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Architectural and growth traits differ in effects on performance of clonal plants: an analysis using a field-parameterized simulation model

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Individual traits are often assumed to be linked in a straightforward manner to plant performance and processes such as population growth, competition and community dynamics. However, because no trait functions in isolation in an organism, the effect of any one trait is likely to be at least somewhat contingent on other trait values. Thus, to the extent that the suite of trait values differs among species, the magnitude and even direction of correlation between values of any particular trait and performance is likely to differ among species. Working with a group of clonal plant species, we assessed the degree of this contingency and therefore the extent to which the assumption of simple and general linkages between traits and performance is valid. To do this, we parameterized a highly calibrated, spatially explicit, individual-based model of clonal plant population dynamics and then manipulated one trait at a time in the context of realistic values of other traits for each species. The model includes traits describing growth, resource allocation, response to competition, as well as architectural traits that determine spatial spread. The model was parameterized from a short-term (3 month) experiment and then validated with a separate, longer term (two year) experiment for six clonal wetland sedges, *Carex lasiocarpa*, *Carex sterilis*, *Carex stricta*, *Cladium mariscoides*, *Scirpus acutus* and *Scirpus americanus*. These plants all co-occur in fens in southeastern Michigan and represent a spectrum of clonal growth forms from strong clumpers to runners with long rhizomes.

Varying growth, allocation and competition traits produced the largest and most uniform responses in population growth among species, while variation in architectural traits produced responses that were smaller and more variable among species. This is likely due to the fact that growth and competition traits directly affect mean ramet size and number of ramets, which are direct components of population biomass. In contrast, architectural and allocation traits determine spatial distribution of biomass; in the long run, this also affects population size, but its net effect is more likely to be mediated by other traits. Such differences in how traits affect plant performance are likely to have implications for interspecific interactions and community structure, as well as on the interpretation and usefulness of single trait optimality models.

Species traits are general, genetically determined characteristics of morphology and physiology. Such traits are often used in ecology to group species; these groups are then used to explain and predict community structure and dynamics (Grime et al. 1988, Smith and Huston 1989, Diaz et al. 1992, Keddy 1992, Thompson et al. 1993, Lavorel et al. 1997, Westoby 1998, Weiher et al. 1998, Weiher and Keddy 1999). A critical assumption of such predictive approaches is that direct straightforward linkages exist between individual traits and species performance. However, organismal traits are inevitably correlated with other traits and therefore their effect is both defined and constrained due to interactions among traits (Reich et al. 1997, 1999). Combined with likely different evolutionary histories in different lineages, the same trait values could thus lead to quite different performances for individual species, and rather than simple universal linkages between traits and performance, such linkages are expected to be highly contingent upon the entire suite of trait values of an organism.

In this paper we explore the degree of contingency of trait-performance linkages for a number of traits across a group of co-occurring plant species. The ideal approach to quantifying such trait-performance linkages would be to manipulate individual traits and observe the consequences for individual or population performance of different species. This can sometimes be accomplished by direct ecological, physiological or genetic manipulation (Berendse 1982, Ballare et al. 1994, Schmitt et al. 1999, Pierik et al. 2004). However, despite recent advances (Ballare 2001), such experimental manipulation is impossible for many ecologically relevant traits. A more common approach is to compare closely-related species on the assumption that common evolutionary history would reduce variation in the correlated trait values, making it easier to isolate the effects of variation in single traits (Silvertown et al. 1997, Huber et al. 1998). This approach can be very useful, but variation in multiple correlated traits is still likely. In addition, this approach is difficult to apply when the question of interest involves comparisons of co-occurring species. Another possible approach is to compare genotypes that differ in trait values within a species (Skalova et al. 1997, Fischer and van Kleunen 2001); this approach is limited to traits in which the species is variable and correlations between traits may still occur at the genotype level.

In this study, we developed a new complementary approach to compare effects of different traits on plant performance: manipulation of traits in a simulation model that has been carefully parameterized for real plants. Such an approach makes it possible to manipulate any single trait independently of all other traits, without the artifacts inevitably introduced when manipulating real plants.

At the same time, because the models are parameterized from real plants, tests of effects of any single trait nevertheless are done in the context of realistic values of the traits not being manipulated. Thus the degree to which effects of single traits are contingent on the combination of traits found in real plants can be detected. This ability to detect contingency of results in the context of realistic trait combinations is what distinguishes our approach based on models parameterized for specific plant species from the widespread use of generalized models to analyze the role of traits in ecological processes and patterns (Stuefer et al. 1998, Oborny et al. 2000, Herben and Suzuki 2001, Oborny and Kun 2001, Chesson and Peterson 2002).

Population-level performance of any particular plant species in a community is due not only to traits affecting growth, allocation and competition, but to traits that determine its spatial spread within the community (Cheplick 1997, Brewer et al. 1998). In this study, we focus on clonal plants, where spatial spread is determined largely by architectural traits such as rhizome length or branching patterns (other models of clonal plants: Bell 1986, Cain 1994, Cain et al. 1995, 1996, Oborny 1994, Oborny et al. 2001, Stuefer et al. 1998, Wolfer et al. 2006). In clonal plants, each "individual" is composed of ramets (=potentially independent units with leafy shoots and roots) that are connected by spacers (e.g. rhizomes and horizontal stems, usually lacking chlorophyll). Such plants have to balance investment into size of individual ramets vs numbers of ramets, and vs growth of spacers.

We distinguish two major sets of traits for detailed analysis of their effects on plant performance: (1) growth traits, including individual ramet growth, resource allocation and competition traits (density-dependence of growth), and (2) architectural traits that determine ramet spacing, such as spacer length or spacer branching frequency and angle. These individual-level traits all influence population dynamics and abundance but, because of tradeoffs among traits and the spatially-explicit nature of plant competitive interactions, may contribute positively or negatively to the outcome of intraspecific competitive interactions. Therefore, we assess the effects of individual level traits, including individual ramet growth rate, on population abundance. For plants with indeterminate growth, biomass is a much better measure of abundance than density; we used total aboveground biomass after a specific time period as our operational definition of performance. We further compared three variables that capture specific components of performance: mean size of produced ramets, number of ramets and total length of spacers, as a measure of colonization ability. Differential investment into these components can dramatically change competitive ability of clonal plants (Gough et al. 2001). In this way we can address whether varying a single trait produces uniform responses in all three performance components, or, alternatively, has qualitatively different effects on each of the components, which could result in tradeoffs among performance components.

The aims of this study are therefore (1) to examine how individual traits affect performance when uncorrelated with other traits and to rank traits according to their effect on plant performance, (2) to examine the contingency of effects of different traits, i.e. how their effects are modified by the values of other traits. The more traits are contingent in this sense, the more likely that effects of trait variation will be highly species specific rather than generally predictable, (3) to examine whether traits affect the three components of performance in similar ways, and (4) to examine whether the two main types of traits (growth/allocation/competition and architecture) affect overall performance in similar ways.

We use a spatially explicit clonal plant growth simulation model developed by Herben and Suzuki (2001). This model combines a ramet growth/allocation model, an individual-based inter-ramet competition model and an architectural model and has sufficient realism to be parameterized for real plants. Although several recent models of clonal growth have employed architectural, resource uptake and competition rules parameterized by real species to attempt to explain and predict their behavior (Cain et al. 1991, Klimeš 2000, Winkler and Stocklin 2002), none of them have been validated by field data. In contrast, before addressing our questions, we parameterized the model to match real plants of six co-occurring species and validated it with an independent garden experiment. We then tested the effects of two major sets of traits (ramet/growth/allocation/competition traits and architectural traits).

Methods

The study system and focal species

To parameterize and validate the model we used six co-occurring wetland clonal sedges (Cyperaceae spp.). These species are the most common sedge species in sotheast Michigan fens (Hershock 2002) and represent a gradient from closely spaced ramets (*Carex stricta* and *Carex sterilis*) to intermediate spacing (*Carex lasiocarpa*) to more widely spaced ramets (*Scirpus acutus*, *Cladium mariscoides* and *Scirpus americanus*). All study species have long-lived rhizomes with sympodial branching (Klimeš et al. 1997). Rhizomes of the three *Carex* species are mainly short, thin and form clumps, although *C. lasiocarpa* and *C. stricta* sometimes produce long rhizomes that connect these clumps. Because these long rhizomes are relatively rare, we only included measurements of short rhizomes in our study. *Cladium* has thin, but somewhat longer rhizomes that are placed deep in the soil. The two *Scirpus* species have thick, long rhizomes that can be as deep as 0.3 m into the soil. Species nomenclature follows Voss (1972).

Plant cultivation

The plants were collected in fens in southeastern Michigan in 1999 (Hershock 2002), with ramets of each species collected a minimum of 0.5 m apart. Each ramet was then vegetatively propagated in artificial pools at the Matthaei Botanical Gardens of the Univ. of Michigan (Ann Arbor, MI). We refer to the descendants of each field-collected ramet as a distinct source clone, although it is possible that some of the source clones for a given species descended from the same genet. Model parameterization and validation were based on measurements of traits and individual plant performance of individuals of the six focal species that had been grown as control treatments for two independent experiments (Hershock 2002, Gough et al., unpubl.) at the Matthaei Botanical Gardens. The plants from one of these were used to parameterize our model, while the plants from the other were used to validate the model. Both sets of plants were grown in 30.5 diameter × 22.9 cm deep plastic pots filled with soil consisting of marl-peat (70:30%) mixtures and pots were placed in kiddie pools kept filled with well water.

Parameterization experiment

In the 2001 growing season, we planted eight replicate pots for each species, each having one pair of connected ramets from a different source clone. The ramets of a given species were all approximately the same age and size. Each ramet pair was planted in the middle of pot, and allowed to grow for 90 d.

At the time of planting, we measured ramet height, then harvested and weighed (dried to constant mass) 50 other individuals of each of the focal species that had been grown under the same conditions. We developed aboveground biomass to height regressions and used them to estimate initial biomass of the planted ramets.

At monthly intervals we marked, with loosely placed wire circles, all new ramets appearing during the interval, and measured heights of all ramets. Ninety days after planting, we harvested all of the plants, dried and weighed separately the ramets and rhizomes of each cohort. To estimate the growth and allocation parameters in Table 1, we used biomass data from the final harvest, and estimated initial and monthly biomass from the biomass regressions. We also measured a number of architectural traits at harvest that were used in the model (Table 1, detailed methods in Appendix 3). The values used for one trait, ramet lifespan, were obtained from a separate long-term competition experiment (Hershock 2002, Petru, unpubl.), where demographic data were collected from 100 ramets of three monitored species during the growing season of 2000 (Appendix 2).

Validation experiment

In May 1999 we planted five unconnected ramets of the same species in each of ten pots per species. All ramets of a species were approximately the same age and size. The five ramets per pot were planted at fixed, evenly spaced positions on one side of a square inner plot 21.6 × 21.6 cm, centered within the 30.5 cm diameter × 22.9 cm deep plastic pots. These plants were

Table 1. Plant traits of architecture and growth (competition, ramet growth and allocation) used in the simulation model, procedures for estimating them to parameterize the model and final estimated values of each trait for individual species. Estimation techniques: M – measured directly from field observations, A – arbitrary value identical for all species, I – indirect estimation from field observations. Species abbreviations used in the table: carlas-*Carex lasiocarpa*, carste-*Carex sterilis*, carstr-*Carex stricta*, clamar-*Cladium mariscoides*, sciacu-*Scirpus acutus* and sciame-*Scirpus americanus*.

Plant traits		Estimation technique	Units	Trait values for individual species					
				carlas	carste	carstr	clamar	sciacu	sciame
Growth (ramets and rhizomes)									
Competitive response	competition	I	unitless	0.03	0.01	0.07	0.07	0.05	0.009
Neighborhood size		A	cm	For all species = 5					
Maximum ramet size	Ramet growth	M	g	0.6815	0.3537	1.663	1.092	1.1252	0.466
Ramet growth rate		M	day^{-1}	0.0517	0.1123	0.0875	0.03079	0.0655	0.0673
Ramet lifespan		M	days	For all species = 140					
Maximum net photosynthetic rate		I	unitless	0.9	0.5	0.9	2	0.5	1
Resource fraction put into new daughter ramet	Allocation	I	1	0.8	0.2	0.5	0.2	0.3	0.6
Internode cost		M	g	0.0029	0.0009	0.0020	0.0835	0.0950	0.0163
Node developmental period		M	days	6	4	8	3	2	1
Architectural (rhizomes)									
Internode length		M	cm	0.233	0.122	0.123	0.503	1.234	2.385
Distance between ramets		M	nodes	4	5	6	18	6	5
Minimum distance between branchings		M	nodes	2	3	4	4	2	2
Branching angle		M	degrees	46	40	44	55	34	38
Probability of non-terminal branching		A	unitless	For all species = 1					

allowed to grow until September 2000. These two years correspond to a total of 300 d during the growing season in the climatic region of southeast Michigan (van den Brink et al. 1971).

At the end of the observation period, we counted the total number of ramets in the square inner plot as well as the number of ramets in only the planted half of the pot. We harvested the aboveground parts of each ramet from each whole pot, dried to constant weight, and weighed (biomass of rhizomes was not measured). After harvesting the aboveground biomass, the belowground part of the pot was sliced down the middle into two halves and the number of rhizomes that crossed the middle line between planted and invaded halves of the plot was counted to characterize one aspect of spatial distribution of clonal growth.

The model

The model simulates vegetative growth of clonal plants, with the nodes and internodes that form the horizontally growing rhizomes as the basic units in the model (Fig. 1). The model runs on a continuous plane with toroidal boundaries (Herben and Suzuki 2001). The simulation plane is initially homogeneous; any heterogeneity is generated by the ramets themselves. The model uses traits of ramet growth, allocation, competitive ability, and spacer (rhizome) architecture to simulate long-term population dynamics (Appendix 1, 2).

Ramets produce "resource" for rhizome growth. This resource may be anything limiting for the plants that is either gathered by the ramet from the environment (e.g. water, nutrients, light) or synthesized by it (photosynthate), and whose accumulation is negatively density-dependent. The rate of resource acquisition by a ramet is determined by competition with neighboring ramets; at each time step, the number of ramets in the neighborhood determines the amount of resource accumulated within each ramet. This amount of resource accumulated can be positive or negative, the latter if the density of neighbors is high. The resource is put into the node bearing the ramet. Resource levels at each node change by resource acquisition by the ramet attached to that node, and by its consumption for growth. Any resource not used is left at the node for the next time step. No translocation is implemented in the model except for production of new nodes and ramets (below) as no data on any translocation traits of real plants were available for our species. A recent field study of translocation effects in these wetland sedges showed that initial physical separation of ramets did not significantly change performance relative to ramets that remained connected, and this was true for all tested growth forms (Pauliukonis and Gough 2004).

Rhizomes grow by adding nodes at terminal positions; the ramet stays at the original node and a new ramet is formed at the newly added terminal node. Therefore, ramets are, by definition, attached to all growing terminal nodes. Non-terminal ramets remain at fixed positions at the nodes where they were formed; they are of fixed lifespan and die after a specified number of steps. Several nodes may be added to a terminal position in one time step to account for different rhizome structures of the modeled species.

A node is always added to a terminal node if the quantity of resource available at the existing terminal node is greater than a species-specific constant (Appendix 1, 2). The resource at the node is reduced by a one-time cost when each immediately subsequent internode is added. If a new node is added, the length and angle of growth of the internode are independent of the amount of resource of the rhizome, and the density of ramets or rhizomes in its neighborhood (neighborhood definition in Appendix 2). After a new node is added, part of the resource accumulated at the maternal node is passed into the daughter node. If the resource is not sufficient, a new node is not added; if it is nevertheless positive the ramet maintains itself to the next step. If the resource is zero or negative, the node bearing the ramet loses the capacity for further growth and dies.

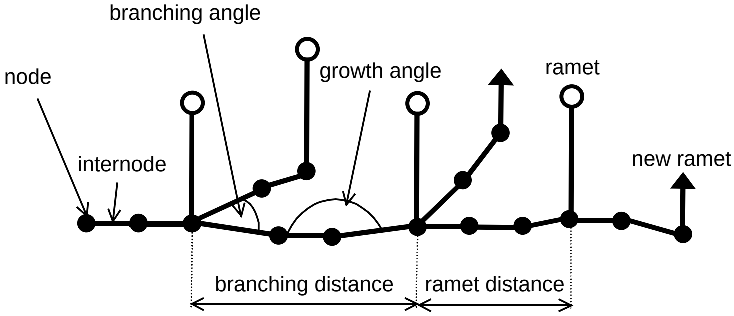

Fig. 1. Definition of architectural traits measured on plants and used in the model. The whole structure represents one rhizome fragment composed of nodes, internodes and ramets.

Nodes may also be added to a rhizome by terminal branching (i.e. by adding two terminal nodes to one at a single time step) or by lateral branching (i.e. by adding a new branch with a new terminal node to a non-terminal node). Both branching processes take place only if the available quantity of resource at that node is sufficient and if the branching is not constrained by architectural rules; the architectural constraint determines the minimum number of nodes between branchings. Branching angle is independent of the resources of the rhizome and of its neighborhood. If a node bearing a branch dies, the branch becomes independent and the rhizome fragments into two.

Simulations

We ran three different sets of simulations: (1) to estimate indirectly several traits using the data from the parameterization experiment; (2) to choose from several plausible parameter sets and to validate the parameterized model using the data from the validation experiment; and (3) to manipulate individual traits to assess their effect on components of performance and total performance. The initial planting design of each set of simulations followed the design of the corresponding parameterization or validation garden experiment (design details in Appendix 3).

Model parameterization and validation

Seven traits were estimated directly from measurements of all ramets in each pot for all eight clones per species in the parameterization experiment. Another three traits, ramet distance, internode length and internode cost were based on four clones only (Table 1, Appendix 2). For six other traits, no field data were available and they were estimated indirectly or set to arbitrary values. Preliminary tests showed that two of them have rather weak (node lifespan) or simple linear (probability of non-terminal branching) effects on plant performance. Therefore, to reduce the multivariate trait space for indirect estimation, these two traits were given arbitrary values identical for all species. Because the effect of neighborhood size was very strongly correlated with that of competitive response in preliminary analyses, we also gave this trait an arbitrary value identical for all species (Appendix 2).

Three remaining traits (competitive response, maximum net photosynthetic rate, and resource fraction put into new daughter ramets) were estimated indirectly by systematic search of the trait space for values that gave the best fit to data from the parameterization experiment (Table 1). The search was done with the model parameterized with the values of all directly and arbitrarily estimated traits (Table 1, Appendix 2). Then we selected a range of values for each of these three traits based on the generation of plausible plants in preliminary tests of the model (for maximum net photosynthetic rate: 0.01 to 9; for competitive response: 0.0005 to 0.1 and for fraction put into new daughter ramet: 0.1 to 0.9). All possible combinations of a range of values of each of these traits were run (4860 combinations for each species).

These simulations ran for 90 steps (corresponding to the 90 d of the parameterization experiment) in five replicate runs of each trait combination. Variation among runs was small and we therefore used the mean responses over the five runs in all analyses. We used several performance variables (number of growing rhizome ends, number of ramets, total length of rhizomes, final mean ramet biomass and number of branchings per pot) to capture the outcome of the simulations. These simulated response variables were compared to observed values and all combinations of values of these three traits that predicted performance within the range of the parameterization observations were selected. This resulted in 34 combinations for *C. lasiocarpa*; 26 for *C. sterilis*; 27 for *C. stricta* and 5 for *S. acutus*. For *C. mariscoides* and *S. americanus*, none of the observed combinations of performance variables were fully matched by any simulation result. For those two species we used the 10 trait combinations that gave the smallest sum of squared differences between observed and simulated values.

For each species, the single combination to be used in subsequent trait manipulation tests was then selected using the data from the validation experiment. We ran the model parameterized with the single values of the directly and arbitrarily estimated traits, and with all successful combinations of the traits estimated indirectly in the parameterization simulations. The model was run in ten replicates for 300 steps corresponding to the total growing season days in the validation experiment.

We then compared simulated and observed performance variables from the validation observations, including total number of ramets, number of ramets in the planted half of the plot, number of rhizomes that crossed the middle line between planted and invaded halves of the plot, and mean ramet biomass. Using these data, we searched for the best fitting combination of indirectly estimated traits for each species using the sum of differences between predicted and observed values of all performance variables with equal weight given to each performance variable. The combination with the smallest average sum of differences over ten replicate runs was taken as giving the best fit and used in the trait manipulations.

Trait manipulations

Values of single traits were manipulated in simulation experiments to quantify the sensitivity of plant performance to changes in each trait separately, while holding all other traits at values found by parameterization/validation (Table 1). For each species, we quantified effects of traits by manipulating each trait from 50% less than to 50% over its observed value. In real plants, most directly estimated traits from our study varied from ±12% up to ±95% of the mean value among measured individuals of each species in the parameterization experiment. For continuous traits (ten out of the total 14 traits), the observed value of the trait was increased by 10, 20, 30 and 50% and decreased by 10, 20, 30 and 50%. Integer values with the range of −50% and 50% were used for the three integer traits (days required to produce one node, distance between ramets, and distance between branchings). Probability of non-terminal branching is defined for a limited range only; its values were distributed regularly to cover the possible range from observed value to a maximum 50% decrease (0.9, 0.8, 0.7, 0.6 and 0.5).

Fifty replicate runs of each trait combination were run for 300 steps each. At the end of each run, number of ramets, ramet size, number of rhizomes and number of branchings were recorded and the total aboveground biomass was calculated as a summary variable. After checking for approximate linearity, we used linear regressions of the response values on the trait values using the mean response from the fifty replicate simulation runs of each trait combination. However, some relationships were better described by quadratic functions indicating more complex responses that would require further exploration exceeding the scope of this paper. We used standardized regression coefficients to compare effects of changes in trait values among species. All calculations were done using SPSS ver. 11.5.1.

Results

Model parameterization and validation

The validated model produced realistic looking plants of different growth forms (Appendix 4). Simulated plants matched the growth of real plants in the validation observations rather well, although the quality of the match differed between species and between performance variables (Fig. 2). The best fits across all performance variables were for *C. sterilis, S. acutus* and *C. mariscoides* followed by *C. stricta* and *C. lasiocarpa*. *S. americanus* was predicted rather poorly in all performance variables (Fig. 2).

The simulated number of ramets was within 30% of the observed values for all species except *S. americanus*. Simulations generally overestimated the mean ramet size for all species (although all differences were within 50% of observed values). Parameters describing spatial arrangement were predicted less well. Relative number of plants that appeared in the planted parts of validation pots was predicted within 25% of observed values for three species and within 50% for two other species; a poorer fit (within 60%) was obtained for *S. americanus*. The number of rhizomes crossing the dividing line between the two halves of the pot was predicted rather poorly for all tested species; three species showed differences within 50% and the other two species (*C. stricta* and *C. lasiocarpa*) within 80% of observed values.

Effects of traits on plant performance

The magnitude and direction of effects of traits on plant performance (= total aboveground biomass) differed strongly among traits within species and among species within traits (Table 2). The performance of the three *Carex* species and *Cladium* was affected by many traits, whereas behavior of *Scirpus* species and especially *S. acutus* was affected by only a few traits (Table 2). Ramet competition traits had strong and similar effects for all species, with only one species, *C. stricta,* being slightly less sensitive to changes in competitive response (Table 2). With the exception of both *Scirpus* species, increasing values of ramet growth traits and one allocation trait, allocation to new daughter ramets, consistently increased plant performance, while increasing values of competition traits decreased plant performance (Table 2).

In contrast, allocation traits that affect rhizome growth and all the architectural traits showed generally smaller effects on total performance (Table 2) and the directions of their effects differed among species, i.e. their effects were more context-dependent. Increasing internode cost strongly decreased performance of *C. mariscoides* and *S. americanus*, both of which have high cost internodes (large biomass per length unit), but had small impacts on other species with less expensive internodes. Increasing node developmental period actually increased performance of all species except *C. mariscoides* and *S. acutus*. The species with the longest rhizomes and inter-ramet distances, *C. mariscoides* and *S. americanus,* were least sensitive to changes in architectural traits, because the slopes of architectural trait responses were very small. Internode length, ramet and branching distances had consistently strong, although contrasting, effects on performance among species, while branching angle and branching probability generally had smaller effects. Longer

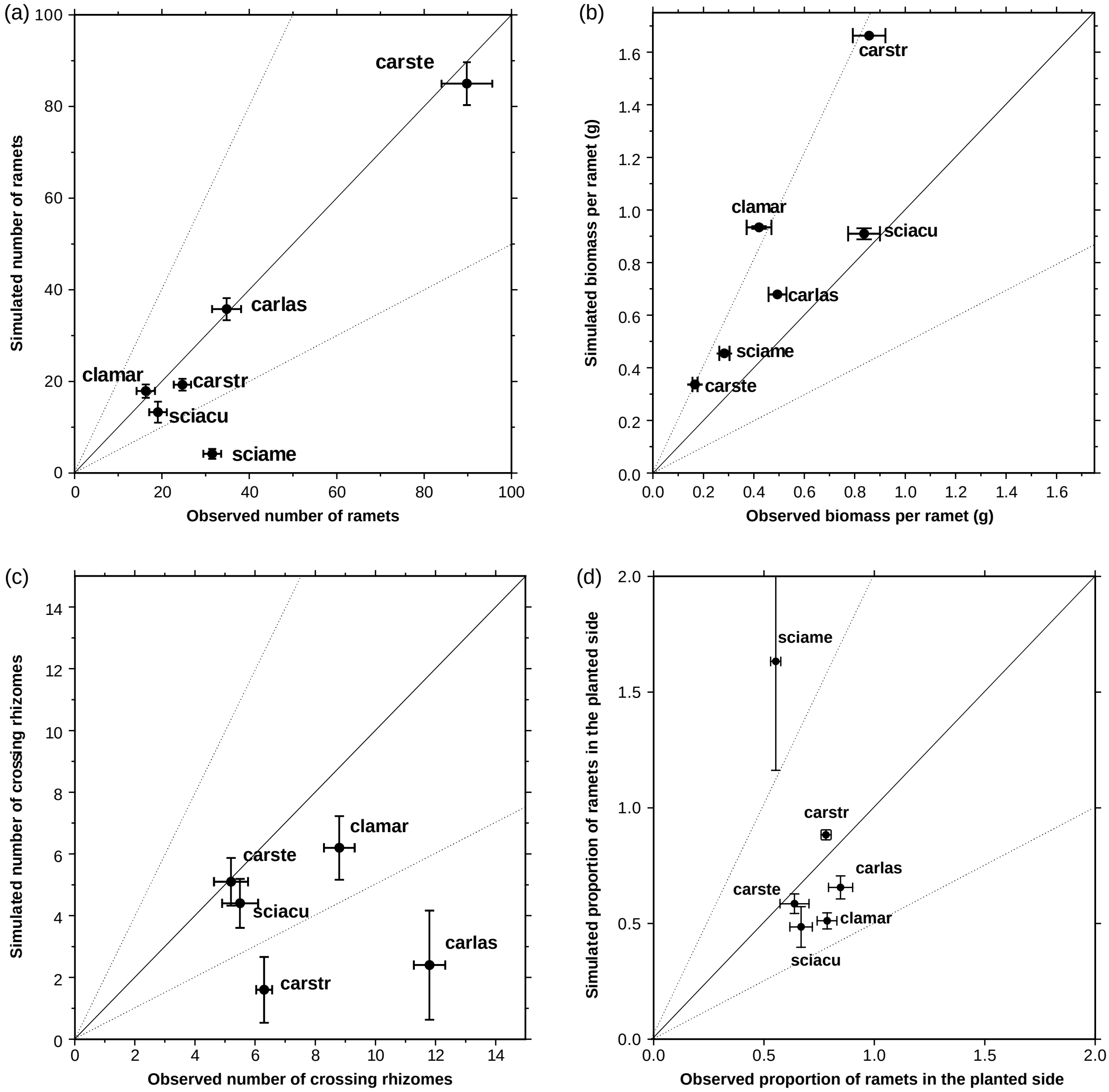

Fig. 2. Comparison of the simulated performance of the final trait combination of individual species with the observed performance in the validation experiment. Each graph represents means and ± SE per species of one performance variable: (a) number of ramets, (b) mean biomass per ramet, (c) number of crossing rhizomes and (d) proportion of ramets on planted side (last two variables are measures of spatial encroachment of clonal growth – for detail description see "Validation experiment" in Methods). The solid line is the 1:1 line (100% fit) and the fine dashed lines indicate 50% fit. Observed and simulated data each represent the mean of 10 replicates. In (c) *Scirpus americanus* was not plotted because simulated results were five times bigger than the observed results, and so off the scale appropriate to show the better-fitting species. For species abbreviations see Table 1.

internodes increased performance of all species except *C. stricta*. More nodes between ramets decreased performance for most species, but increased performance for *C. mariscoides* and *S. americanus*. Longer distance between branchings increased performance of all *Carex* species, had no effect on *C. mariscoides* and decreased performance of both *Scirpus* species. Increased probability of branching had a strong negative effect on *C. mariscoides* while performance of the other species was only slightly affected.

Trait effects on components of performance

When total biomass is broken into components of performance, a given trait often had opposite effects on the individual components. This was the case in 40 out of 84 possible effects (species × trait combinations examined, Table 3). Such tradeoffs among performance variables occurred for all species, although the traits involved differed. Tradeoffs were particularly common in *C. lasiocarpa* and *S. acutus*. The most commonly

Table 2. The effect of changes in trait values on total plant performance (=total aboveground biomass), summarized by slopes (standardized regression coefficients) of linear regressions. Results are based on simulations where trait values were manipulated from −50 to +50% of observed values. For each changed trait value, the mean performance from 50 replicate simulations was used as the dependent variable. Traits with the strongest effect on plant performance ($R^2 \geq 0.750$) are in bold. For species abbreviations see Table 1.

Traits	Standardized slope					
	carlas	carste	carstr	clamar	sciacu	sciame
Growth						
Competitive response	**−0.870**	**−0.857**	−0.499	**−0.965**	**−0.792**	**−0.906**
Neighborhood size	**−0.927**	**−0.874**	**−0.974**	**−0.950**	**−0.878**	**−0.935**
Maximum ramet size	**0.996**	**0.950**	**0.995**	**0.996**	−0.106	0.270
Ramet growth rate	**0.976**	**0.962**	**0.968**	**0.927**	0.266	**0.93**
Ramet lifespan	**0.792**	**0.786**	**0.879**	**0.919**	−0.324	−0.040
Maximum net photosynthetic rate	**0.951**	**0.854**	**0.989**	**0.987**	−0.198	**0.960**
Resource fraction put into new daughter ramet	**0.958**	**1.000***	**0.999**	**0.987**	−0.133	**0.929**
Internode cost	−0.491	0.216	0.174	**−0.977**	0.366	**−0.969**
Node developmental period	**0.889**	0.410	**0.812**	−0.221	**−0.878**	0.485
Architectural						
Internode length	0.666	**0.889**	**−0.844**	**0.826**	**0.963**	0.702
Distance between ramets	0.695	**−0.757**	**−0.748**	−0.537	**0.761**	**−0.847**
Minimum distance between branchings	**0.957**	**0.791**	**0.791**	0.097	**−0.995**	−0.643
Branching angle	0.530	0.687	0.044	0.006	−0.161	0.122
Probability of non-terminal branching	−0.196	0.480	0.236	**−0.752**	0.241	−0.298

* There were only two points for regression because only two trait values produced valid results in simulations. The simulation of *Carex sterilis* failed when new ramet cost was larger than the observed value

found type of contrasting effect of a trait on different performance components (22 times out of 40 total) involved mean ramet biomass vs number of ramets and rhizome length; if a trait increased the former, it decreased both the latter, and vice versa. This tradeoff is shown by many different traits, for example internode length (*C. lasiocarpa*, *C. mariscoides* and *S. americanus*), node developmental period and branching probability (*C. mariscoides* and *S. acutus*), branching distance (*C. lasiocarpa* and *S. acutus*), and branching angle (*C. lasiocarpa* and *C. sterilis*). Further, if changing a trait increased number of ramets and rhizome length, but decreased mean ramet size, total biomass almost always followed the positive effect on number of ramets and rhizome length. For architectural and allocation traits, the types of tradeoffs were more variable among species than was the case for growth/competition traits.

Discussion

Realism of the parameterized model

In general, the model was able to capture growth patterns of plants observed in the garden experiments; with the possible exception of one species (*S. americanus*), it could be parameterized with realistic values that matched fairly well with the independent data set from the validation experiment. This in itself constitutes a check on the realism of model's structural assumptions. Therefore, in spite of the necessary structural simplifications made in the model, these assumptions may be considered to capture all the major processes accounting for growth of a clonal plant. Out of these simplifications, the lack of seasonal dynamics of ramet growth (Pitelka et al. 1985, Laterra et al. 1997, Egli and Schmid 2000), and possibly the lack of complex translocation interactions between ramets (Pennings and Callaway 2000) are likely to be most important. In the model we only employed simple translocation into new ramets, because more complex processes are not well understood for real plants. However, the absence of more complex translocation might have contributed to differences between simulated and real plants. In a simulation study, Herben (2005) showed that translocation traits can be rather important for performance parameters such as number of ramets and competitive ability, especially in species with long rhizomes. This may explain why, in general, lower fits were obtained for the rhizomatous species, especially *Scirpus americanus*, than for the tussock-forming species. Both simplifications above may account for the observed lack of fit, although their relative importance cannot be determined. Ramet growth rates do change during the growing season (Bernard et al. 1985), and among ramets of different ages (Wildová, unpubl.). This in itself produces variation in ramet size distribution and might have accounted for the smaller mean sizes of ramets in real, compared to simulated, plants (Fig. 2).

Table 3. Signs of slopes of linear regressions of performance components on traits (L – total length of rhizomes, S – mean ramet size (biomass), N – number of ramets and T – total biomass), where traits were manipulated from −50 to +50% of the observed value. Regressions based on mean results from 50 replicate simulations of each trait value over the manipulated range. (No effect (0) was used when $R^2 < =0.1$). A tradeoff is defined as opposing effects of a trait on different components of performance. Simulated plants produced several types of tradeoffs where different combination of effects on components of performance were identified.

Traits	carlas				carste				carstr				clamar				sciacu				sciame				No. of species with tradeoffs (max = 6)	No. of tradeoff types (max = 6)
	L	S	N	T	L	S	N	T	L	S	N	T	L	S	N	T	L	S	N	T	L	S	N	T		
Growth																										
Competitive response	−	+	−	−	−	0	−	−	−	+	−	−	−	−	−	−	−	+	−	−	−	0	−	−	3	1
Neighborhood size	−	+	−	−	−	0	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	0	−	−	2	1
Maximum ramet size	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	0	+	+	0	0	1	1
Ramet growth rate	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	0	+	+	+	+	1	1
Ramet lifespan	−	+	+	+	−	+	+	+	−	+	+	+	−	+	+	+	−	+	−	−	−	+	0	0	6	2
Maximum net photosynthetic rate	+	−	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	−	0	+	+	0	+	3	2
Resource fraction put into new daughter ramet	−	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	0	0	+	+	+	+	2	2
Internode cost	−	0	−	−	−	−	0	0	0	0	0	0	−	−	−	−	−	−	+	+	−	−	−	−	1	1
Node developmental period	−	+	+	+	−	−	+	+	−	0	+	+	−	+	−	−	−	+	−	−	0	+	+	+	5	4
Architectural																										
Internode length	+	−	+	+	+	0	+	+	+	−	−	−	+	−	+	+	+	+	+	+	+	−	+	+	4	2
Distance between ramets	+	+	+	+	−	+	−	−	+	+	−	−	+	0	−	−	−	−	+	+	+	0	−	−	5	4
Minimum distance between branchings	+	−	+	+	+	0	+	+	+	0	+	+	0	+	0	0	−	+	−	−	0	−	−	−	2	2
Branching angle	+	−	+	+	+	−	+	+	0	+	0	0	0	+	0	0	−	0	0	0	−	0	0	0	2	1
Probability of non-terminal branching	+	0	−	0	+	+	+	0	+	+	0	0	−	+	−	−	+	−	+	0	0	+	0	0	3	3
No. of traits with tradeoffs (max = 14)	10				4				8				5				10				3				40	

Despite these structural simplifications, we obtained reasonable predictions for relative differences in growth and behavior of our study species. The model can therefore be used to test effects of individual traits on plant performance within a realistic context of other traits.

Sensitivity of performance to single traits

Most of the traits we tested had strong effects on plant performance, at least for some species. However, architectural traits and rhizome allocation had different patterns of effects than did ramet growth/competition traits and new ramet allocation. First, the effects of growth traits on performance were generally stronger than those of architectural traits. Second, effects of ramet growth on plant performance were quite consistent across species, while effects and even directions of architectural traits tended to vary among species. Response to architectural traits and allocation into rhizomes is also much more often non-linear (unpubl.).

These findings from trait manipulations in simulated plants are consistent with results of two studies using different genotypes to assess effects of changes in trait values. Both Cheplick (1997) and Skalova et al. (1997) found that the relationships between performance and architectural trait values differed among environments, while the relationships were similar among environments for size-related traits.

We suggest that the difference between effects of architectural and growth traits is due to the fact that ramet growth traits affect mean ramet size directly, and, in turn, mean ramet size is a straightforward component of overall performance expressed as total population biomass. On the other hand, architectural traits determine the spatio-temporal distribution of aboveground biomass. This affects resource distribution within a clonal fragment, which underlies spreading and colonization ability of the plant and ultimately determines how often and where ramet interactions will take place. Thus, their effect on performance is more indirect and is much more likely to be mediated by values of other traits. This does not mean that architectural traits are unimportant; rather, they yield less to generalizations than do ramet growth and competition traits. For this reason current architectural models (Winkler et al. 1999, Klimeš 2000, Wolfer et al. 2006) can provide insight into the specific cases they study, are less likely to be more generally relevant. Their usefulness is also likely to be much more dependent on good parameterization than models of growth, allocation and ramet competition.

Further, context dependence of architectural traits may mean that selection on ramet growth traits should generally be of greater magnitude – in all environments it is preferable to be big, than selection on architectural traits – in different environments different architecture can be successful. This finding, however, should be interpreted with caution, as the effect of traits has always to be assessed relative to the potential variation in the trait values (Caswell 2000); a trait with a strong effect in the model may still have a low potential to vary and thus may be of little significance for future evolutionary trends. The actual variation in a trait is generally constrained by the evolutionary history of the species in question and therefore cannot be addressed here. However, it can be assessed experimentally by measuring trait variation of different genotypes under different sets of conditions; these values could then be compared with the strength of the effect determined by the model.

Effects of traits on components of performance and tradeoff effects

In our simulations, manipulation of a particular trait often affected different components of performance in opposite directions, an effect that we refer to as a tradeoff. The most common tradeoff is between ramet size vs number of ramets and rhizome length, i.e. changing a trait value either led to a few large ramets connected by short rhizomes or to many small ramets connected by long rhizomes. A similar tradeoff between ramet size and short-distance colonization ability has often been observed in field experiments with clonal plants (Huber and Wiggerman 1997, Stuefer et al. 2002, Lepik et al. 2004). Such tradeoffs are likely to be generated by traits that affect how the plant distributes resource within the clonal fragment, but do not strongly alter the total amount of resource available to the plant. Most notably, the two key traits that most directly alter total resources available for growth, maximum ramet size and ramet growth rate, do not generate any tradeoffs among performance components. Instead, with the single exception of the poorly parameterized *Scirpus acutus*, increasing the value of these two traits always increase all three performance components and total performance.

The existence of such tradeoffs between components of performance represents an important cost of space encroachment via clonal growth that has not yet been thoroughly explored (Hutchings and Bradbury 1986, van Groenendael et al. 1996, Dietz and Steinlein 2001). The existence of a tradeoff means that the plant is not able to maximize the values of all of the components of performance by the trait in question; in contrast, maximizing one performance component incurs a cost on the other components. The best value of the trait is therefore determined by some optimality criterion. In the modeling approach used here, maximizing overall biomass is used as such a criterion, but this choice is necessarily based on specific assumptions on environmental conditions of the plant. Specifically, overall biomass is likely to be a good measure of success if disturbance or density-independent mortality are not important elements of community dynamics. In the real world, however, different environments (depending, for example, on the level of disturbance or productivity) will favor different combinations of these components and may lead to widely differing values of the traits that produce tradeoffs in plant performance components (Fahrig et al. 1994, Klimeš et al. 1997). In real plants, the tradeoff between these components thus reflects evolutionary constraints in a plant species due to their histories and may differ between species, even if the final growth form of species developing under different constraints may seem convergent.

Implications for community structure

The differences in importance and contingences of effects of growth and competition traits versus architectural traits may have important implications for community structure. Because effects of ramet growth and ramet competition traits are rather consistent across species in their effects on plant performance, they are likely to lead to a competitive hierarchy of species. Thus if, in a given set of species, only ramet growth and ramet competition traits vary, we expect there will be a consistent transitive performance ranking of species according to their growth rate. This should be the case in communities where the rate of horizontal spread over space is less important for the success of a species than vertical competition. Such constant rankings are commonly found when large sets of species of varying sizes are compared in short-term experiments (Keddy et al. 2002) and we contend that they are due primarily to growth traits similar to those in the model. As a corollary, in communities with such clear transitive competitive hierarchies, one or a few dominants should occupy most of the space in the community, resulting in a species-poor community.

On the other hand, if variation in growth and ramet competition traits is narrow relative to variation in architectural (i.e. colonization/space encroachment) traits, consistent hierarchies of competitive ability are much less likely. Variation in architectural traits can generate many different kinds of space occupation strategies (for clonal plants see Wildova 2004). Each of these strategies may be successful in competition with a certain set of species, but these sets will not necessarily be hierarchically arranged for two reasons. First, these traits do not affect directly the total amount of resource available to a ramet and second, the role of these traits is much more context-dependent. Communities where colonization/space encroachment traits are important, and growth traits of involved species are similar, will thus not be ordered along competitive hierarchies; non-transitive community networks are likely to arise instead (Aarssen 1988). Such traits may thus generate more complex structure of species interactions in the communities such as that found for grassland communities of clonal plants (Aarssen 1988, van der Maarel and Sykes 1993) and may result in much more species-rich communities. It should be noted that many experiments reporting consistent species hierarchies (Keddy et al. 2002) have been done with clonal plants, but often in small pots and during so short times that the effects of architectural traits are likely to be unimportant. We hypothesize that the hierarchies shown by such experiments might have been much less pronounced for long-term and larger-scale experiments in which clonal growth becomes much more important.

Conclusions

Consistent with the common assumption that directions and magnitude of linkages between traits and performance measures are universal, rather than highly species-specific, we found that traits related to individual ramet growth and production usually had similar effects on components of fitness and on overall population abundance across the six study species. However, in contrast to this common assumption, traits related to architecture often had highly contingent effects, where the magnitude and even direction of effect of a particular change in trait value depended on values of other traits. These results contain an important warning for simple models exploring the evolution of architectural traits and suggest that the power to generalize from such models may be more limited than we would like. The results also may have important implications for community structure; we suggest that highly contingent trait-performance linkages may be much less likely to lead to consistent competitive hierarchies and therefore dominance and low diversity than are simple general trait-performance linkages that hold for all interacting species.

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Appendix 1. Main structural assumptions and formulae used in the model

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

$$R_{avail} = R(t-1) + A.(1-\beta.N)/(1+\beta.N) - C_i, \qquad (1)$$

where R (t-1) is the resource status of the node at time t-1 (i.e. the previous step), A is the productivity of the environment (Maximum net photosynthetic rate in Table 1), is the density-dependence constant of resource accumulation for that species (Competitive response in Table 1), C_i is the internode cost (including the new ramet) and N is the number of all ramets within a specified circular neighborhood of that ramet.

A terminal node always forms a new node when it has sufficient resource for the daughter node, i.e. when the following condition is met:

$$R_{new}(t) > R_{min}/f_g \qquad (2)$$

where R_{avail} is the value defined by Eq. 1, f_g is the fraction of resource put into the new ramet at the growing tip, and R_{min} is the minimum resource required for ramet formation (ramet cost). Both these parameters are species-specific constants. When a new node is added, it is formed at a distance from the current terminal node drawn from a defined Gaussian distribution with mean and standard deviation (using parameters Internode length and Variation coefficient of the internode length). The angle of the newly formed internode (Growth angle – for this study we used standard value 10 degrees for all species, this parameter is not listed in the Table 1) with the previous internode is drawn from a defined Gaussian distribution with mean zero and a given standard deviation.

The initial ramet resource in the mother and daughter ramets is consequently

$$R_{daughter}(t) = R_{avail} \times f_{g,} \qquad (3a)$$

$$R_{mother}(t) = R_{avail} \times (1 - f_g), \qquad (3b)$$

where R_{avail} is the value defined by Eq. 1, and f_g is the fraction of resource put into the new ramet at the growing tip. This is identical also for branching.

Ramet growth follows this formula:

$$x_{t+1} = \max(x_t + r_c \times R_{avail} \times (1 - f_c) \times (K_c - x_t),\ x_{init}) \qquad (4)$$

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, f_c is the fraction of resource not used for the size growth (used for rhizome growth and branching) and R_{avail} is the resource available at the node supporting the ramet. The same formula is used for terminal and lateral ramets.

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 age as the tip) with the specified probability (Probability of terminal branching – in this study for all species this parameter was equal to 1, i.e. branching is possible at each node) if the following conditions are met

$$R_{avail}' > R_{min}/f_g \qquad (5)$$

where R_{avail}' is the value defined by Eq. 1 reduced by the cost of producing the terminal ramet and the internode, R_{min} is the minimum resource required for ramet formation, and f_g is the fraction of resource put into the new ramet at the growing tip.

A non-terminal (adventive) 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:

$$R_{avail} > R_{min} \qquad (6)$$

$$(1 - k.\beta.N) > 0$$

where R_{avail} is defined by Eq. 1, R_{min} is the resource required to produce a ramet, is the density-dependence constant of resource accumulation for that species, k is a positive constant and N is the number of all ramets in the neighborhood 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 $N \ll 1/$).

A ramet dies if its resource calculated by Eq. 1 is $<=$ zero. 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 time step of its formation) exceeds a specified constant (Node lifespan in Table 1).

The processes are simulated in the following order: (1) terminal internode growth (including associated translocation), (2) branching, (3) adventive ramet formation and adventive branching, (4) ramet mortality, (5) resource production, (6) translocation. Along the rhizome, nodes are always evaluated in basipetal direction (i.e. starting with the youngest node).

Appendix 2. The description of traits directly estimated from measurements on plants

Name of trait	Description of trait estimation
(1) Directly estimated traits	
Internode length	Mean length of all internodes measured on rhizome systems.
Node developmental period	Represents number of days required to produce one node. Ratio between number of nodes on the main axis of the rhizome system (=longest path) and number of days during which that system was developed (90 d of observation). Nodes on lateral branchings were not included because of their simultaneous growth with the main axis.
Distance between ramets	Mean number of nodes between two nodes bearing ramets.
Minimum distance between branchings	5th percentile of number of nodes between two branching nodes.
Branching angle	Mean size of angle between two branches. Branching angles were measured on fresh plants during the harvesting.
Maximum ramet size	95th percentile of all ramet sizes. Ramet size was defined as the dry weight of biomass of a single ramet.
Ramet initial size*	5 percentile of the estimated biomass of all approximately 1–30 days old ramets. This trait is determined to differentiate individual species at the very beginning of their growth.
Ramet growth rate	Mean change of ramet biomass during one month. Because significant differences in growth rate between ramets of different cohorts were revealed, we included only growth rate of youngest ramets (growth rate in June/July of ramets born at the start of June/July). Ramet growth rate we calculated as the natural log of [final biomass (at last day of selected time period) divided by initial estimated biomass (at first day of selected time period)], divided by growth period (30 d).
Ramet lifespan	Median of ramet lifespan of three species (*Carex lasiocarpa, Carex stricta and Scirpus acutus*; Petru unpubl.) was used for approximation of ramet lifespan for all species. Estimated length of ramet lifespan corresponded with length of vegetation season.
Internode cost	Mean internode biomass. This is a proxy value indicating the real cost under the assumption that investment in a plant part is equivalent to the biomass of that part.
Variation of internode length	Coefficient of variation of the internode length.
(2) Traits with arbitrary values	
Node lifespan*	Nodes were immortal in all simulations.
Probability of terminal branching if there is no density-dependence	Probability that a plant could branch at each node if it had enough resources.
Neighborhood size	Distance where target ramet is influenced by competition with neighborhood ramets. We used a simple exponential model for neighborhood size estimation based on size of plants (Czárán 1998). We modified the Zou and Wu (1995) formula for space utilization of a biological entity where competition (utilization) is calculated as $\text{competition effect} = \text{plant height} \times \exp\left[\frac{-(\text{neighborhood size})^2}{\text{plant height}}\right]$ For plant height we used mean height of adult ramets of all species (=15 cm). The final neighborhood size was taken as the size where competition effect was bigger than 10%.
(3) Indirectly estimated traits (process of estimation described in the text)	
Competitive response	Density-dependence constant of resource accumulation.
Maximum net photosynthetic rate.	The rate in which species produces photosynthetic resource; can be also understand as a productivity of the environment.
Resource fraction put into new daughter ramet	The proportion of resource that is transferred from mother ramet into the daughter ramet at the time of its formation.

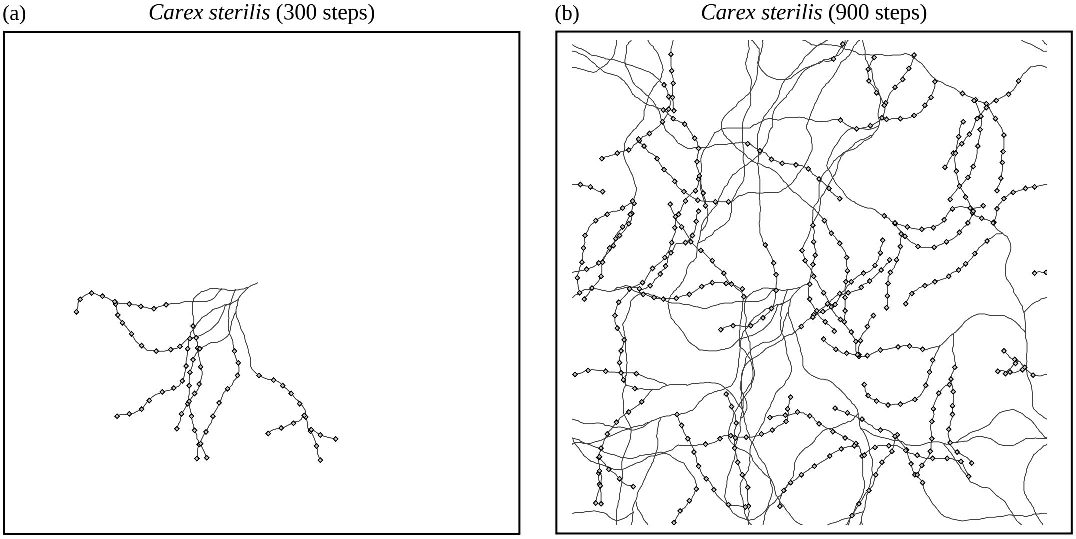
* Only used as traits in the model but not in the trait manipulations: ramet initial size because of its close correlation with maximum ramet size and node lifespan because the real number of days is higher then the number of days (steps) in traits manipulation.

Appendix 3. Simulation approach

In the parameterization simulations, one ramet was placed in the center of the simulation plot. In the validation simulations, five evenly-spaced ramets were placed into one side of the simulation plot, similar to the design of the validation experiment. The trait manipulation experiments followed the same design as the validation experiment. At the beginning of all simulations, ramets started with non-zero species-specific sizes that were estimated as the bottom 5th percentile of 1–30 d old ramets measured for each species in the parameterization experiment. The whole simulation area was four times as big (43.2 × 43.2 cm) as the experimental pots to avoid edge effects of toroidal boundaries; however, a simulation subplot 21.6 × 21.6 cm that corresponded with the inner square plot size of the experimental pots was used to collect data from simulations. In all simulations, one step corresponded to one day; the number of days during the growing season were used to decide the number of simulation steps so that field and simulated values would be comparable.

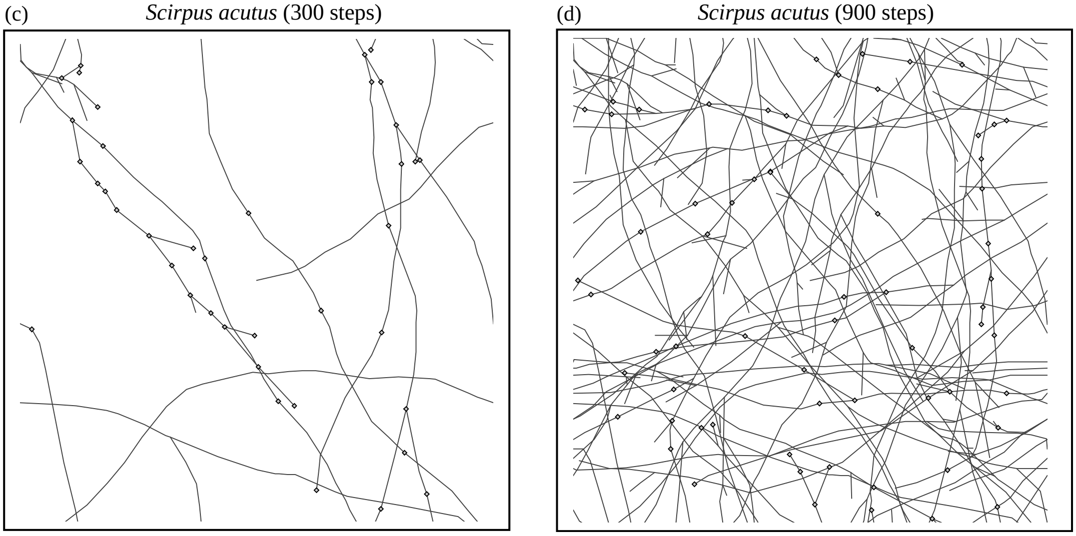
Appendix 4.

Examples of two simulated species *Carex sterilis* (a, b) and *Scirpus acutus* (c, d) parameterized by real plants. The simulated space represents pot of 21.6 × 21.6 cm where one single ramet was planted in the middle. Clones depicted after 300 steps of simulation correspond to two vegetation seasons (a, c) and after long-term simulation is (900 steps) (b, d). Lines indicate rhizomes, diamonds are ramets drawn from a bird's eye perspective.



(a) *Carex sterilis* (300 steps)

(b) *Carex sterilis* (900 steps)



(c) *Scirpus acutus* (300 steps)

(d) *Scirpus acutus* (900 steps)