



A simulation study of the effects of architectural constraints and resource translocation on population structure and competition in clonal plants

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Abstract. (1) Spatially explicit simulation of clonal plant growth is used to determine how ramet-level traits affect ramet density, spatial pattern of ramets and competitive ability of a clonal plant. The simulation model used combines elements of (i) an individual-based model of plant interactions, (ii) an architectural model of clonal plant growth, and (iii) a model of resource translocation within a set of physiologically integrated plant individuals. (2) The effects of two groups of parameters were studied: growth and resource acquisition parameters (resource accumulation, density-dependence of resource accumulation, resource translocation between ramets) and architectural rules (branching angle and probability of branching, internode length). The model was parameterised by values approximating those of clonally growing grasses as closely as possible. The basic parameter values were chosen from a short-turf grassland. Sensitivity analysis was carried out on relevant parameters around three basic points in the parameter space. Both single-species and two-species systems were studied. (3) It is shown that increasing resource acquisition and growth parameters increase ramet density, genet number and competitive ability. Translocation parameters and architectural parameters modify the effects of resource acquisition and growth, but their effect in single-species stands was smaller. (4) The simulations of species with fixed ramet sizes showed that ramet density in single-species stands cannot be used for predicting competitive ability. Increase in resource acquisition and growth parameters was correlated with an increase in equilibrium ramet density and competitive ability. Increasing branching angle, branching probability or internode length lead to an increased competitive ability, but did not affect equilibrium ramet density. Change of architectural parameters could therefore affect competitive ability independently of their effect on the final ramet density. (5) Spatial pattern both in single-species and two-species stands was also highly parameter-dependent. Changes in architectural parameters and in translocation usually lead to pronounced change in the spatial pattern; change in growth and resource acquisition parameters generally had little effect on spatial pattern.

Key words: architectural model, architectural rules, competitive ability, genet coexistence, individual-based simulation model, resource acquisition, spatial autocorrelation

Introduction

The ability to maintain connections between ramets and to translocate resource is one of the most intriguing features of clonal plants. Translocation can support growth of ramets and buds (Marshall and Price, 1997). Many experiments have also shown that, in heterogeneous environments, clonal plants can transport resources obtained from resource-rich patches to support plant parts located in resource-poor patches (Birch and Hutchings, 1994; Stuefer *et al.*, 1996; Alpert and Stuefer, 1997; Jónsdóttir and Watson, 1997; Wijesinghe and Hutchings, 1997; Hutchings *et al.*, 2000), and thus maintain higher total biomass than if the same amount of resource were homogeneously distributed. Both analytical treatments (Caraco and Kelly, 1991) and simulation models (Oborny and Cain, 1997; Piqueras *et al.*, 1999; Oborny *et al.*, 2000) have demonstrated that under rather general assumptions of environmental covariance, maintenance of inter-ramet connections is beneficial for the plant and can optimise usage of a heterogeneously distributed resource. However, it is important to note that while resource concentration varies in space under field conditions (Caldwell and Pearcy, 1994), this heterogeneity often changes over time scales comparable with that of the plant growth (Robinson *et al.*, 1994; Farley and Fitter, 1999). In particular, much of the environmental heterogeneity found in the field is due to uneven distribution of plant individuals themselves (Jackson and Caldwell, 1993).

Mechanisms of vegetative growth that give rise to the spatial arrangement of daughter ramets are the second intriguing process in clonal plants. Plant form is constrained by architectural and developmental rules (Mogie and Hutchings, 1990; de Kroon *et al.*, 1994; Newton and Hay, 1995; Geber *et al.*, 1997; Huber *et al.*, 1999; Watson *et al.*, 1997). Many studies of foraging by stolons or rhizomes have shown that the extent and importance of the foraging response to environmental conditions is limited (de Kroon *et al.*, 1994; Hutchings and de Kroon, 1994; Oborny and Cain, 1997). Thus the distribution of ramets in space is largely determined by internal regulation of branching and growth and rather independent of the momentary distribution of resource patches surrounding the plant.

Architectural constraints on plant form have profound consequences. First, the lack of mechanisms to compensate for environmental heterogeneity may actually increase environmental heterogeneity due to unequal spatial distribution of plant parts. The capacity of a clonal plant to exploit a heterogeneous environment must therefore operate in an environment in which heterogeneity is partly shaped by the architectural rules of the plant itself (Fig. 1). Second, the architectural constraints determine spatial patterns found at the level of whole populations. Studies of tree architecture have demonstrated that crown shape is very sensitive to minor variations in parameters such as branching

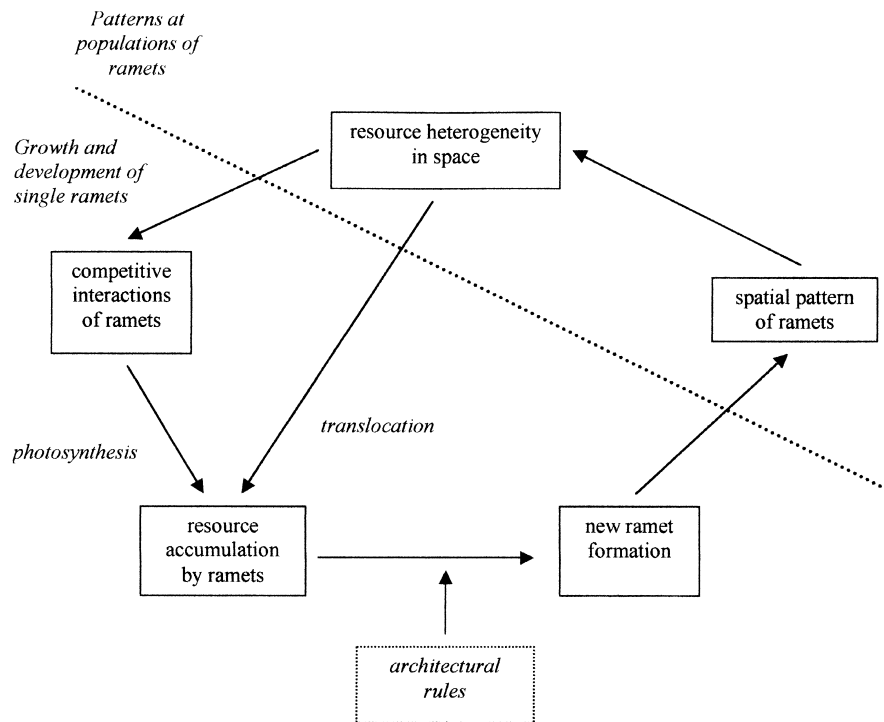


Figure 1. Links between architectural constraints, resource dynamics and spatial pattern. Arrows indicate effects. The effects of resource dynamics (photosynthesis and translocation) on new ramet formation is filtered through architectural rules.

angle (Takenaka, 1994). Similar constraints operate in clonal plants (Bell, 1986; Klimeš, 1992, 2000; Adachi *et al.*, 1996); architectural rules may thus affect both intra- and inter-specific interactions (Bell, 1984; Cain *et al.*, 1995; Cowie *et al.*, 1995). In spite of the recent interest in spatial effects on ecological interactions (Bascompte and Sole, 1997; Tilman and Kareiva, 1996; Dieckmann *et al.*, 2000), little attention has been paid to architectural constraints. Such constraints may be neglected in plants with roots as organs of clonal growth (Klimeš and Klimešová, 1999), but many other plants have long spacers (Eriksson and Jerling, 1990; Wilhalm, 1995) and the role of architectural rules cannot be disregarded.

Surprisingly, the feedback relationships between architectural constraints, resource heterogeneity and spatial pattern in ramet distribution (Fig. 1) have been little explored (see review by Oborny and Bartha, 1995). Architectural models have shown how ramet-level processes determine the shape of a plant, but usually do not take into account the facts that the plant's shape also determines resource acquisition (but see Oborny, 1994a, b; Piqueras *et al.*, 1999) and plays a role in translocation. The most intriguing questions here are:

- (1) How do different traits of resource dynamics (including resource translocation) affect the density and spatial pattern of ramets in a clonal plant in which growth is constrained by architectural rules?
- (2) How does alteration in the architectural rules affect the equilibrium density and spatial pattern of ramets and the architectural features of a clonal plant?
- (3) Can a change in an architectural trait compensate for a change in a trait of resource dynamics?
- (4) How do these traits affect the success of a clonal plant in competition? Under what circumstances can these traits lead to a spatial segregation of competing species?

To address these issues, we developed a spatially explicit simulation model of a clonal plant that combines elements of three different modelling approaches: (i) an individual-based model of plant interactions in a local neighbourhood, (ii) an architectural model of clonal plant growth, and (iii) a model of resource (photosynthate) translocation within a set of physiologically interconnected ramets. We used this model to determine the effects of individual plant traits (both of resource dynamics/competition and of architecture) on the final density and spatial structure of ramets in a single-species stand of a clonal plant, and to determine how these plant traits affected the success of the plant in competition with a similar species. The effects of plant traits on single-species stands were analysed by determining changes in stand variables such as ramet density relative to changes in model parameters. The effects of plant traits on competitive success were determined by the outcome of competition between two plants with identical values for all parameters except the parameter being tested. Since the model inevitably has many parameters, we restricted ourselves to study its behaviour only around a few points in the whole parameter space. The chosen points represent three kinds of 'model plants' and explore the effects of changes of one parameter at a time only.

Methods

The model

The model simulates growth of clonal plants on a continuous plane with toroidal boundaries. (For a more detailed description of the model see the Appendix 1 and Table 1.) It works with a set of species; each of these species has a different set of growth and architectural parameters. Basic objects in the model are rhizomes (rhizome fragments) that grow horizontally (Fig. 2). Each rhizome fragment has its own genetic identity (all descendants of one seedling have the same genetic identity). The rhizome fragments are composed of nodes

Table 1. Summary of the model parameters

Name	Units	Base value	Other values tested	Meaning
Accumulation rate	1/Time step	3.5	2, 3, 4, 5	A , Constant of resource production during one time step. Its value after subtraction of 1 means how many new ramets a ramet would be able to form per one time step under no-competition conditions
Density-dependence of resource accumulation	Area/biomass	0.1	0.3, 0.2, 0.05	β , Through the direct effect on resource accumulation, this constant determines actual branching rate of rhizomes and mortality of ramets
Resource retained	1/Time step	1	0.095, 0.9, 0.8, 0.7	S , Proportion of the resource from the earlier step retained to the next step. It expresses maintenance cost of the node.
Integration range	Nodes	0	1, 2, 3, 4	T , range of physiological integration
Internode cost	Biomass	0	0.25, 0.5, 1	C_i , Cost of adding one internode to a terminal node or a branch; relative to resource needed to produce a new ramet
Fraction of available resource put into the terminal ramet	1	0.7	0.4, 0.6, 0.8, 0.9	f_g , Applied after the cost of the internode production has been subtracted
Mean internode length	Distance	0.01	0.002, 0.005, 0.02, 0.03, 0.04	
Node lifespan	Time step	20	10, 30, 40	After how many time steps since its formation the basipetal (oldest) node dies
Probability of terminal branching	1/Time step	0.5	0.2, 0.4, 0.6, 0.8	Probability of terminal branch formation, provided the resource is sufficient
Branching angle	Degrees	30	10, 20, 50, 70	Angle of main and lateral axes
Dormant bud activation probability	1/Time step	0	0.005, 0.01, 0.02, 0.05	Probability that a non-terminal node forms a branch (provided resource is sufficient)
Non-terminal ramet formation probability	1/ time step	0	0.005, 0.01, 0.02, 0.05	Probability that a dormant bud will form a ramet (provided resource is sufficient)
<i>Parameters of non-zero translocation</i>				
Fraction of resource translocated	1/Time step	0.7		f_{tr} , Fraction of the resource translocated to the tip; rest is available for the growth of non-terminal ramets and translocation in next steps
Translocation cost	1/Time step	0.1		C_i , Fraction of the resource that is lost when translocated over one node

Table 1. (Continued)

Name	Units	Base value	Other values tested	Meaning
<i>Parameters with fixed values</i>				
Neighbourhood size	Distance	0.05		Relative to the size of the simulation plane, which is scaled from 0 to 1
Variation coefficient of the internode length	1	0.1		
Standard deviation of the branching angle	Degrees	10		Standard deviation of the branching angle and angle of rhizome growth
Branching constraint	Nodes	3		Architectural constraint for branching: how many nodes after an earlier branching the terminal node may branch again, provided resource is sufficient
<i>Parameters with fixed values (only for plants with variable size)</i>				
Ramet growth rate	1	0.8		r_c
Maximum ramet size	Biomass	1		K_c
Density dependence of ramet growth in size	Area/biomass	0.8		α , Determines the effect of neighbours on size growth of ramets
Minimum ramet size	Biomass	0.1		R_{min} , Resource needed for branching and node survival

Symbols of variables are identical to those used in the appendix. Biomass and distance (area) values are scaled in relative units. Biomass is relative to the maximum ramet size; distance is expressed as a fraction of the size of the simulation plane (which is scaled from 0 to 1). Values in bold were used to calculate the slope of the response surface for that parameter (see the Methods section).

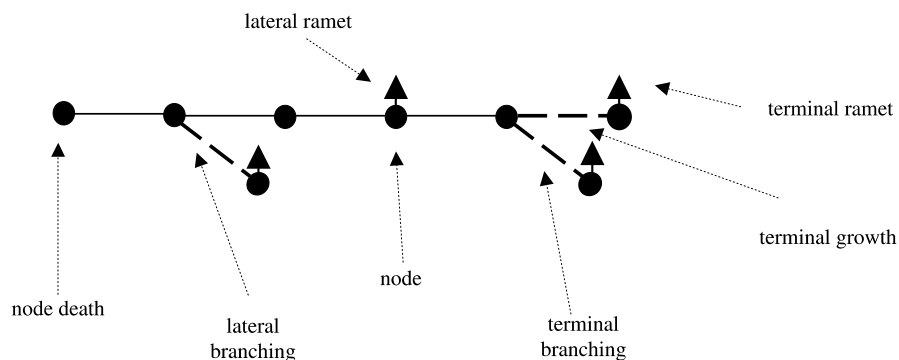


Figure 2. Definition of some terms used in the model. The whole structure represents one rhizome fragment composed of nodes, internodes and ramets. Dashed lines indicate rhizome segments added in the last simulation step.

and internodes. Each node of a rhizome has an amount of internal resource as a state variable. This resource may be anything that is limiting for the plants and whose accumulation (i) depends on the ramet size and (ii) is density-dependent. In the current formulation of the model it is a proxy for photosynthate, but the predictions of the model are more general and valid for any resource that satisfies these two conditions. Resource levels at each node change because of resource acquisition by the ramet attached to that node, acropetal translocation and by resource consumption.

Rhizomes grow by adding nodes at terminal positions. This process takes place if the quantity of resource available at the current terminal node is sufficient. If a new node is added, the length and angle of growth of the internode are independent of the internal state of the rhizome and of its neighbourhood. If the resource is not sufficient, a new node is not added; if the resource is zero or negative, the node loses the capacity for further growth and the terminal ramet dies. Further, nodes may be added to a rhizome by terminal branching (i.e. by adding two parallel terminal nodes at a single time step) and by lateral branching (i.e. by adding a new branch with a new terminal node to a non-terminal node). Both branching processes again take place only if the available quantity of resource at that node is sufficient. Branching angle is independent of the internal state of the rhizome and of its neighbourhood. The decision to branch to the left or right depends on the neighbourhood ramet density. The branch is formed always in the direction of lower density. The oldest (basipetal) nodes of a rhizome die depending on their age. If a node bearing a branch dies, the branch becomes independent and the rhizome fragments into two.

The nodes may produce ramets. Ramets are the photosynthetically active plant parts that provide resources for rhizome growth; the rate of their resource acquisition is determined by competition with neighbouring ramets and by their own size. Ramets may be of fixed size or may grow in size; in the latter case growth depends on the resource acquisition by that ramet. Ramets are by definition attached to all growing terminal nodes. At each time step when a new node is added, terminal ramets move to the new node in order to remain in the terminal position (e.g. as in *Anemone nemorosa*, see Shirreffs, 1985). Non-terminal ramets are formed with a specified probability at non-terminal nodes. A ramet dies if the resource level at the node to which it is attached is zero or negative. Non-terminal ramets remain at fixed positions that are determined by the nodes and have the potential to live indefinitely, provided they are not outcompeted by other ramets.

Simulation experiments

The model has a large number of parameters (see Table 1 and Appendix 1). All simulations were performed on three types of 'model plants' (Table 2) repre-

Table 2. 'Model plants' used in simulations

Parameter	Basic (B)	With dormant bud activation (D)	Of variable size (V)
Maximum ramet size	1	1	1
Minimum ramet size	1	1	0.1
Dormant bud activation probability	0	0.05	0
Non-terminal ramet formation probability	0	0.05	0

senting three specific points in the parameter space. These were (i) a plant with no variation in ramet size and no ability to activate older dormant buds (further denoted B for basic), (ii) a plant with no variation in ramet size and with an ability to activate dormant buds, both to form ramets and rhizomes (further denoted D for dormant) and (iii) a plant with variable ramet size, but with no ability to activate older dormant buds (further denoted V for variable size). To minimise arbitrariness in the choice of parameter values, basic parameter values for these model plants were selected to approximate values from a stand of grass ramets in short-turf grassland in an area of $1 \times 1 \text{ m}^2$ in size. We used data on architectural and growth parameters from a studied previously mountain grassland system (Table 1; Herben *et al.*, 1993; Hara and Herben, 1997; Wildová, unpublished data; see also Suzuki *et al.*, 1999; Pecháčková *et al.*, 1999).

All variable parameters from Table 1 were tested for each model plant. In the tests, separate simulations were run with different parameter sets. In each test, only one parameter was changed (using four to five parameter values from Table 1) while all other parameters were held at the basic values. The larger range of values was used to find not only the slope/sign of the response of the model but also its shape (concave, convex, unimodal) around that parameter value. The effect of each parameter was determined in two different scenarios:

(1) a single-species system starting with 50 'seedlings' of one 'species' randomly positioned in the simulation plane. Each of these seedlings gave rise to a two-node rhizome with one terminal ramet. No new plants were allowed to establish in later steps. Simulations were run for 200 time steps; preliminary simulations showed that this was long enough to attain stable values of the ramet number and architectural parameters.

(2) a system of two species starting with 25 'seedlings' of each 'species'. The two competing 'species' had identical values of all the parameter except the parameter being tested; one species always had the basic set of parameters; the other one had one parameter changed. Again, no new plants were allowed to establish in later steps. Both species were always of the same type (B, D, or V). Simulations were run always for 100 time steps; 100 time steps was enough for

the overall number of ramets to reach a plateau and competition to take place. We used a shorter time interval than in (1) since 200 time steps often lead to a complete disappearance of one of the two species. If neither species was fully outcompeted after 100 steps, the proportion of the ramet number of each species was used as a measure of their relative success in competition. Ten realisations were run for each parameter combination, both in single-species and in two-species systems.

Simulation results were used to produce three response variables for each parameter combination. Two of them were based on one-species systems: (i) number of ramets, and (ii) the number of genets. Proportion of number of ramets of the two species at the end of the two-species simulation was used as the third response variable; it is assumed to express a 'competitive' (dis-)advantage conferred by the parameter in question.

These response variables were plotted against the model parameters. To compare effects of individual parameters on ramet number and competitive performance the following procedure was used. First, response in both ramet number and competitive performance were plotted against each model parameter, and the largest range of values of the parameter that produced an approximately linear response, both in ramet number and competitive performance was found (for these ranges, see Table 1). The response in ramet number was measured by $2(a - b)/(a + b)$, a and b being average values of the ramet number at each endpoint of the range of the parameter values tested. The response in competitive performance in two-species systems was measured as $(a_1 - a_2 - b_1 + b_2)/(a_1 + a_2 + b_1 + b_2)$, a_1 and b_1 being ramet numbers for species 1 at each endpoint of the range tested, and a_2 and b_2 the same values for species 2. The slope over this range approximates the slope of the response surface for ramet number and competitive performance. The slope thus expresses the type and strength of the effect of the parameter on ramet number and competitive performance. These slopes in ramet number and competitive performance (for all model parameters studied) were then plotted against each other.

At the end of each simulation, ramet densities were converted to a grid of 30×30 cells and exploratory spatial analysis was performed on these data. For single-species systems, spatial autocorrelation using Moran's I was calculated (Upton and Fingleton, 1985). Approximate significance of the spatial correlation was determined by full randomisation of the grid data (200 randomisations); a significance threshold of 0.05 was used. In the two-species system, spatial correlations between the two species, from a lag of 0 (i.e. in the same cell) up to a lag of 3 cells, were also assessed using Moran's I. Since some parameter combinations resulted in (almost) complete disappearance of one of the species after 100 steps, it was impossible to calculate meaningful autocorrelations after such periods of time. Therefore autocorrelations were studied in

two-species systems after 55 steps, when both species were still present in sufficient quantities; this time span was sufficient for both species to fully fill the plot and for the competitive processes to have begun, but not long enough for the disappearance of one of the species. These data were used only to assess spatial correlation between the species.

Results

Most of the parameters tested had a strong effect on most of the response variables. Parameters of resource accumulation/maintenance (Fig. 3a, d) and density dependence strongly affected ramet density; the effect of architectural parameters was weaker, but still pronounced. In most cases, if a change in the parameter value led to a higher number of ramets, it also led to a higher number of genets. Two parameters (translocation range and accumulation rate; the latter in B plants only) deviated from this pattern; a change in these parameters that increased ramet number led to a marked decrease in number of genets.

The effects of individual parameters on competitive ability in the two-species system were not independent of their effect on the ramet number (Fig. 4); the change in parameter value that increased the ramet number in the single-species system often conferred a competitive advantage in the two-species system. In particular, changes in resource accumulation rate, density dependence, investment into the terminal ramet and integration range that increased ramet number in the single-species system also had the same effect in the two-species system (Fig. 3a, b vs. d, e). Some parameters did not fit this pattern. Branching angle had very little effect on ramet number in single-species systems of plants with fixed ramet size. In contrast, the range of values tested had a strong effect on the success of the species in mixture, with higher branching angles conferring a competitive advantage (Fig. 3c vs. f). The same was true, to a lesser degree, for resource retained and branching probability. The most striking effect was caused by change in the internode length. In single-species systems, increasing internode length brought about a slight decrease in ramet density (in B and D plants). In contrast, in two-species systems, increasing internode length over the same range of values conferred a strong competitive advantage (Fig. 4).

There were some differences between the model plants. The D plant differed from the other two plants by a very weak response (in all response variables) to change in branching probability; on the other hand, it was the only plant strongly affected by the node lifespan. It also showed the strongest response to the 'resource retained' parameter, mainly in two-species systems. Plants with variable size (V) generally responded more strongly to most of the parameters.

Spatial pattern in single-species systems was generally fairly homogeneous with no spatial variation in density. At a spatial lag of 1 grid cell (-0.03 of the

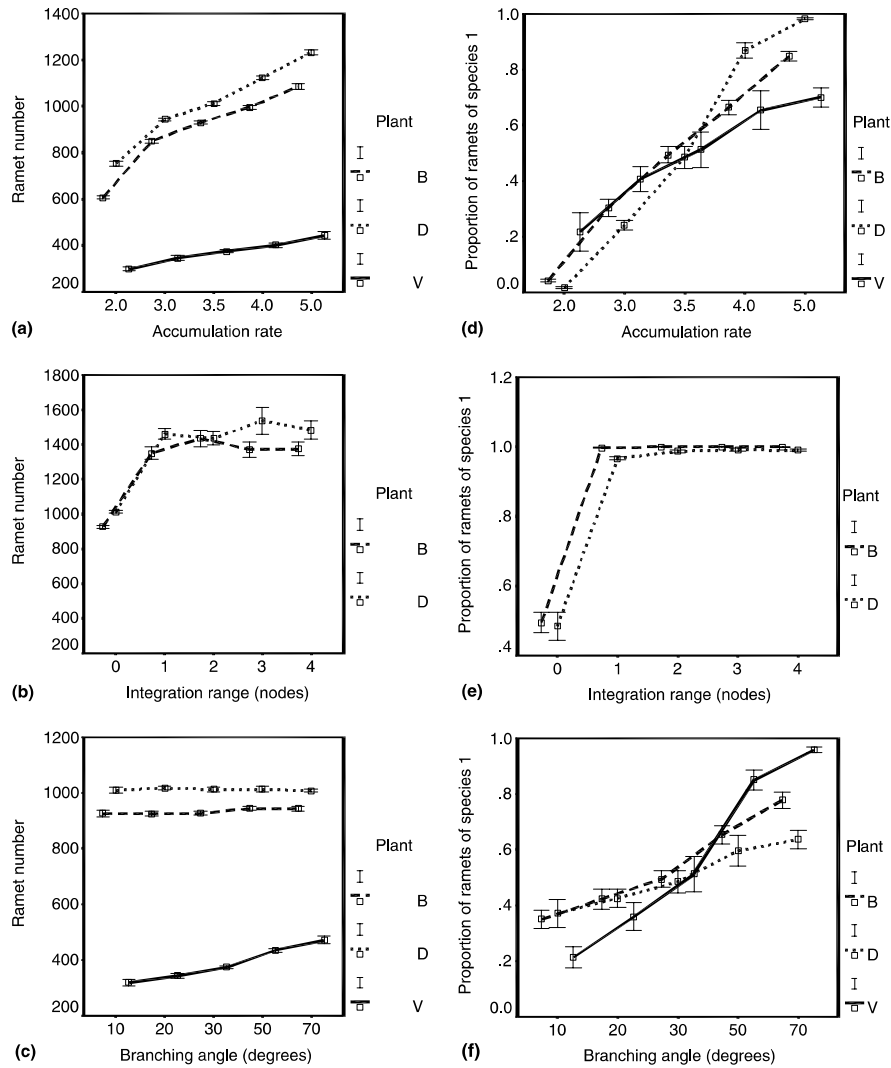


Figure 3. Effects of accumulation rate (a, d), integration range (b, e) and branching angle (c, f) on ramet density in a single-species system (a, b, c), and competitive performance in the two-species system (d, e, f). In the two-species system, always species 1 had the altered value of the parameter tested; the species 2 had standard values (Table 1) of all parameters. Bars indicate two standard errors of the mean ($n = 10$ in all cases).

plane side), some parameters (internode length, branching angle, translocation distance, node lifespan and investment into the terminal node; the last two only in D plants) had a marked effect on spatial structure. Ramet density in plants with short internode lengths and small branching angles was significantly negatively autocorrelated over spatial lags of 1 cell. Plants with non-zero

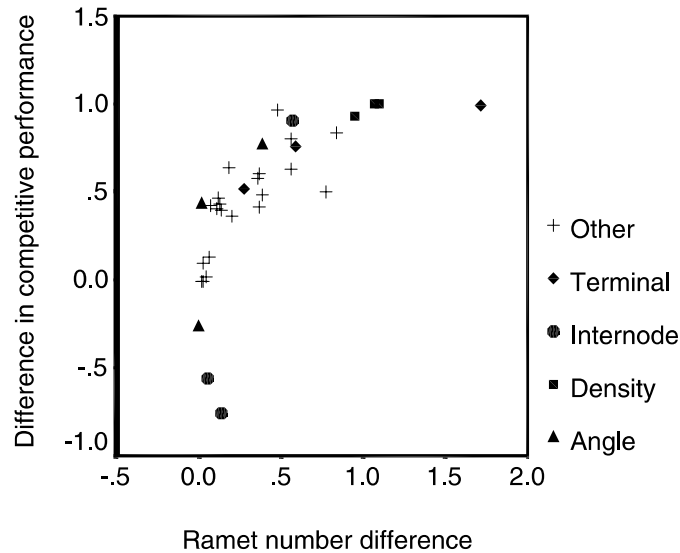


Figure 4. Summary of effects of individual parameters on ramet number in the single-species system and on competitive performance in the two-species system. Values on the abscissa are standardised effects of the change of the parameter on the ramet number; values on the ordinate are standardised effects of the same change of the parameter on the competitive performance (see methods for the details). A values of 0 on the abscissa means that the change of a particular parameter had no effect on the ramet number; values of 1 means that the parameter range led to the twofold increase in the ramet number. Ordinate values of 0 mean that the particular parameter had no effect on competitive performance; a value of 1 mean that the parameter change led to complete dominance of the species with higher ramet number in the single-species system, while value of -1 mean that the parameter change led to complete disappearance of the species with higher ramet number. Each point represents an effect on one parameter in one model plant system.

translocation showed significantly positive autocorrelation of ramet density over the same spatial lag; in addition, the D plants showed higher aggregation over this lag if they had longer node lifespan or less investment into terminal nodes. No systematic significant correlation was found at lags greater than 1 grid cell (~ 0.03 of the plane); this means that no spatial correlations extend beyond the neighbourhood size (0.05 of the plane).

In two-species systems, there was also no large scale spatial structures in ramet populations. In addition, variation between different realisations of one parameter combination was often rather large. Consistent spatial segregation of plants developed if the competitors differed in one of the following parameters (Fig. 5): translocation range (both for B and D plants), 'resource put into the terminal node' (mainly for B plants), internode length (mainly in D plants with short internode lengths), branching angle (mainly small angles in D plants). The spatial segregation of species was usually strongest at a lag of 0 cells (exclusion within the range of ~ 0.03 of the plane) and got weaker at increasing spatial lags. In contrast, no spatial segregation developed with

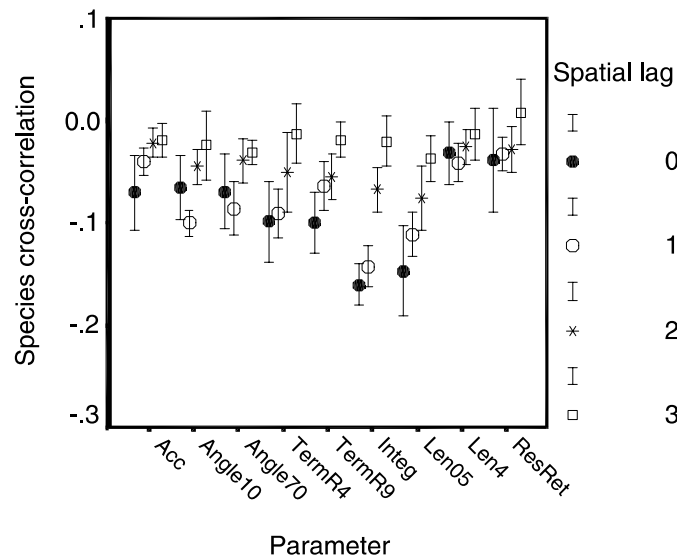


Figure 5. Spatial segregation in systems of two competing species differing in one parameter (after 55 steps; D plants). Species cross-correlation is measured by Moran's I, spatial lag is in cells (~ 0.03 of the plane side). Always a species with the standard parameter combination was competing with a species with: accumulation rate of 2 (Acc), branching angle of 10 (Angle10), branching angle of 70 (Angle70), terminal ramet resource of 0.4 (TermR4), terminal ramet resource of 0.9 (TermR9), integration range of 2 (Integ), internode length of 0.005 (Len05), internode length of 0.04 (Len4) and Resource retained of 0.9 (ResRet). Bars indicate two standard errors of the mean ($n = 10$ in all cases).

competition if plants differed in resource retained, internode length (plants with internode lengths of 0.01 and 0.04 competing with each other) and resource accumulation. There was no correlation between the tendency to develop spatial structure and intensity of the competitive exclusion (i.e. the proportion of the species after 100 time steps).

Discussion

Limitations of the approach

Here that the results obtained by our approach are only valid under rather specific assumptions. First they are valid only for the range of parameters tested; in a non-linear system with many parameters no inference can be made over regions of parameter values that have not been explored. A comparison of B and D plants shows that parameters such as node lifespan or branching probability have very different effects on each of these plants, indicating non-additive effects between parameters. This makes the results strongly dependent

on good qualitative and quantitative choice of 'model plants'. Different choices may not produce the same types of model behaviour. While we attempted to mimic parameter values for real plants for which there is information available, a few parameters had to be provided by 'educated guesses'. This is mainly the case of resource parameters; as the model shows that these parameters generally have strong effects on the outcome, different choices might have led to very different results.

Second, the outcome of each simulation is determined both by the parameter choice and by initial conditions. While preliminary simulations showed that the effect of initial conditions on ramet density and branching pattern is generally negligible, this cannot be taken for granted for all parameter combinations. The present data do not enable the effects of processes that take place at full density (i.e. when the species has/have filled the simulation plane up to their carrying capacity) to be distinguished from those that take place at the transient stage. The effect of initial conditions is particularly important for the genet number as the response variable (and correlations that involve it), since all the scenarios studied were based on initial seedling recruitment only (Eriksson, 1993); this makes the effect of initial conditions for this response variable critical. Differential effects of individual parameters on the correlation between ramet density and genet number may be caused by the way in which these parameters affect competition before full density has been attained.

Single-species systems

The model was able to closely mimic many higher-level (i.e. populations of ramets) patterns found in clonal plants. Some of these patterns have been long known from other models of single-species systems, such as change in equilibrium density with change in competition intensity or resource accumulation rate (Piqueras *et al.*, 1999) or dependence of spatial structure on internode length or branching angle (Bell, 1984, 1986; Winkler and Schmid, 1995). Some effects have been less explored. In particular, it turned out that resource translocation as implemented in the model had profound effects on the structure of the simulated stands. It increased ramet density and made the plant more competitive; it also made the density of a species in a cell positively correlated with the density of the same species in nearby cells. This is likely to be due to the fact that translocation may partially compensate for competitive effects of nearby ramets (Alpert, 1995). A patch of high ramet density in non-translocating plants reduces density in nearby patches by competition. If translocation is involved, some of the plants in a highly competitive neighbourhood are likely to get support from outside the high-competition patch. As a result, the high-density patch may be less affected by density-dependent mortality due to neighbourhood competition which could show up as autocorrelations at a distance of one

cell. The support due to translocation may also help a rhizome to survive when it has to pass through a locally dense patch of ramets. This is likely to lead to lower ramet/rhizome mortality, and thus both to a higher overall density in single-species systems and to an increased competitive ability of such a physiologically integrated plant in two-species systems.

In terms of differences between the model plants, the D plant (i.e. the one that is able to activate dormant buds) differs from the other two plants in number of critical parameters. It is not affected by branching probability; clearly the activation of the dormant buds can compensate for a low terminal branching probability. On the other hand, it is the only plant that responded in competition, ramet density and spatial structure to change in node lifespan; increasing node lifespan increases the size of the bud bank.

Spatial structure emerging

The modelling framework we employed did not lead to the formation of any large scale structures; in contrast, smaller-scale structures were rather common, but their formation was parameter-dependent. Architectural parameters and parameters that affected resource distribution between nodes usually changed the spatial pattern, while other parameters did not. These results thus can shed some more light on the old controversy of whether spatial segregation can be used as an indication of competitive interactions (Wilson, 1995). The results show that the degree of spatial segregation may depend strongly on the exact trait involved in competition and it will develop under a certain subset of competitive mechanisms; therefore the spatial pattern itself can hardly be used to infer a competitive process. Species segregation in a homogeneous system is very likely to be due to neighbourhood competition, but the reverse implication does not necessarily hold.

Relationship between performance in single-species and two-species systems

One of the striking results of this study is the fact that changing a parameter value to increase the equilibrium ramet density in a single-species system does not necessarily mean that the same parameter change would increase competitive ability in the two-species system. These responses are correlated for parameters directly affecting resource accumulation and maintenance, viz. resource accumulation rate, density dependence and resource retention. For these parameter, the positive correlation is rather trivial: resource parameters determine how effectively the species can draw resources from its environment. This directly affects both equilibrium density and competitive performance. In contrast, architectural parameters (branching probability, branching angle, dormant bud activation probability and internode length) affect competitive

ability and ramet density in opposite ways (i.e. the change in the parameter value that decreased density in the single-species system improved competitiveness). Presumably, changing these parameters in two-species systems changes the relative amounts of interspecific vs. intraspecific competition. If internode length is short or the branching angle is small, a ramet is more likely to compete with ramets of the same species (Winkler and Schmid, 1995). It is therefore positioning new plants into positions that are a priori less favourable because of spatially constrained intraspecific competition. This is likely to give a competitive disadvantage if neighbouring plants are of a different species. In contrast, a plant that places daughter ramets farther away is distributing them into sites that may be just as favourable as unfavourable.

The absence of correlation between equilibrium ramet density or biomass and competitive ability shows that these traits have to be treated as different. This absence of correlation may have important evolutionary implications. Namely, a plant can maximise its competitive ability by changing different subsets of underlying growth and developmental processes. Since different plants are likely to be constrained in different ways because of their evolutionary histories, there will be a variety of means by which maximum competitive ability could be attained. Some of these evolutionary changes will also lead to a higher density in the single-species stand; there will be a positive correlation between ramet density and competitive ability in such a group of evolutionarily related plants. In contrast, if the plant attained the higher competitive ability by some other ramet-level trait, the correlation may be negative.

The weak correlation between density in the single-species system and competitive ability holds for systems where maximum plant size is constrained (Suzuki and Hutchings, 1997) and this constraint is similar in both competing species. If species that compete differ markedly in their maximum sizes, the resulting pattern is strikingly different. In such a case, growth rate or the maximum size a plant can attain is often the important trait that determines competitive success (Keddy, 1990; Pacala and Silander, 1990; Silander and Pacala, 1990). In non-clonal plants it is thus possible to predict the outcome of competition between two species from the value of this parameter only (Keddy, 1990). In contrast, our simulation results show that in clonal plants there does not seem to be a similar proxy variable that would enable prediction a priori of the outcome of interaction between several species.

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Appendix 1: Main structural assumptions in the model

Resource accumulation and ramet growth in size

Ramet sizes (for the V plants; B and D plants have ramets of fixed sizes) are expressed in arbitrary units (with the meaning of mass). The scale of these units is given by the parameter K , which means the maximum ramet size that the species can attain relative to the initial ramet size (ramet size formed after seedling establishment). The ramet growth follows the formula:

$$x_{t+1} = x_t + r_c(K_c - x_t)/(1 + \alpha N), \quad (\text{A1})$$

where x_t is the ramet size at the time t , r_c is the growth rate for that species, K_c is the maximum ramet size for that species, α is the density-dependence constant for that species and N is the sum of sizes of all ramets within a circular neighbourhood of that ramet.

In all nodes with ramets present, the resource is accumulated at individual nodes following this formula:

$$R_{t+1} = SR_t + A(x_t/x_{\text{init}})(1 - \beta N)/(1 + \beta N), \quad (\text{A2})$$

where R_t is the resource of the node at the time t , x_t is the ramet size at the time t (when $\beta N < 1$) and x_{init} otherwise, S is the resource retained, A is the accumulation rate, β is the density-dependence constant of resource accumulation for that species and N is the sum of sizes of all ramets within a circular neighbourhood of that ramet. In nodes without ramets, resource is affected only by maintenance costs (S) and translocation.

Acropetal translocation takes place at terminal buds for branching, and horizontal tip growth (addition of a new node). At each time step (i.e. plastochron), the growth the terminal node evaluates the following quantity:

$$R_{\text{avail}} = R_0 + \sum_{j=1}^T (1 - C_T)^j R_j f_{\text{tr}} \quad (\text{A3})$$

where R_i is the resource level of i th ramet in basipetal direction (the terminal ramet is coded 0), f_{tr} is proportion of the resource that is available for translocation, C_T is the cost of translocation (a resource fraction that is lost when translocated over one node) and T is the translocation distance (number of nodes over which translocation takes place). Note that for $T = 0$ the model defaults to a usual architectural model without translocation. The resource in each node involved in translocation (as source, i.e. $i > 0$) has its resource diminished to $R_i(1 - f_{\text{tr}})$; the difference between this quantity and the quantity brought to the sink node is due to translocation cost. This translocation takes place always, no matter whether the terminal node happens to have sufficient resource for growth or branching or not.

Acropetal translocation also takes place at non-terminal nodes before dormant bud activation and non-terminal ramet formation. The formulas are identical, but the translocation takes place only if the resource to be translocated will be sufficient for bud activation. Only resource positioned basipetally from the node can be translocated and translocation takes place only after the conditions for activation (including evaluation of the potentially translocable resource) are satisfied. For the dormant bud activation and non-terminal ramet formation, R_{avail} is hence calculated inde-

pendently using the resource left in the rhizome, i.e. the apex takes priority as a sink; only when its requirement is satisfied, the rest of the resource can be used for other processes.

A terminal node forms a new node and put its own ramet to that node always when the following condition is met:

$$R_{\text{avail}} > C_i + R_{\text{min}}/f_g, \quad (\text{A4})$$

where R_{avail} is the value defined by Equation (A3), C_i is the internode cost, f_g is the proportion of resource put into the new ramet at the growing tip, R_{min} is the minimum resource required for ramet formation (ramet cost). When a new node is added, it is formed at a distance from the current terminal node drawn from the Gaussian distribution with the mean and standard deviation given by the values from the Table 1. The angle of the newly formed internode with the previous internode is drawn from the Gaussian distribution with the mean zero and a given standard deviation.

Ramet size after branching or non-terminal ramet formation is set to

$$x_t = \min(R_t, K_c), \quad (\text{A5})$$

where R_t is the initial resource of the newly formed ramet at the time t , x_t is the ramet size at the time t , K_c is the maximum ramet size for that species. This expresses the dependence of the initial ramet size on available resource; the higher the available resource in the rhizome when a branch with a ramet or a non-terminal ramet are formed, the bigger the ramet will be.

The initial ramet resource is

$$R_t = (R_{\text{avail}} - C_i)f_g, \quad (\text{A6})$$

where R_{avail} is the value defined by Equation (A3), C_i is the internode cost, and f_g is the proportion of resource put into the new ramet at the growing tip. This is identical also for branching.

A node forms a lateral branch (after the new terminal node has been formed; the branch is consequently attached to the second youngest node and is thus of the same plastochron age as the tip) with the specified probability (probability of terminal branching) if the following conditions are met

$$R'_{\text{avail}} > C_i + R_{\text{min}}/f_g \quad (\text{A7})$$

distance to the previous branch is greater than a specified value
(branching constraint),

where R'_{avail} is the value defined by Equation (A3) reduced by the cost of producing terminal ramet and the internode (following Equation (A6), i.e. $R'_{\text{avail}} = (R_{\text{avail}} - C_i)(1 - f_g)$), C_i is the internode cost, R_{min} is the minimum resource required for ramet formation, and f_g is the proportion of resource put into the new ramet at the growing tip. The left/right decision in branching is made on the basis of ramet density in the position where the new node is being put (to simulate red/far red ratio sensing of the neighbourhood density).

A non-terminal ramet (i.e. a ramet attached to a non-terminal node) is formed with a specified probability (parameter probability of non-terminal ramet formation) if the following condition is met:

$$(1 - k\beta N) > 0, \quad R_{\text{avail}} > R_{\text{min}} \quad (\text{A9})$$

where R_{avail} is defined by Equation (A3), R_{min} is the resource required to produce a ramet, β is the density dependence constant of resource accumulation for that species, k is a positive constant and N is the sum of ramet sizes of all neighbours of that ramet. The second part of the condition assures that ramet is formed only when it is likely to have a positive photosynthetic balance (i.e. when $N \ll 1/\beta$).

A ramet dies if its resource calculated by Equation (A2) is ≤ 0 . The same process applies to non-terminal and terminal ramets. A node at the basipetal position dies if its age (i.e. current time step time minus step of its formation) exceeds a specified constant (Node Lifespan).

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A branch (i.e. an internode with a node with a terminal ramet attached) is formed by activation of a dormant bud with a specified probability (dormant bud activation probability) if the following conditions are met:

$$R_{\text{avail}} > R_{\text{min}} + C_i/f_g \quad (\text{A10})$$

distance from the tip is bigger than a specified constant,

where R_{avail} is defined by Equation (A3), R_{min} is the resource required to produce a ramet, C_i is the internode cost, and f_g is the proportion of resource put into the new ramet at the growing tip.

The conditions are evaluated in the order: (1) terminal internode growth (including associated translocation), (2) branching, (3) non-terminal ramet formation and dormant bud activation. Along the rhizome, nodes are always evaluated in basipetal direction (i.e. starting with the youngest node). Ramet size growth (for V plants) and resource accumulation are evaluated in separate passes through rhizomes.

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