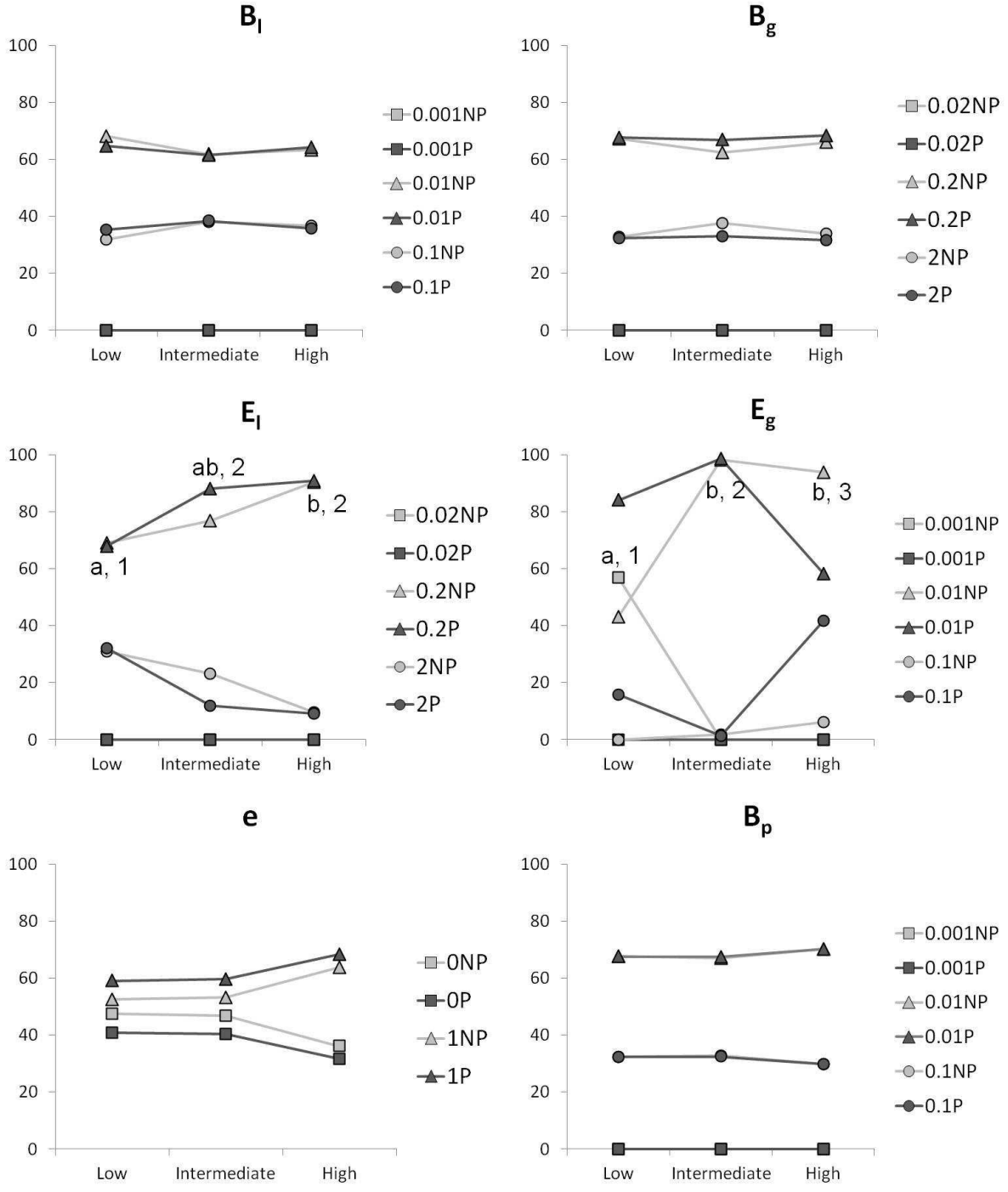


Table 1. Input parameters of the CLONAL plant model determining clone architecture. The numbers within brackets correspond to the equation in which the parameter was involved. The parameter values tested were determined through experimentation or literature surveys.

Significance	Label	Values
Structural blueprint		
Maximum number of branches developing from the initial ramet	n_0	2; 4; 6
Maximum number of branches developing from non-initial ramets	n_b	1; 2
Minimum inter-ramet distance (3)	d_0	1; 2; 3; 4
Variability in the inter-ramet distance (3)	d_1	0; 2
Threshold probability for the elongation process compared with the branching process (apical dominance) (1)	$P_{el/br(0)}$	0.2; 0.5; 0.8
Ontogeny		
Elongation process		
Dependence of elongation on the length of the rhizome (2)	E_l	0.02; 0.2; 2
Dependence of elongation on the generation level of the rhizome (2)	E_g	0.001; 0.01; 0.1
Branching process		
Dependence of branching on the rhizome length (4)	B_l	0.001; 0.01; 0.1
Dependence of branching on the generation level of the rhizome (4)	B_g	0.02; 0.2; 2
Constant in (5)	e	0; 1
Dependence of the branching location on the distance from the ramet to the base of the rhizome (5)	B_p	0.001; 0.01; 0.1

Table 2. Comparison of trait distributions between the three competition intensities in plastic and non-plastic clones (see Data analysis for trait distribution assessment). Trait distributions were compared using Chi-square tests. If significant differences were detected, partial Chi-square tests were performed (results are given in Fig. 4). For d_0 and d_1, no Chi-square tests were performed as their distributions remained constant regardless of competition intensity.

Traits	**Non-Plastic**			**Plastic**		
	χ^2	**df**	**P-value**	**χ^2**	**df**	**P-value**
Structural blueprint						
n_0	5.62	4	ns	3.80	4	ns
n_b	16.28	2	***	29.53	2	***
$P_{el/br(0)}$	54.27	2	***	92.42	2	***
Ontogeny						
E_l	13.85	2	***	21.58	2	***
E_g	145.0	2	***	53.03	2	***
B_l	0.57	2	ns	0.05	2	ns
B_g	0.93	2	ns	0.24	2	ns
e	3.29	2	ns	2.30	2	ns
B_p	0.25	2	ns	0.22	2	ns

Note: Asterisks indicate significant differences: ns not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 3. Comparison of trait distributions with and without plasticity under low, intermediate, and high competition intensity (see Data analysis for trait distribution assessment). Trait distributions were compared using Chi-square tests. For d_0, d_1, and $P_{el/br(0)}$ at low and intermediate competition intensity, no Chi-square tests were performed as their distributions remained constant regardless of competition intensity.

Traits	Low			Intermediate			High		
	χ^2	df	P-value	χ^2	df	P-value	χ^2	df	P-value
Structural blueprint									
n_0	1.64	2	ns	0.75	2	ns	0.83	2	ns
n_b	0.02	1	ns	11.03	1	***	0.002	1	ns
$P_{el/br(0)}$	-	-	-	-	-	-	4.72	1	*
Ontogeny									
E_l	0.001	1	ns	3.62	1	ns	0.01	1	ns
E_g	85.93	1	***	0.36	1	ns	0.01	1	ns
B_l	0.006	1	ns	0.27	1	ns	0.04	1	ns
B_g	0.13	1	ns	0.01	1	ns	3.10^{-4}	1	ns
e	0.62	1	ns	0.60	1	ns	0.27	1	ns
B_p	0.02	1	ns	0.007	1	ns	0.02	1	ns

Note: Asterisks indicate significant differences: ns not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.